65th Palaeontological Association Annual Meeting

18–20 December 2021

The University of Manchester

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PROGRAMME
ABSTRACTS
AGM papers

The Palaeontological Association

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The programme and abstracts for the 65th Annual Meeting of the Palaeontological Association are provided after the following information and summary of the meeting.

Venue

The Annual Meeting will take place at the University of Manchester. The symposium and regular sessions will be at University Place on Oxford Road opposite the Manchester Museum. This is a short walk from Manchester Piccadilly train station (or a short bus journey: #147).

Format

The hosting committee are keen to welcome delegates to a safe in-person meeting with its concomitant benefits, whilst maintaining and enhancing the internationalism and diversity of the Annual Meeting during pandemic times. We will be holding in-person scientific sessions at the University of Manchester, and streaming/sharing oral and poster presentations for virtual delegates who are unable to attend in person. Presentations will be delivered by both in-person and virtual delegates. This is a new way of approaching the Palaeontological Association Annual Meeting that we hope will be beneficial for both in-person and remote delegates.

Public health arrangements

The meeting will follow all University of Manchester and national UK COVID-19 guidelines. The former currently includes wearing a face covering in all indoor areas. We will be asking and reminding delegates to wear masks during sessions. Beyond these guidelines, we note that the Palaeontological Association is a scientific organization, and we will follow the best available evidence-based policy to ensure the welfare of all those sharing space during the meeting and associated activities. As such, we expect all in-person attendees and exhibitors to be fully vaccinated unless medically exempt. Delegates who are unvaccinated or at high risk for COVID-19 should register as virtual delegates. We also expect in-person delegates to complete lateral flow tests before attending the meeting. We will be asking delegates to share evidence of vaccination/test status at registration. In the event of a positive test, or if a delegate is required to self-isolate whilst the meeting takes place, registrations can be transferred to virtual attendance. If in-person attendance is no longer possible for an individual due to travel restrictions or to allow them to isolate then virtual attendance will be made available to that delegate. If the meeting cannot go ahead in person due to UK government guidelines/restrictions then all registrations will become virtual. Should such a situation occur then all presenters will be invited to submit a pre-recorded talk and attend a live virtual Q&A session. Unfortunately no refunds will be given in these instances. These measures are in place for the safety of conference delegates, but all delegates attend at their own risk.

Oral Presentations

This year, to facilitate engagement for both in-person and remote delegates and presenters, talks slots will be a strict **12-minute** length with a separate Grouped Q&A session from presenters at the end of each session. Oral presentations will predominantly be in-person, live talks, with some pre-recorded video presentations from remote delegates. Talks have been organized into themed sessions. Morning sessions will be in parallel in two separate rooms, afternoon sessions a single session. In-person oral presenters should prepare PowerPoint or PDF slides and talk for no longer than **11 minutes**. We ask that delegates upload and share their slides with organizers in advance of the meeting. Remote presenters of oral presentations will be asked to pre-record their talks and share a video file or upload with the organizers by **15th December** at the latest. We ask that both in-person and remote delegates submit their questions to oral speakers via an online Slack text channel (instructions to follow). Oral questions can be received during the live grouped Q&A at the end of each session, but we encourage use of the online Slack text channel to facilitate dialogue.

Due to the uncertain nature of the pandemic there may be last-minute changes to the programme. See the webpage for updates: <**https://www.palass.org/meetings-events/annual-meeting/2021/annual-meeting-2021-manchester-uk-programme**>.

Poster presentations

All posters, from both in-person and remote presenters, will be submitted electronically via the website. Electronic posters will be available for all delegates, both in-person and remote, via the website. We also encourage in-person poster delegates to bring a physical printed poster with them. Posters will be landscape format, A1 size.

Travel grants to student members

Students who have been awarded an Association travel grant should see the Executive Officer Dr Jo Hellawell at the Association's stand to receive their reimbursement.

Childcare

There are baby-changing facilities on campus, and a nursing room can be made available as required.

Accessibility

All buildings in the University are accessible via ramps and/or lifts. For assistance during the meeting please speak to volunteers at the registration desk.

Sponsors

The Palaeontological Association gratefully acknowledges the support of the Annual Meeting's sponsors, as detailed on the Association's website.

Manchester

Manchester is a large city with an historic industrial past, currently undergoing an energetic period of growth and regeneration. There is a long history of engineering and science innovation at the University, from Ernest Rutherford's work in physics and Alan Turing's pioneering approaches in computing, to Kathleen Drew-Baker's work on botany and marine aquaculture. Evidence of Manchester's industrial, political, cultural and sporting heritage can be found all over the city centre and its museums, alongside modern architecture and vibrant nightlife. Close to the University campus is Manchester's famous gay village, historic music venues, the curry mile, and a wide range of pubs and restaurants. A guide to getting to Manchester, things to see and do, and places to eat and drink, can be found on the Annual Meeting webpage at <**www.palass.org**>.

Summary of Schedule

Please note: all times are given in GMT.

Friday 17th December

A virtual pre-conference workshop "Social justice in palaeontology: case studies and future actions" coordinated by Emma M. Dunne and Nussaïbah B. Raja will take place before the Annual Meeting. This event is open to both delegates and non-delegates and requires separate registration.

Saturday 18th December: Workshops, Symposium and Reception

The morning of 18th December features a workshop for in-person delegates on "Science communication for palaeontologists", coordinated and delivered by Elspeth Sinclair, Liz Hide, Susannah Lydon and Zoë Hughes from the Palaeontological Association's Public Engagement Group. This workshop also requires pre-registration, but might be able to accommodate last-minute requests. This will take place in the Williamson building, next to University Place.

The Annual Meeting will begin at 13:30 with a symposium entitled "The Problem with Problematica: pushing the limits of the fossil record". Registration will be available from 12:00 to 17:30 on the ground floor of University Place.

Following the Symposium there will be an icebreaker reception at University Place, starting at 17:30.

Sunday 19th December: Conference, AGM, Annual Address and Annual Dinner

The conference will start at 09:00 in University Place, registration opening at 08:30. Talks will be held in double and single sessions in two lecture theatres in University Place. The Annual General Meeting (AGM) will be held at 14:45 followed by a brief coffee break, returning to the Annual Address at 16:00. Posters will be set up across University Place foyer and the Williamson building and will be available during lunch and tea breaks. Please note that lunch and refreshments are included in your registration fee.

The afternoon will have a dedicated poster session (17:00–18:30).

The Annual Dinner will be held at the historic Midland Hotel, beginning at 20:00. The dinner will feature a three-course meal accompanied by drinks, and an open cash bar. The Midland Hotel is approximately 20 minutes' walk from the University campus. Most buses heading North on Oxford Road will take you close (ask for St. Peter's square).

Friday 20th December: Conference and prizes

Talks will begin at 09:00 in double and single sessions in the same two lecture theatres as those the previous day. Posters will continue to be on display. Talks will end by 17:00, after which time the conference will close with presentations by the organizing committees of upcoming meetings, the award of the President's Prize and the Council Poster Prize, and concluding remarks.

The Palaeontological Association thanks the Organizing Committee:

Chair:

- Dr Robert Sansom

Committee:

- Dr Russell Garwood
- Dr Katrina Jones
- Dr Marta Pina
- Dr Victoria Egerton

Support team:

- Amun Dubro
- Ellis Jones
- Euan Malpas
- James Chester
- Jane Reeves
- Jenna Davenport
- Jesse Hennekam
- Laura Austin Sydes
- Meghan Jenkinson
- Priya Gordon
- Sam Coatham
- William Rutter

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 (anonymously if you choose to) via the online reporting form: <**https://www.palass.org/meetings-events/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

Saturday 18th December

Pre-meeting in-person workshop

Participants must be pre-registered as spaces are limited.

10:00 – 12:30 "Science communication for palaeontologists"
Instructors: Elspeth Sinclair, Liz Hide, Susannah Lydon and Zoë Hughes
Williamson Building G12

REGISTRATION

12:00 – 17:30 University Place

Symposium: *"The Problem with Problematica: pushing the limits of the fossil record"*

University Place, Lecture Theatre B

13:30 – 13:45 Welcome address

13:45 – 14:15 **The Possibilities of Problematica**
Derek E. G. Briggs

14:15 – 14:45 **Proterozoic microfossil problematica: a window into the ecology and evolution of early eukaryotes**
Heda Agić

14:45 – 15:15 **The Gabonionta: a new perspective in understanding the emergence of multicellularity**
Abderrazak El Albani

15:15 – 16:00 Tea/coffee break

16:00 – 16:30 **Ecological insights into Ediacaran evolution**
Emily G. Mitchell

16:30– 17:00 **Systematic error and the problems of the phylum level (molecular) phylogeny of the animal kingdom**
Max J. Telford

17:00 – 17:30 **A Can of Cambrian worms**
Xiaoya Ma (** – a virtual presentation)

Ice-Breaker Reception

17:30 – 19:00 University Place Foyer

Sunday 19th December

Conference, Association AGM, and Annual Dinner

Underlined author denotes designated speaker.
*Candidates for the President's Prize are marked with an asterisk.
**Presentations delivered as pre-recorded videos from remote delegates are indicated with a double-asterisk

08:30 – 09:00 Registration and Poster set-up, University Place, Williamson Building.

Session 1: Precambrian & Cambrian life (in parallel with session 2)

University Place, Lecture Theatre B

09:00 – 09:12 **"Conga Lines" of small fronds: implications for reproduction and clonality in the Ediacaran**
*Katie Delahooke, Alexander G. Liu and Emily G. Mitchell

09:12 – 09:24 **Priapulid trace fossils from the late Ediacaran of Namibia**
*Katherine Turk, Katie Maloney, Marc Laflamme and Simon A. F. Darroch

09:24 – 09:36 ***Charniodiscus* and *Arborea* are separate genera within the Arboreomorpha: using the holotype of *C. concentricus* to resolve a taphonomic/taxonomic tangle ****
*Daniel Pérez Pinedo, Christopher McKean, Rod S. Taylor and Duncan McIlroy

09:36 – 09:48 **Cambrian tentaculate deuterostomes reveal ancestral body plans**
Yujing Li, Frances S. Dunn, Duncan J. E. Murdock, Imran A. Rahman and Peiyun Cong

09:48 – 10:00 **Complex growth and sexual maturity in a *c.* 512-million-year-old trilobite**
James D. Holmes, John R. Paterson and Diego C. García-Bellido

10:00 – 10:12 **Cambrian stem group chaetognaths dominated the top of early pelagic food chains**
Jakob Vinther, Tae-Yoon Park, Luke A. Parry, Morten Lunde Nielsen, Mirina Lee, Ji-hoon Kim *et al*.

10:12 – 10:30 ***Grouped Q&A for speakers in session 1***
Delahooke, Turk, Dunn, Holmes, Vinther
(Perez Pinedo will be in the Q&A for virtual delegates in session 11)

Session 2: Mesozoic life (in parallel with session 1)

University Place, Lecture Theatre 1.219

09:00 – 09:12 **Fossil evidence suggests the first amniote displayed extended egg retention**
Baoyu Jiang, Yiming He, Armin Elsler, Shengyu Wang, Joseph N. Keating, Junyi Song, Stuart Kearns and Michael J. Benton

09:12 – 09:24 **New information on the archosaurs from the Late Triassic fissure fills locality of Pant-y-ffynnon, Wales**
Stephan N. F. Spiekman, Martín Ezcurra, Richard J. Butler, Nicholas C. Fraser and Susannah C. R. Maidment

09:24 – 09:36 **Dinosaur etymology reflects and reinforces global inequities in palaeontology**
Thomas J. D. Halliday, Emma M. Dunne, William J. Foster, Bryan M. Gee, Sarah E. Greene, Thomas W. Hearing, Emmanuel Tschopp, Evangelos Vlachos and Nussaïbah B. Raja

09:36 – 09:48 **Simple and branched pterosaur feathers with distinct melanosome geometries reveal deep origins of visual signalling in feather evolution**
Aude Cincotta, Michaël Nicolaï, Hebert B. Nascimento Campos, Maria E. McNamara, Liliana D'Alba, Matthew D. Shawkey *et al*.

09:48 – 10:00 **A juvenile rhynchosaur specimen from the Otter Sandstones of Southern England (Anisian, Middle Triassic)**
*Thitiwoot Sethapanichsakul and Michael J. Benton

10:00 – 10:12 **Here be dragons: the perplexing patterns in the distribution, growth and evolution of non-pterodactyloid pterosaurs**
*Natalia Jagielska, Stephen L. Brusatte and Michael O Sullivan

10:12 – 10:30 ***Grouped Q&A for speakers in session 2***
Benton, Spiekman, Halliday, Cincotta, Thitiwoot, Jagielska

10:30 – 11:00 **Tea/Coffee Break and Posters**

Session 3: Comparative morphology and feeding A (in parallel with session 4)

University Place, Lecture Theatre B

11:00 – 11:12 **Multivariate dental topographic metrics demonstrate the dietary breadth and specialisms of conodonts**
*Christopher Stockey, Philip C. J. Donoghue, Thomas. H. P. Harvey, Duncan J. E. Murdock and Mark A. Purnell

11:12 – 11:24 **Geometric evolution of the galloanseran quadrate**
*Pei-Chen Kuo, Roger B. J. Benson and Daniel J. Field

11:24 – 11:36 **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

11:36 – 11:48 **Marine tetrapod feeding guilds using automated high-density D geometric morphometrics**
Valentin Fischer, Jamie A. MacLaren, Rebecca F. Bennion, Pierre Sparla and Nathalie Bardet

11:48 – 12:00 **Developing a taste: Connecting skull shape ontogeny and evolution of different feeding adaptations in Cetacea using D geometric morphometrics**
Agnese Lanzetti, Vincent Fernandez, Brett Clark and Anjali Goswami

12:00 – 12:15 ***Grouped Q&A for speakers in session 3***
Stockey, Kuo, Hennekam, Fischer, Lanzetti

Session 4: Phylogeny and Evolution (in parallel with session 3)

University Place, Lecture Theatre 1.219

11:00 – 11:12 **In search of ancestors: benchmarking parsimony and likelihood methods of ancestral state estimation**
Joseph N. Keating, Philip C. J. Donoghue and Michael J. Benton

11:12 – 11:24 **Examining postcranial evolution in Crocodylomorpha using discrete characters** **
Pedro L. Godoy, Felipe C. Montefeltro, Mario Bronzati, Candice M. Stefanic, Hans C. E. Larsson, Richard J. Butler and Alan H. Turner

11:24 – 11:36 **Origins of the echinozoan body plan**
Jeffrey Thompson, Imran A. Rahman, Timothy A. M. Ewin, Nicolas Mongiardino Koch, Zoe X. Schultz, Paola Oliveri, Ferdinand Marletaz and Samuel Zamora

11:36 – 11:48 **Does time matter in phylogeny? A perspective from the fossil record** **
Pauline Guenser, Rachel C. M. Warnock, Walker Pett, David De Vleeschlouwer, Philip C. J. Donoghue and Emilia Jarochowska

11:48 – 12:00 **An estimate of the deepest branches of the tree of life from ancient vertically-evolving genes**
Edmund R. R. Moody, Tara A. Mahendrarajah, Nina Dombrowski, James W. Clark, Celine Petitjean, Pierre Offre *et al*.

12:00 – 12:15 ***Grouped Q&A for speakers in session 4***
Keating, Thompson, Moody
(Godoy and Guenser will be in the Q&A for virtual delegates in session 11)

12:15 – 13:30 **Lunch Break and Posters**

Session 5: Sampling and biases

University Place, Lecture Theatre B

13:30 – 13:42 **Occurrences of Palaeozoic ray-finned fishes exhibit major biases which confound diversity estimates**
*Struan Henderson, Emma M. Dunne and Sam Giles

13:42 – 13:54 **Completeness patterns of the Palaeozoic chondrichthyan fossil record**
*Lisa Schnetz, Richard J. Butler, Michael I. Coates and Ivan J. Sansom

13:54 – 14:06 **Gone fishing: using the soft-tissue taxa to explore the fidelity of the early Palaeozoic fossil record of vertebrates**
*Jane Reeves, and Robert S. Sansom

14:06 – 14:18 **Diversification through the looking glass: the continuum of mass radiation and extinction**
Jennifer Hoyal Cuthill, Nicholas Guttenberg and Graham E. Budd

14:18 – 14:30 **The impact of mass extinctions on the morphological disparity of vertebrates**
*Tom A. Trapman, Matthew Wills and Natalie Cooper

14:30 – 14:42 ***Grouped Q&A for all speakers in session 5***
Henderson, Schnetz, Reeves, Hoyal Cuthill, Trapman

Annual General Meeting

14:45 – 15:30 **Annual General Meeting**
University Place, Lecture Theatre B

15:30 – 16:00 **Tea/Coffee Break and Posters**
University Place, Lecture Theatre B

Annual Address

University Place, Lecture Theatre B

16:00 – 17:00 **Decoding the evolution of form and function in the fossil record: why are animals shaped the way they are?**
Emily J. Rayfield

Poster Session

Williamson Building G12, G14, G16 and Foyer

17:00 – 19:00 **Poster Session with refreshments**

Annual Banquet

Midland Hotel, St. Peter's Square

20:00 – 23:00 **Annual Banquet, with council awards and speeches**

Monday 20th December

Conference

Underlined author denotes designated speaker.
*Candidates for the President's Prize are marked with an asterisk.
**Presentations delivered as pre-recorded videos from remote delegates are indicated with a double-asterisk

REGISTRATION AND POSTER SET-UP

08:30 – 09:00 Registration and Poster set-up, University Place, Williamson Building

Session 6: Exceptional preservation (in parallel with session 7)

University Place, Lecture Theatre B

09:00 – 09:12 **An early Cambrian window into mechanisms for phosphatization of labile soft tissues**
*Morten Lunde Nielsen, Philip R. Wilby, Mirinae Lee, Arne T. Nielsen, Tae-Yoon S. Park and Jakob Vinther

09:12 – 09:24 **Exceptionally preserved soft tissues of *Vampyronassa rhodanica* provide new insights on the evolution and palaeoecology of vampyroteuthidsa**
*Alison Rowe, Isabelle Kruta, Henk-Jan Hoving, Neil Landman, Löic Villier and Isabelle Rouget

09:24 – 09:36 **A new marrellomorph arthropod from southern Ontario and the potential for soft tissue preservation on late Ordovician open marine shelves ****
*Joseph Moysiuk, Alejandro Izquierdo-López, George Kampouris and Jean-Bernard Caron

09:36 – 09:48 **Darwin's Dilemma: Constraints on the origin of animals from taphonomic studies**
Ross P. Anderson, Christina R. Woltz, Nicholas J. Tosca, Susannah M. Porter and Derek E. G. Briggs

09:48 – 10:00 **How soft-bodied fossils from the Lower Devonian of southern Belgium can help to decipher the early stages of vertebrate evolution**
Sébastien Olive, Pierre Gueriau, Philippe Janvier and Bernard Mottequin

10:00 – 10:12 **Physical characterization of the conodont white matter tissue**
Carlos Martinez Perez, Ayse Atakul-Özdemir, Xander Warren, Peter Martin, Manuel Guizar-Sicairos, Mirko Holler *et al*.

10:12 – 10:30 ***Grouped Q&A for speakers in session 6***
Nielsen, Rowe, Anderson, Olive, Martinez Perez
(Moysiuk will be in the Q&A for virtual delegates in session 11)

Session 7: Climate, environment, conservation (in parallel with session 6)

University Place, Lecture Theatre 1.219

09:00 – 09:12 **Climatic controls on the ecological ascendancy of dinosaurs**
Richard J. Butler, Emma M. Dunne, Alexander J. Farnsworth, Roger B. J. Benson, Pedro L. Godoy, Sarah E. Greene, Paul J. Valdes and Daniel J. Lunt

09:12 – 09:24 **It's a trap! Environment and biogeography of Siberia across the Frasnian–Famennian**
Elizabeth M. Dowding, Trond H. Torsvik and Mathew Domeier

09:24 – 09:36 **Palaeontology, Geodiversity, and the International Geodiversity Day**
Jack J. Matthews, José Brilha, Murray Gray and Zbigniew Zwolinski

09:36 – 09:48 **Assessing the impact of climate change on the structural integrity of benthic foraminifera during the Palaeocene Eocene Thermal Maximum – implications for future climate change**
*James M. Mulqueeney, Leanne A. Melbourne, Danna Titelboim and Suman Sarkar

09:48 – 10:00 **Biome specialization promotes diversification in swallowtail butterflies ****
*Sara Gamboa, Fabien Condamine, Juan L. Cantalapiedra, Jonathan S. Pelegrín, Iris Menéndez, Sara Varela *et al*.

10:00 – 10:12 **A second 'Great American Biotic Interchange' signals the Anthropocene impact of humans**
*Stephen Himson, Mark Williams, Jan Zalasiewicz, Anthony D. Barnosky, Colin N. Waters and Mary McGann

10:12 – 10:30 ***Grouped Q&A for speakers in session 7***
Butler, Dowding, Matthews, Mulqueeney, Himson
(Gamboa will be in the Q&A for virtual delegates in session 11)

10:30 – 11:00 **Tea/Coffee Break and Posters**

Session 8: Comparative morphology and feeding B (in parallel with session 9)

University Place, Lecture Theatre B

11:00 – 11:12 **Cranial muscle reconstructions quantify adaptation for high bite forces in Oviraptorosauria**
*Luke E. Meade and Waisum Ma

11:12 – 11:24 **Dental form and function and feeding diversity during the early evolution of Dinosauria**
*Antonio Ballell Mayoral, Michael J. Benton and Emily J. Rayfield

11:24 – 11:36 **Diet of the toothed and long-snouted longipterygid birds (Avialae: Enantiornithes) determined with reference to quantitative analysis of extant bird dietary proxies ****
*Case Vincent Miller, Michael Pittman and Jen A. Bright

11:36 – 11:48 **Did Carboniferous chimaeras suck? Evidence for high-performance suction feeding in the Pennsylvanian stem-group holocephalan Iniopera**
Richard P. Dearden, Anthony Herrel and Alan Pradel

11:48 – 12:00 **How *in vivo* data can shed light on jaw evolution during the fish–tetrapod transition**
Hugo Dutel, Anne-Claire Fabre, Laura B. Porro, Michael J. Fagan and Emily J. Rayfield

12:00 – 12:15 ***Grouped Q&A for speakers in session 8***
Meade, Ballell Mayoral, Dearden, Dutel
(Vincent Miller will be in the Q&A for virtual delegates in session 11)

Session 9: Cenozoic life (in parallel with session 8)

University Place, Lecture Theatre 1.219

11:00 – 11:12 **First known fossil ratite eggshells from the Siwalik Frontal Range near Chandigarh (northern India) and their multidisciplinary scientific analysis ****
*Anubhav Preet Kaur, Rajeev Patnaik, Prabhin Sukumaran, Stanley H. Ambrose, Raj Sekhar Roy and Parth R. Chauhan

11:12 – 11:24 **Radial Porosity Profiles: a new quantitative histological method for studying dynamics of diametric limb bone growth**
Edina Prondvai, Ádám T. Kocsis, Anick Abourachid, Dominique Adriaens, Pascal Godefroit, Dong-Yu Hu and Richard J. Butler

11:24 – 11:36 **Comparative morphology of the passerine carpometacarpus: Implications for interpreting the fossil record of crown Passeriformes**
*Elizabeth Steell, Jacqueline M. T. Nguyen, Roger B. J. Benson and Daniel J. Field

11:36 – 11:48 **New unworn dentitions illuminate the dental morphology and diversity of puzzling early eutherian mammals, Taeniodonta**
*Zoi Kynigopoulou, Sarah L. Shelley , Thomas E. Williamson, Ornella C. Bertrand, Ian B. Butler and Stephen L. Brusatte

11:48 – 12:00 **First fossil of *Styriofelis* (Felidae, Carnivora) from the middle Miocene of Madrid basin**
*Jesús Gamarra González, Gema Siliceo, Mauricio Antón, Jorge Morales, Manuel J. Salesa

12:00 – 12:15 **Grouped Q&A for speakers in session 9**
Prondvai, Steell, Kynigopoulou, Gamarra González
(Kaur will be in the Q&A for virtual delegates in session 11)

Session 10: Palaeozoic Life

University Place, Lecture Theatre B

13:30 – 13:42 **Analysis of skeleton space reveals early unique excursions in the evolution of spiralian hard parts**
Luke A. Parry and Roger B. J. Benson

13:42 – 13:54 **Radiodont oral cones from the Fezouata Biota (Early Ordovician, Morocco) ****
Gaëtan J.-M. Potin and Allison C. Daley

13:54 – 14:06 **Evolutionary analysis of swimming speed in early vertebrates challenges the 'New Head Hypothesis'**
Humberto G. Ferron and Philip C. J. Donoghue

14:06 – 14:18 **Quantifying conodont crystals: controls of biomineralization in early vertebrates**
*Bryan Shirley, Isabella Leonhard, John E. Repetski and Emilia Jarochowska

14:18 – 14:30 **An exceptionally diverse Early Devonian flora from the Lochkovian of South Africa**
Cyrille Prestianni and Robert W. Gess

14:30 – 14:42 **Giant articulated *Arthropleura* remains from the Mississippian of northern England**
Neil S. Davies, Russell J. Garwood, William J. McMahon, Joerg Schneider and Anthony Shillito

14:42 – 15:00 ***Grouped Q&A for speakers in session 10***
Parry, Ferron, Shirley, Prestianni, Davies
(Potin will be in the Q&A for virtual delegates in session 11)

15:00 – 15:30 **Tea/Coffee Break and Posters**

Session 11: Macroevolution and Close

University Place, Lecture Theatre B

15:30 – 15:42 **Is early euarthropod evolution characterised by 'creeps' or 'jerks'?**
*Alavya Dhungana and Martin R. Smith

15:42 – 15:54 **The morphological disparity of Fungi**
Thomas J. Smith and Philip C. J. Donoghue

15:54 – 16:06 **Decoupled morphological disparity trends during the early diversification of ammonoids**
Ninon Allaire, Samuel Ginot, Nicolas Goudemand, Kenneth De Baets, Claude Monnet and Catherine Crônier

16:06 – 16:18 **Understanding the diversification dynamics of the Permo–Triassic archosauromorph radiation using occurrence-based Bayesian approaches**
Roland B. Sookias, Luciano Pradelli, Eduardo Ascarrunz, Daniele Silvestro and Martin Ezcurra

16:18 – 16:30 **Cenozoic slowdown in placental skull evolution**
Anjali Goswami, Eve Noirault, Ellen J. Coombs, Julien Clavel, Anne-Claire Fabre, Thomas J. D. Halliday *et al*.

16:30 – 16:45 ***Grouped Q&A for speakers in session 11***
Dhungana, Smith, Allaire, Sookias, Goswami

16:45 – 17:00 ***Grouped Q&A for all remote presenters of oral presentations, joining Lecture Theatre B via Zoom***
Pérez Pinedo, Godoy, Guenser, Moysiuk, Gamboa, Vincent Miller, Kaur, Potin

Closing business

17:00 – 17:30 **Concluding Remarks, Announcement of best presentation prizes, Invitation to next year's Palaeontological Association Annual Meeting and *Progressive Palaeontology* Meeting**
Robert Sansom, Paddy Orr, Maria McNamara, Sean Smart

Abstracts of symposium presentations

The Problem of Problematica: pushing the limits of the fossil record

The Symposium will take place on Saturday 18th December.

Proterozoic microfossil problematica: a window into the ecology and evolution of early eukaryotes

Heda Agić
University of California, Santa Barbara, USA

The fossil record through most of Earth's history, including time before onset of macroscopic multicellular life, is dominated by organically-preserved remains of soft-bodied microorganisms: organic-walled microfossils (OWM). These eclectic problematica include single-celled prokaryotes and eukaryotes, and filaments and cellular aggregates in marine and lacustrine sediments. Some Precambrian OWM provide clues about one of the most fundamental events in the history of life: the origin of a complex cell and the subsequent diversification of eukaryotic life. Yet little is known about their metabolisms, biological affinities, and habitats. New Meso-Neoproterozoic microfossil assemblages contain characters that allows us to reconstruct the timeline of eukaryotic radiation. It is unclear, however, whether the early eukaryotes were restricted to oxygenated surface waters, or if they also inhabited the rest of the water column that was mostly anoxic ferruginous throughout Proterozoic. This information is critical to understand if and how different environmental conditions, *e.g.* ocean oxygenation during the Neoproterozoic, impacted eukaryotic evolution. Novel approaches, like organic C-isotope analyses of individual microfossils, can provide insight into short-term environmental variability and early eukaryote palaeoecology. Initial analyses from Mesoproterozoic–Neoproterozoic microfossils show heterogenous C-isotopic composition of eukaryotic OWM, suggesting habitat heterogeneity including deep and anoxic parts of the water column.

The Possibilities of Problematica

Derek E. G. Briggs
Yale University, USA

At the simplest level fossils are problematic if we cannot determine their relationships. The most interesting represent unfamiliar morphologies, but incomplete preservation can compromise attempts to place them in a phylogeny. The preservation of anatomical features may allow different interpretations, and homologies are difficult to establish. Problematica may lose their status with new discoveries and further research: better preserved specimens flesh out morphology; new techniques (CAT scans, synchrotron data, elemental maps) generate additional evidence of anatomical features; experiments show how decay can lead to artefacts and also allow us to identify taphonomic thresholds that help to differentiate between characters that have degraded and those that are truly absent; phylogenetic analysis allows taxa to be placed, with support values depending on character coding, in a scheme of relationships. Even then, because these organisms are inherently unusual, conclusions about their nature and affinities may remain controversial.

Nonetheless, fossils often have considerable influence in revealing relationships among extant taxa, and problematica, with their extinct character combinations, provide critical possibilities for documenting the history of clades. Classic examples, such as radiodonts, conodonts, machaeridians and the Tully Monster, provide illustrations of these topics.

The Gabonionta: a new perspective in understanding the emergence of multicellularity

Abderrazak El Albani
University of Poitiers, France

The emergence of complex life more than five hundred million years ago marked the beginning of a change in the Earth's biosphere during the so called "Cambrian Explosion". However, several studies have reported that scattered fossils of large individual multicellular macro-organisms that use cells as building blocks existed during most of the Proterozoic Eon. The recent discovery of centimetre-sized fossils of more than 1,500 specimens from the 2.1 Ga Palaeoproterozoic black shales in Gabon reveals the growth of macro-organisms in a coordinated manner. The biogenicity of the fossils resemble irregularly shaped cookies with split edges and a lumpy interior. X-ray tomography revealed their structures that are too complex to be simple products of inorganic processes. Some of these species showed evidence of organism motility in oxic shallow marine waters and provide support for the presence of multicellular life about 2.1 billion years ago. The evolution of the Gabonese biota represents an early step toward large-sized multicellularity and may have become possible by the first boost in oxygen during the Great Oxidation Event (GOE). Why it took around 1.4 billion years for the multicellular organisms to take over is currently one of the great unsolved mysteries in the history of the biosphere.

Ecological insights into Ediacaran evolution

Emily G. Mitchell
University of Cambridge, UK

Ediacaran fossils include some of the earliest animals known from the fossil record (572–550 Ma). However, understanding Ediacaran evolution is hampered by the lack of clear morphological analogues between Ediacaran and extant organisms. Fortunately, Ediacaran preservation is exceptional, with thousands of soft-bodied, sessile organisms preserved in their in-life positions. This *in situ* preservation means that the position of the specimens on their bedding-planes captures their entire life-history: how they reproduced and interacted with each other and their local environment. As such, spatial analyses can be used to reconstruct Ediacaran eco-evolutionary dynamics. We have systematically mapped Ediacaran palaeocommunities using LiDAR, photogrammetry and a laser line probe, and used spatial analyses to infer the underlying processes governing community dynamics. We found a lack of influence of the local environment on the older deep-water organisms, which suggests that early metazoan diversification may not have been driven by systematic adaptations to the local environment, but instead may have resulted from stochastic demographic differences. This pattern shifts for younger, shallow-water communities, which were heavily influenced by local environmental patchiness. Our results provide quantitative support for the "Savannah" hypothesis for early animal diversification – whereby Ediacaran diversification was increasingly driven by patchiness in the local benthic environment.

Systematic error and the problems of the phylum level (molecular) phylogeny of the animal kingdom

Max J. Telford and Paschalia Kapli
University College London, UK

While molecular data have been a powerful tool for understanding the deep relationships between animal phyla, there remain hotly disputed aspects of the animal tree. Notable amongst these are the ongoing arguments over the affinities of Ctenophora and Xenacoelomorpha. Recent molecular phylogenetic studies have not even consistently supported deuterostome monophyly – a group that had not been questioned in over a hundred years. With a focus on these three problematic aspects of the molecular tree, I will ask where the uncertainty comes from; how we might address it; and what resolving these questions might mean for our understanding of animal evolution.

Abstract of Annual Address

The Annual Address will be given on Sunday 19th December at 16.00.

Decoding the evolution of form and function in the fossil record: why are animals shaped the way they are?

Emily J. Rayfield
University of Bristol, UK

Throughout their evolutionary history, animals have evolved a multitude of shapes and sizes. The focus of this seminar is how quantification of animal form and function in the fossil record can help address: Why are organisms shaped in the way they are? How and why does shape evolve? And what are the functional controls on form? I will discuss how imaging analysis combined with the application of biomechanical principles and computational methods drawn from engineering structural analysis can be applied to understand the function and evolution of animals. Fossils typically preserve only part of the puzzle; studies on living animals are also key, to provide the whole organism and phylogenetic context to form-function evolution. As the fields of palaeobiomechanics and organismal anatomy and comparative methods advance, there is great potential to synthesise multiple lines of evidence to better constrain and better understand the functional evolution of extinct animals. To demonstrate this multi-modal approach, I will present a case study on the function and evolution of the skull across the water to land transition, drawing on X-ray tomographic data, studies on extant musculoskeletal anatomy and in vivo function, computational analysis of function and morphometric and network analysis approaches.

Abstracts of oral presentations

* Candidates for the President's Prize are marked with an asterisk.
Underlined author denotes designated speaker.

talks

Decoupled morphological disparity trends during the early diversification of ammonoids

Ninon Allaire[1,2,3], Samuel Ginot[2], Nicolas Goudemand[2], Kenneth De Baets[1], Claude Monnet[3] and Catherine Crônier[3]
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[2]*Ecole Normale Supérieure de Lyon, France*
[3]*Université de Lyon, France*

Ammonoids constitute an invaluable fossil record for documenting macroevolutionary patterns. Our study investigates the morphological evolution of ammonoids during their initial radiation through the Early and Middle Devonian. Previous morphological disparity analyses were restricted to conch geometry; here we have also explored the evolutionary patterns of the suture lines, using the exceptional early ammonoid record from Morocco. We quantified the conch geometry and the suture line shape by classical, linear morphometrics and by geometric morphometrics, respectively. These morphometric data enabled the reconstruction of ammonoid empirical morphospaces, for which standard disparity indices were computed. These metrics enabled us to quantify the changes in morphological disparity through time, using the ammonoid biozonation as a temporal scale. The results reveal important fluctuations in morphological disparity. Despite a well-known covariation relationship (*i.e.* second Buckman's rule, the more compressed conchs displaying more frilled sutures), the evolution of disparity in, respectively, conch geometry and suture lines, are temporally decoupled: conch geometry reached maximum disparity at the end of the Early Devonian, while suture line disparity climaxed much later, at the end of the Middle Devonian, when multilobate sutures first appeared. This decoupling may reflect the influence of distinct ecological tasks (*e.g.*, buoyancy, hydrodynamics) associated with these different traits.

Darwin's Dilemma: constraints on the origin of animals from taphonomic studies

Ross P. Anderson[1], Christina R. Woltz[2], Nicholas J. Tosca[3], Susannah M. Porter[2] and Derek E.G. Briggs[4]
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[2]*University of California, Santa Barbara, USA*
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[4]*Yale University, USA*

Charles Darwin famously lamented the absence of animal fossils in Precambrian strata as a valid argument against his theory of evolution. Today, a version of Darwin's Dilemma remains with molecular clocks placing the origin of animals as far back as ~800 Ma whereas animal fossils extend maximally to ~574 Ma. The disconnect between these major lines of evidence for the timing of the origin of animals requires explanation. Darwin

argued that taphonomy was key: perhaps Neoproterozoic environments were unconducive to animal fossilization. We compiled data from recent taphonomic studies on Burgess Shale-type (BST) deposits, which are proven repositories for early animal fossils and capable of capturing small/fragile taxa composed of a variety of tissue biopolymers, to address this issue. The clay minerals kaolinite and berthierine suppress decay and interact directly with decaying organic matter in ways that favour its fossilization. They are major constituents of BST deposits and are commonly associated with their soft-bodied fossils. Yet Neoproterozoic mudstones rarely display the same clay mineralogy. Fossils of basal animals are consequently likely to be rare, but even where conditions favour BST preservation in Tonian strata they are absent. Thus, taphonomy places a maximum ~800 Ma constraint on animal antiquity.

Dental form and function and feeding diversity during the early evolution of Dinosauria

*Antonio Ballell Mayoral, Michael J. Benton, and Emily J. Rayfield
University of Bristol, UK

Dinosaurs evolved varied craniodental morphologies during the Late Triassic and Early Jurassic, suggesting an early dietary diversification. Tooth shape comparisons with extant reptiles have been central to dietary classifications: carnivores having recurved bladed teeth and herbivores having denticulated lanceolate teeth. However, quantitative studies of dental form and function in early dinosaurs and its link to diet are scarce. Here we use 3D modelling to reconstruct tooth morphology in the main dinosaurian lineages, in comparison with extant crocodylians and lepidosaurs. We characterize dental form and function using a combination of geometric morphometrics and finite element analysis, and use machine-learning algorithms to infer the potential diet of key early-branching dinosaurs. Extant herbivores show the most diverse dental morphologies, and omnivores experience relatively low stress under simulated bite-like compressive loads. Carnivorous taxa show the highest stress values compared to other dietary categories. Among early dinosaurs, sauropodomorphs are the most diverse in dental shape and mechanical behaviour. Early theropods and herrerasaurids are classified as carnivores. Early ornithischians and post-Carnian sauropodomorphs are recovered as herbivores, while most Carnian species were likely omnivores. Our results confirm the wide variety of feeding habits exploited by early dinosaurs, which was fundamental for the evolutionary success of the clade.

Climatic controls on the ecological ascendancy of dinosaurs

Richard J. Butler[1], Emma M. Dunne[1], Alexander J. Farnsworth[2], Roger B.J. Benson[3], Pedro L. Godoy[4], Sarah E. Greene[1], Paul J. Valdes[2] and Daniel J. Lunt[2]
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Dinosaurs have been extensively studied, but the impacts of large-scale environmental changes on their evolution remain contentious. Climate has been hypothesized to have been a fundamental control on dinosaur distribution and evolution, particularly during their early diversification in the Late Triassic and Early Jurassic. However, hypotheses of

climatic influences on early dinosaurs are based on indirect or qualitative observations. We test the influence of climate on early dinosaur evolution using a general circulation climatic model (HadCM3L), combined with comprehensive phylogenetic and occurrence data. We find that in the Late Triassic, early sauropodomorph dinosaurs occupied generally cooler regions with more seasonably variable temperatures. Unlike other tetrapods, including theropod dinosaurs, Late Triassic sauropodomorphs were excluded from the hottest, low-latitude climate zones. The Early Jurassic saw sauropodomorphs expand their biogeographical distribution, entering low-latitude regions for the first time. However, quantitative evolutionary models do not support a marked shift in sauropodomorph climate niche evolution across the Triassic–Jurassic boundary, suggesting that this biogeographical expansion might reflect more widespread occurrence of climatic conditions favourable for this group in the Early Jurassic. Our results suggest that climate played a key role in the biogeographical expansion and evolutionary ascendancy of early dinosaurs.

Simple and branched pterosaur feathers with distinct melanosome geometries reveal deep origins of visual signalling in feather evolution

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Preserved soft tissues in Mesozoic fossils have yielded substantial insights into the evolution of feathers and their functions. Recent discoveries of branched feathers in pterosaurs suggest that feathers originated in the ancestor of pterosaurs and dinosaurs in the Early Triassic, but the functions of these early feathers are not fully resolved. Reports of pterosaur feathers with homogeneous ovoid melanosome geometries suggest limited variation in feather colour, supporting hypotheses that early feathers functioned primarily in thermoregulation. Here we report geometry data for preserved melanosomes in soft tissues associated with the cranial crest of a tapejarid pterosaur (Lower Cretaceous Crato Formation, Brazil). The tapejarid melanosomes have distinct geometries in simple and branched feather types and the skin, a feature previously known only in theropod dinosaurs, including birds. Tissue-specific melanosome geometries in pterosaurs confirm that the ability to manipulate feather colour has deep evolutionary origins and that visual communication was an important function of early feathers. Further, genetic regulation of melanosome chemistry and shape by α-MSH, ASIP and MC1R was already active during early stages of feather evolution. The genomic regulatory framework controlling melanin-based colouration of plumage and hair likely originated in the common ancestor of birds and mammals in the Late Palaeozoic.

Giant articulated *Arthropleura* remains from the Mississippian of northern England

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Newly discovered partial remains of the giant millipede-like organism, *Arthropleura*, are reported from the Serpukhovian (Pendleian) aged Stainmore Formation in the Northumberland Basin of northern England. The reported specimen is a rare example of its kind, as only two other partially articulated giant *Arthropleura* fossils are previously known. Measuring 76 x 36 cm, the specimen is remarkable as one of largest arthropod fossils known from the global geological record, and the largest arthropleurid, from an interval pre-dating Palaeozoic oxygen peaks. The specimen is preserved in three dimensions within fine sandstone and exhibits a number of unusual taphonomic characteristics due to its moderate deformation by synsedimentary tectonics. Sedimentological evidence for a lower delta plain environment supports the contention that *Arthropleura* preferentially occupied open woody habitats rather than swampy environments, and shared such habitats with tetrapods. The new datapoint for *Arthropleura* remains is compared with other global evidence to show that the organism was closely associated with the location of the palaeoequator, and relatively unaffected by climatic events in the late Carboniferous, prior to its extinction in the early Permian.

Did Carboniferous chimaeras suck? Evidence for high-performance suction feeding in the Pennsylvanian stem-group holocephalan *Iniopera*

Richard P. Dearden, Anthony Herrel and Alan Pradel

Muséum national d'Histoire naturelle, Paris, France

High-performance suction feeders are found in all four of the major phylogenetic divisions of jawed vertebrate but one: holocephalans (chimaeras and relatives). Instead, the handful of living holocephalans share an unusual and highly conservative anatomy adapted to demersal durophagy. By contrast, in the Carboniferous stem-group holocephalans dominated entire marine ecosystems with vastly more varied and sometimes bizarre forms. These animals surely filled a wider range of ecological niches than living holocephalans, but interpreting them is difficult as their fossils are almost always flattened. In this study we investigate the functional morphology of a rare exception: the Carboniferous iniopterygian *Iniopera*. We use 3D methods and a new reconstruction of the cranial musculature to show that the mandible of *Iniopera* is unsuited to durophagy, with an extremely low mechanical advantage and estimated bite force. Instead, we argue that *Iniopera*'s small, anteriorly-oriented mouth aperture, pectoral girdle with strong muscular links to the neurocranium and robust ventral pharyngeal skeleton, and expandable pharynx are consistent with high-performance suction feeding. *Iniopera*'s anatomy is unexpectedly more similar to living tetrapod high-performance suction feeders than to more closely-related elasmobranchs, and offers a rare glimpse into the breadth of holocephalan ecologies before the dominance of neopterygians.

'Conga Lines' of small fronds: implications for reproduction and clonality in the Ediacaran

*Katie Delahooke, Alexander G. Liu and Emily G. Mitchell
University of Cambridge, UK

The Ediacaran biota of Newfoundland, Canada (~565 Ma) comprise some of the oldest examples of complex macro-organisms, preserved in census populations on large bedding planes. On the H5 surface on the Bonavista Peninsula, we discovered four instances of 'conga lines'; three to five very closely spaced, aligned small frondose specimens. This surface was subsequently mapped out from large-scale casts to create a community spatial point distribution. We then constructed an algorithm to detect linear series of proximal points, which successfully recovered the conga lines. 10,000 Monte-Carlo simulations of clustered point patterns, parameterized by models fitted to the H5 surface, in concert with this algorithm determined that the probability for finding that particular number of conga lines on the studied surface was 0.0004. This result shows that conga lines are not a consequence of chance alignments, but have instead arisen from a distinct phenomenon. Competing hypotheses to explain these linear patterns were tested by modelling larval settlement in the lee of a larger frond using discrete phase modelling (DPM), as well as assessing stolonic connections between series of frondose specimens. Discriminating between these theories expands our knowledge of Ediacaran reproductive mode and clonality.

Is early euarthropod evolution characterized by 'creeps' or 'jerks'?

*Alavya Dhungana and Martin R. Smith
Durham University, UK

A new reading of the euarthropod fossil record suggests a stepwise acquisition of key characters, rather than a compressed 'Big Bang' of sudden morphological innovation. We test these hypotheses by explicitly coding ambiguity in contested characters in a phylogenetic framework, in order to identify the most parsimonious interpretation of observed fossil morphology. Our results reveal quantitative support for the 'stepwise' hypothesis. Despite support for gradual ('creeping') evolution of the euarthropod body plan, one fossil on the euarthropod stem remains at odds morphologically with closely related fossils – implying sudden ('jerky') changes and suggesting that 'weird wonders' obfuscate Cambrian studies by representing evolutionary dead ends. We use comparative anatomy to redescribe the anterior morphology of the 'weird wonder' *Opabinia regalis*. Our results show that the morphological oddities of *O. regalis* are actually *informative* of changes in the euarthropod stem, rather than being highly derived. Together our results show Cambrian fossils support gradual morphological evolution throughout the euarthropod stem group.

It's a trap! Environment and biogeography of Siberia across the Frasnian–Famennian

Elizabeth M. Dowding, Trond H. Torsvik and Mathew Domeier
University of Oslo, Norway

The Late Devonian was a period of biotic turbulence, prolonged climate instability, and oceanic anoxia on a global scale. It was also a critical period of biotic evolution, hosting

diverse fish fauna and the earliest limbed tetrapods. Geologically and biotically active, the Late Devonian consistently presents new insights into the conditions and patterns of ecosystem development. Here we report the results of palaeoenvironmental review and biogeographical assessment of Siberia in the Late Devonian. Late Devonian Siberia hosts terrestrial, marginal and marine settings, presenting a unique cross-section of the local environment. The Viluy Traps, a large igneous province (LIP), is considered a key feature of the Siberian landscape; its active pulses have been correlated to Late Devonian extinction across the region. Taxic distributional data were collected from museum collections and published literature, and supplemented by the Paleobiology Database. Once cleaned and validated, the data were tested across time, area and geological regime. Using fossil occurrences, different types of survivorship were marked and ranked within a geological province. This was then tested against the temporal distribution of LIP events. The assessment of changing palaeoenvironmental and biogeographic profiles across the Frasnian–Famennian events provides unique insight into the spatial structure of extinction and recovery.

How *in vivo* data can shed light on jaw evolution during the fish–tetrapod transition

Hugo Dutel[1], Anne-Claire Fabre[2], Laura B. Porro[3], Michael J. Fagan[4] and Emily J. Rayfield[1]

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[4]*University of Hull, UK*

Despite the advances in understanding the assembly of the tetrapod body plan, it is still unclear how the dramatic morphological changes in the skull impacted feeding function during the fish–tetrapod transition. Previous studies have focused on the morphological and biomechanical evolution of the jaws of fossils spanning the fish–tetrapod–amniote transitions. Yet, fossil taxa have never been analysed along with living vertebrates for which soft tissue anatomy and performance measurements can be collected. We aimed to fill this gap by investigating the morphological and functional variation of the jaw of six fossil early tetrapods and lobe-finned fishes with a sample of 30 living vertebrates (non-tetrapods, amphibians and amniotes). Using 3D geometric morphometrics and phylogenetic comparative methods we determined the pattern of variation in jaw shape and assessed the influence of phylogeny, allometry and ecology on morphological variation. We then deciphered how the variation in the shape of the jaw of the living vertebrates sampled relates to bite force, muscle mass, and selected functional and biomechanical parameters. These new data will contribute to better understanding the determinants of phenotypic variation in living taxa, and reconstruct the evolution of soft tissue anatomy and functional performance in fossils.

talks

Evolutionary analysis of swimming speed in early vertebrates challenges the 'New Head Hypothesis'

Humberto G. Ferron and Philip C. J. Donoghue
University of Bristol, UK

The ecological context of early vertebrate evolution is envisaged as a long-term trend towards increasingly active food acquisition and enhanced locomotory capabilities culminating with the emergence of jawed lineages. However, support for this hypothesis has been anecdotal and drawn almost exclusively from the ecology of living taxa, despite knowledge of extinct phylogenetic intermediates that can inform our understanding of this formative episode. Here we analyse the evolution of swimming speed in early vertebrates based on caudal fin morphology using ancestral state reconstruction and evolutionary model fitting. We predict the lowest and highest ancestral swimming speeds for jawed and microsquamous jawless groups, respectively, and find complex patterns of swimming speed evolution with no support for a trend towards more active lifestyles in the line leading to jawed groups. Our results challenge the hypothesis of an escalation of Palaeozoic marine ecosystems and shed light into the factors that determined the disparate palaeobiogeographic patterns of microsquamous and armoured Palaeozoic jawless vertebrates. Ultimately, our results offer a new enriched perspective on the ecological context that underpinned the assembly of vertebrate and gnathostome body plans, supporting a more complex scenario characterized by diverse evolutionary locomotory capabilities reflecting their equally diverse ecologies.

Marine tetrapod feeding guilds using automated high-density 3D geometric morphometrics

Valentin Fischer[1], Jamie A. MacLaren[1,2], Rebecca F. Bennion[1], Pierre Sparla[1] and Nathalie Bardet[3]
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Defining feeding guilds based on tooth morphology is an entire subfield in marine tetrapod science. However, these assessments have mostly been qualitative, relying on gross tooth shape, rarely preserved gut content and killing behaviour. Moreover, some of the data at the foundation of these guilds have proven to be debatable and there is an ever clearer need for a testable, quantitative framework to assess feeding guilds. We develop a novel protocol that incorporates the pseudo-landmarking technique into high-density geometric morphometrics procedures, sampling 3D surface models of tooth crowns automatically and densely (*e.g.* 2,000 surface landmarks) after placing just five fixed landmarks on each tooth. A crushing-to-piercing transition is evident along the first axis of the PCA-based morphospace, while the presence and shape of carinae, as well as crown curvature, are captured by the second axis. This allows an efficient visualization of tooth shapes with just two axes. Peculiar structures such as strong crown curvature or carinae are mostly recorded on medium-sized teeth, suggesting that a scaling factor is at play. We attempt a new definition of marine reptile feeding guilds based on tooth morphology and size, using extant polarizers.

First fossil of *Styriofelis* (Felidae, Carnivora) from the middle Miocene of the Madrid Basin

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Príncipe Pío-2 is one of the richest middle Miocene fossil sites of Madrid. Here we describe a fairly well preserved hemimandible of a medium-sized felid from this site. Based on diagnostic characters, such as poorly developed talonid and metaconid on m1, gently curved mandibular symphysis, and presence of a vestigial m2, the specimen is determined as belonging to *Styriofelis turnauensis* (Hoernes, 1882). The hemimandible is almost complete, showing all the teeth except the incisors. Both the mandibular corpus and ramus are very robust in comparison to extant similarly-sized felids. The angular process shows a strong lateral expansion under the masseteric fossa, indicating relatively large deep and superficial masseter muscles. This suggests that *Styriofelis* had more powerful masticatory muscles than other known fossil and extant small felines and, therefore, a more powerful bite. The coronoid and mandibular processes and the mandibular condyle are also present, which make this hemimandible one of the most complete specimens of all the known early felines. Also, it constitutes the first presence of *Styriofelis* in the Madrid basin, adding this taxon to the extraordinarily rich fossil record of felids from this region, one of the most relevant places in the world for the study of Miocene Felidae.

Biome specialization promotes diversification in swallowtail butterflies

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One of the main goals in macroevolutionary research is to test hypotheses linking climate changes with diversification patterns. For instance, it is generally thought that biome specialists (species restricted to a single biome) have higher speciation and extinction rates than generalists, as the former are more prone to population fragmentation and genetic divergence when facing environmental change. This and other related predictions are encapsulated under the resource-use hypothesis, previously tested using both fossil and living species data. However, previous works have been focused on vertebrate clades. Thus, the universality of such predictions in other key groups such as insects is still unknown, preventing us from understanding the impact of climate shifts in a significant part of the global biota. In this work, we test some of the predictions from the resource-use hypothesis in swallowtail butterflies (Papilionidae) by estimating the degree of biome specialization of each species and testing for its correlation with species-level diversification

rates estimated from the most complete Papilionidae time-calibrated phylogeny to date. We found a higher prevalence of biome specialists than expected under null models, which also showed higher diversification rates than biome generalists, and the proportion of specialists in climatically extreme biomes was higher than in transitional biomes.

Examining postcranial evolution in Crocodylomorpha using discrete characters

Pedro L. Godoy[1,2], Felipe C. Montefeltro[3], Mario Bronzati[4], Candice M. Stefanic[2], Hans C. E. Larsson[5], Richard J. Butler[6] and Alan H. Turner[2]

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talks

Most macroevolutionary studies exploring crocodylomorph morphological variation have focused on the skull. These works provided important insights, such as the association between ecology and changes in cranial morphology. However, similar questions remain untested for the postcranium. Here we investigate the influence of ecological transitions on the postcranium, by estimating and comparing cranial and postcranial morphological disparity from discrete characters, using two of the most comprehensive phylogenetic matrices available. A principal coordinate analysis reveals that, when only postcranial characters are considered, more overlap is observed in the morphospace of different crocodylomorph lifestyles (*e.g.* terrestrial, freshwater and marine), suggesting that changes in the postcranium are not associated with changes in lifestyle. However, it could also indicate that such variation has yet to be incorporated into published data matrices. Indeed, the vast majority of characters in our analyses (> 80% in both datasets) are based on cranial features. We also fitted distinct evolutionary models, including a multi-regime model aimed at testing if morphological changes were associated with ecological transitions. The results varied depending on the dataset used, with either cranial or postcranial characters receiving more support for a multi-regime model, demonstrating a significant effect of taxon sampling.

Cenozoic slowdown in placental skull evolution

Anjali Goswami[1,9], Eve Noirault[1], Ellen J. Coombs[1], Julien Clavel[1], Anne-Claire Fabre[3], Thomas J. D. Halliday[1], Morgan Churchill[4], Abigail A. Curtis[5], Akinobu Watanabe[1,6,7], Nancy B. Simmons[6], David L. Fox[8], Brian L. Beatty[7], Jonathan H. Geisler[7,9] and Ryan N. Felice[1]

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Placental mammals make up 94% of extant mammalian diversity, with ~6,144 recognized extant species and an immense variation in ecology and morphology. However, significant uncertainty in the timing of the initial divergence and frequent exclusion of fossils from macroevolutionary analyses are driving continued debate on the tempo, mode and drivers of the placental radiation. Here we present the first quantitative analysis of skull evolution spanning living and extinct placental diversity, with 757 3D landmarks and sliding semi-landmarks for 322 species representing every extant family and most extinct orders, analysed across a distribution of 1,800 exvolutionary trees. Placental cranial variation is highly concentrated, with only whales and rodents occupying distinct regions. Rates of evolution peak early in the radiation and generally decline through the Cenozoic. Whales, armadillos and extinct "ungulate" orders consistently display rapid evolution, while stem placentals evolve much more slowly than the crown group. Rodents and bats display moderate to low evolutionary pace, demonstrating a dissociation of taxonomic and morphological diversification. Social, precocial, aquatic and herbivorous species evolve fastest among placentals. Finally, ancestral shape estimates for three of the four extant superorders are highly similar, suggesting that the earliest representatives of the placental radiation may continue to elude unambiguous identification.

Does time matter in phylogeny? A perspective from the fossil record

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The role of time (*i.e.* taxa ages) in phylogeny has been a source of intense debate within palaeontology for decades and has not yet been resolved fully. The fossilized birth–death range process is a model that explicitly accounts for information about species through time. It presents a fresh opportunity to examine the role of stratigraphic data in phylogenetic inference of fossil taxa. Here we apply this model in a Bayesian framework to an exemplar dataset of well-dated conodonts from the Late Devonian. We compare

the results to those obtained using traditional unconstrained tree inference. We show that the combined analysis of morphology and stratigraphic data under the FBD range process reduces overall phylogenetic uncertainty, compared to unconstrained tree inference. We find that previous phylogenetic hypotheses based on parsimony and stratophenetics are closer to trees generated under the FBD range process. However, the results also highlight that irrespective of the inclusion of age data, a large amount of topological uncertainty will remain. Bayesian inference provides the most intuitive way to represent the uncertainty inherent in fossil datasets and new flexible models increase opportunities to refine hypotheses in palaeobiology.

Dinosaur etymology reflects and reinforces global inequities in palaeontology

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Taxonomy is foundational to the study of life on Earth in Western science approaches. Each species is assigned a binomial (two-part) name in the Linnaean system of classification, established almost three centuries ago. This allows us to categorize species and unambiguously discuss different organisms across language barriers. These names, however, carry meanings beyond simply identifying a species. Some names refer to anatomical features of interest, hypothesized behaviours or ecologies, while others honour people, places and folkloric entities. The choice of whom or what to honour is a power held by the authors describing the holotype, and overseen by reviewers and editors. We examined the historical patterns in the etymology of Mesozoic dinosaur genera and species names to survey who holds these naming rights and how their choices reinforce prevailing power structures and value systems in palaeontology. A plurality of dinosaurs are named for people, but there are significant geographic, gender and linguistic disparities in who authors have chosen to celebrate and recognize. These discrepancies, mirroring patterns observed in the scientific names of extant dinosaurs, reflect historical, colonial structures associated with the natural sciences and the inequitable access to material and funding, structures that persist to this day.

Occurrences of Palaeozoic ray-finned fishes exhibit major biases which confound diversity estimates

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Actinopterygians (ray-finned fishes) are the most diverse living group of vertebrates, but the patterns of diversity in their early evolutionary history are far from understood. There have been limited attempts to investigate biases in the early actinopterygian fossil record, and previous studies of 'global' diversity have conglomerated regional fossil records, with results subject to significant spatial biases. Palaeontologists have sought to untangle

sampling biases and estimate true diversity patterns with new sampling standardisation techniques. These have been applied to numerous vertebrate groups, but never to ray-finned fishes. Here we present raw occurrence data for Palaeozoic actinopterygians and identify major spatial biases and gaps in sampling. We also attempt to estimate diversity trends. We find that biases effectively swamp any underlying signal, and our richness estimates show explicable, though likely inaccurate, temporal variation. Available methods are therefore unable to produce accurate trends in Palaeozoic actinopterygian diversity due to compounding taxonomic, spatial and temporal biases that plague the actinopterygian fossil record. Future work addressing problematic taxonomy, exploring under-represented regions, and harnessing unpublished museum data, will be vital to understanding the rise of ray-finned fishes. More broadly, our work highlights that researchers should take care that their data are suitable for estimating diversity.

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. Furthermore, insular dwarfism seems to occur more frequently than insular gigantism. Fossil dormice (Gliridae) are known to have increased their body size during isolation on various Mediterranean islands. Here we compare 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.

talks

Complex growth and sexual maturity in a *c.* 512-million-year-old trilobite

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The exceptional trilobite fossil record provides our best insights into early arthropod growth, although detailed analysis has so far been restricted to a handful of species. Here we present a detailed examination of axial growth in the Cambrian Series 2 (Stage 4) trilobite *Estaingia bilobata* from the Emu Bay Shale, South Australia. We use threshold models to show that abrupt allometric changes occurred in two phases, close to the anamorphic–epimorphic and meraspid–holaspid transitions. It is likely that these reflect the transition to sexual maturity based on observations of similar changes in extant arthropods such as millipedes and crustaceans. We also observe growth gradients across the sequence of meraspid and holaspid trunk segments and fit contrasting non-linear models to test hypotheses about likely growth controls. We suggest that overall size, rather than moult stage, may better explain observed patterns of trunk segment size through ontogeny. The observation of multiple phases of allometric change across ontogeny suggests that trilobite growth is more complex than previously thought.

Diversification through the looking glass: the continuum of mass radiation and extinction

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Palaeodiversity studies have previously focused strongly on a small number of mass extinctions and their subsequent recoveries. This is in line with macroevolutionary narratives of creative destruction, in their strongest forms suggesting that major radiation requires preceding extinction to clear its path. However, machine-learning-assisted analysis of the relative levels of species extinction and origination across Phanerozoic geological boundaries shows a full continuum of events ranging from predominant diversification, with little extinction, to its converse of extinction with little associated diversification. Within this continuum, events which correspond most closely to classic macroevolutionary narratives of extinction and recovery include first, relatively balanced events of extinction and radiation (such as the Ordovician, where radiation has often been emphasized) and second, mass extinctions followed shortly by significant radiations (such as the end-Permian and early-middle Triassic). However, such events are only a small component of a continuum in which the extinctions and radiations that are most comparable in scale (looking glass events, exemplified by the Cambrian explosion and end-Permian extinction) are not significantly correlated in time. Such analyses, conducted at the biologically fundamental species level, show no significant decline in extinction magnitude across the Phanerozoic, in contrast to widely reported trends among higher taxa.

Here be dragons: the perplexing patterns in the distribution, growth and evolution of non-pterodactyloid pterosaurs

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The non-pterodactyloid pterosaurs were a successful group of flying reptiles, appearing in the Late Triassic and reaching global distribution by the Late Jurassic. Despite low disparity and conservative bauplan, they occupied a range of depositional environments and continents. Even with temporal longevity and success, these animals vanished from the record by the Early Cretaceous, seemingly replaced by related pterodactyloid pterosaurs and birds. With preservation biases and debatable phylogenies, the macroevolutionary patterns of pterosaur evolution are hard to study. Our recent discovery of a large Middle Jurassic non-pterodactyloid from Scotland prompted a re-evaluation of basal pterosaur phylogeny and distribution to address what may have caused such a successful grade of animals to vanish. Our review of the distribution of non-pterodactyloid specimens indicates that immature individuals are over-represented in marine environments whereas larger individuals are more likely to be found in marginal marine or terrestrial settings. Our new phylogeny, created from combined published datasets, suggests a post-Toarcian diversification event, reaching a morphological zenith by the Middle Jurassic followed by morphological stasis throughout the Late Jurassic. This stagnation might have resulted in the clade failing to adapt to global climate changes across the Jurassic–Cretaceous boundary.

Fossil evidence suggests the first amniote displayed extended egg retention

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The amniotic egg with its complex foetal membranes was a key innovation in vertebrate evolution that enabled the great diversification of reptiles, birds and mammals. Did these foetal membranes evolve in eggs on land as an adaptation to the terrestrial environment or to control antagonistic foetal–maternal interaction in association with extended embryo retention (EER)? Extant amniotes (turtles, crocodilians and birds) generally lay eggs at an early developmental stage (obligate oviparity), whereas most squamates (lizards and snakes) and mammals either display oviparity with EER or viviparity (produce live young). Evolutionary studies based on extant amniotes give equivocal results about whether oviparity or viviparity arose first. Fossil data, which show eggshell type and sometimes viviparity and even EER, allow more accurate reconstruction of ancestral states. Here we report an archosauromorph (choristodere) embryo of *Ikechosaurus* sp. inside a parchment-shelled egg from the Lower Cretaceous of northeast China. The fossil confirms this archosauromorph displayed EER across oviparity to viviparity, as seen in numerous extant squamates, and the even older mesosaurs. Phylogenetic analysis on amniotes including fossils shows that obligate oviparity evolved multiple times, and viviparity was the primitive reproductive mode, supporting the EER model for the origin of the amniotic egg.

talks

First known fossil ratite eggshells from the Siwalik Frontal Range near Chandigarh (northern India) and their multidisciplinary scientific analysis

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Fossil ratite eggshells and struthioid (ostrich-like) skeletal remains have been known from Miocene to Middle Pleistocene deposits of the Siwalik Hills in Pakistan and India since the nineteenth century. Siwalik exposures in Pakistan have yielded aepyornithid and struthioid fossils in deposits dating to 11.35–1.25 Ma and 1.15–0.58 Ma, respectively. Ratite eggshells from Haritalyangar, the 10.1 million-year-old Miocene fossil ape locality in northwestern India, show close affinity with the Neogene fossil taxon *Struthiolithus*. Here we report discovery of the first known fossil ratite eggshells (n = 36) from three localities in the Siwalik Frontal Range near Chandigarh in northern India. Collected from a surface of fine sediments mapped earlier as the Pinjore Formation at Choti-Badi Nangal, the specimens fill critical geographic and chronological gaps in South Asian struthioid palaeobiogeography. We applied optical and scanning electron microscopy to understand the ultrastructure and pore pattern. Pore morphology shows close affinity to *Struthio camelus* subsp. *molybdophanes* (Somali blue ostrich). Energy dispersive X-ray analysis was used to understand the elemental composition of the eggshells and was supplemented by X-ray diffraction to check for the extent of diagenesis. We also present preliminary results of stable carbon and oxygen isotope analysis of ostrich eggshell to infer their environmental context and diet.

In search of ancestors: benchmarking parsimony and likelihood methods of ancestral state estimation

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Ancestral state estimation is a formal phylogenetic method for inferring the nature of ancestors and performing tests of character evolution. As such, it is among the most important tools available to palaeobiologists. However, the precision and accuracy of different methods remain unclear. Here we use simulations to test among parsimony and likelihood methods for discrete unordered characters. We simulated 500 binary and multistate characters under a range of tree sizes and topologies. Data were simulated under the equal-rates (ER), symmetric (SYM) and all-rates-different (ARD) models. Ancestral states were subsequently estimated under the aforementioned models and parsimony. Our results demonstrate that all approaches obtain higher accuracy with increasing tip data. Parsimony outperforms all other methods when branch length heterogeneity is low, but is outperformed by likelihood methods when heterogeneity is high. The ARD model is least accurate irrespective of the model used to simulate the data, suggesting that it may be overparameterized. We find no correlation between difference in accuracy and difference in model fit; a better fitting model is not necessarily more accurate. Finally, our results highlight the importance of incorporating fossils, which break long branches, lower overall branch length heterogeneity and thereby increase the accuracy of ancestral state estimates.

Geometric evolution of the galloanseran quadrate

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In birds and other reptiles, the quadrate acts as a hinge connecting the lower jaw and the skull, and plays an important role in avian cranial kinesis. Though previous studies have qualitatively described its substantial morphological variability, none have tried to quantify evolutionary changes in its shape. Here we investigate shape changes of the quadrate in Galloanserae, a major clade of extant birds uniting relatives of living chickens and ducks. We quantified morphological variation in the quadrate across 35 extant galloanseran taxa covering all major extant subclades using three-dimensional geometric morphometrics, and performed ancestral shape reconstructions in the context of an up-to-date neornithine phylogeny. Our results suggest that the quadrate of ancestral galloanserans may have shared features associated with both extant Galliformes and Anseriformes. For example, the ancestral condition of the orbital process is reconstructed as robust and strongly protruding (anseriform-like) with a pointed tip (galliform-like). The quadratojugal contact is reconstructed as a shallow fossa (anseriform-like), but the squamosal and otic capitula are more similar to the condition in galliforms. Notably, our ancestral reconstructions closely approximate aspects of quadrate morphology observed in early galloanseran fossil quadrates, such as *Asteriornis* and *Presbyornis*, suggesting that both these fossils and our reconstructions may provide useful insight into the plesiomorphic galloanseran condition.

New unworn dentitions illuminate the dental morphology and diversity of puzzling early eutherian mammals, Taeniodonta

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Taeniodonta is a group of North America Palaeogene mammals that lived after the end-Cretaceous mass extinction. Taeniodonts show an extreme degree of dental wear, indicative of an abrasive diet, leading to hypsodonty in the most derived species. The rarity of fossils and their highly worn teeth makes their dental morphology difficult to study. We examined five new partial mandibles from the San Juan Basin, New Mexico, USA, most of which preserve unworn molars. One of the specimens preserves a deciduous ultimate premolar and using 3D micro-CT we were able to segment and study the unworn permanent tooth embedded in the jaw. We then conducted multivariate analyses on dental measurements to compare the new specimens to known teeth of early taeniodonts. We assigned the new specimens to at least three genera of Conoryctidae, a taeniodont subclade. Our results suggest that there is a broader dental diversity of the studied genera than previously thought. Morphological observations also suggest that progressive loss of cingulids and the addition of cuspids started early in the evolution of taeniodonts. These distinctive dental specializations strengthen the hypothesis that early Palaeocene mammals were able to rapidly adapt to fill the vacant ecological niches after the end-Cretaceous extinction.

talks

Developing a taste: connecting skull shape ontogeny and evolution of different feeding adaptations in Cetacea using 3D geometric morphometrics

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Baleen and toothed whales (Mysticeti and Odontoceti, Cetacea), while sharing a deep evolutionary history, present distinct feeding adaptations most visible in their skull morphology. Ontogeny plays a key role in the evolution of organisms, as changes during this complex process can allow for new traits to arise. Identifying changes in allometry from fossil ancestors to modern groups can reveal important insights into the evolutionary processes at play. We aim to conduct a novel study to investigate the influence of allometric changes in Cetacea evolution. We hypothesize that allometric trajectories are markedly different between Mysticeti and Odontoceti, and among families of toothed whales with different skull morphologies. We assembled a 3D dataset of over 120 specimens, spanning the developmental and phylogenetic spectrum. Skull shape morphology was acquired using both CT and surface scanning. We quantified variation using 3D geometric morphometrics and conducted statistical analyses in R. Our results show that the two groups have distinct allometric trajectories, with Mysticeti displaying a decelerated growth relative to the reconstructed ancestral trajectory. Odontoceti instead present an accelerated growth, with significant differences among families. This shows the profound influence of developmental changes in the evolution of the disparate feeding adaptations present in Cetacea.

Cambrian tentaculate deuterostomes reveal ancestral body plans

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Reconstructing the common ancestor of deuterostomes is crucial for uncovering the earliest steps in the evolution of this hyper-diverse clade. Comparative anatomy, developmental biology and molecular phylogenetics have provided valuable insights into patterns of character evolution, but important aspects remain unclear due to the widely divergent body plans exhibited by extant deuterostomes. Putative stem-deuterostomes, stem-chordates, stem-echinoderms and stem-hemichordates have been reported from the Cambrian, potentially bridging these morphological gaps, but the phylogenetic positions of these taxa are contentious. Here we describe new exceptionally-preserved specimens of the discoidal metazoan *Rotadiscus grandis* from the early Cambrian Chengjiang biota of China. These reveal a previously unknown bispiral structure, which we interpret as a coelomopore, located adjacent to a pair of hollow tentacles that bifurcate and branch unilaterally along their lengths. Phylogenetic analyses recover *Rotadiscus* and other eldonioids as stem-ambulacrarians. Additionally, our analyses recover another group of putative Cambrian deuterostomes, the vetulicolians, as stem-group chordates. Together, these data indicate that a branched tentacular system is plesiomorphic for ambulacrarians and that the post-anal regions of chordates and hemichordates were acquired independently. This allows us to reconstruct the ancestral body plans of major clades, revealing that key traits of extant deuterostomes evolved through convergence.

Physical characterization of the conodont white matter tissue

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Conodont elements are phosphatic tooth-like microfossils that comprised the dentition of an extinct clade of primitive vertebrates that thrived in marine environments from the Cambrian to the Triassic, and are commonly exploited as mineral archives of past ocean chemistry. The elements are histologically differentiated into a base and a crown, the latter comprised of lamellar crown tissue and the tissue white matter which has been the focus of geochemical assays. However, the nature of the white matter has been the subject of controversy, including claims that it is macrocrystalline, microcrystalline or even non-crystalline; concerns have also been raised that its porous structure may reflect permeability and, as such, an imperfect geochemical archive. Using electron backscatter diffraction (EBSD), ptychographic X-ray computed nanotomography (PXCT) and pore network analysis, we demonstrate that white matter is crystalline, comprised of a single crystal that is typically tens of microns in dimension. PXCT and pore network analysis reveals that while tissue is extremely porous, the pores are unconnected. Combining these data reveals that conodonts enlarged their dentition through syntactic growth of their denticles and provides support for the exploitation of conodont white matter as a closed geochemical system suitable for inferring the changing chemistry of Cambrian–Triassic oceans and atmospheres.

Palaeontology, Geodiversity and the International Geodiversity Day

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Geodiversity is the abiotic equivalent of biodiversity and has been defined as "the natural range (diversity) of geological (rocks, minerals, fossils), geomorphological (landforms, topography, physical processes), soil and hydrological features. It includes their assemblages, structures, systems and contributions to landscapes" (Gray 2013). Fossils represent an important component of Earth's geodiversity and are of particular interest within geodiversity to engagement with education (Sustainable Development Goal (SDG)4.7), geotourism (SDG8.9), conservation (SDG11.4), climate change awareness (SDG13.3), and understanding ocean acidification (SDG14.3). Palaeontology, as part of geodiversity, has a meaningful role to play in supporting global efforts for a more peaceful and prosperous planet. We have been working to persuade international governments to establish an International Geodiversity Day on 6th October each year. UNESCO's Executive Board has already approved the proposal, with a final decision being taken at the UNESCO General Conference in November. We will outline the important role that palaeontology plays within geodiversity, and the reasons palaeontologists should support this proposal. Finally, noting the increasing prominence of policy engagement in research, we will discuss the methods used to engage policy makers, and how these were used to build a global partnership to raise the profile of palaeontology and geodiversity as a whole.

Cranial muscle reconstructions quantify adaptation for high bite forces in Oviraptorosauria

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Oviraptorosaurians are an unusual and probably herbivorous group of theropod dinosaurs that evolved pneumatized crania with robust, toothless jaws apparently adapted for producing a strong bite. Using 3D retrodeformed skull models of oviraptorid oviraptorosaurians *Citipati*, *Khaan* and *Conchoraptor*, along with the earliest diverging oviraptorosaurian *Incisivosaurus*, we digitally reconstruct jaw adductor musculature and estimate bite force to investigate cranial function in each species. We model muscle length change during jaw opening to constrain optimal and maximum gape angles. Results demonstrate oviraptorids were capable of much stronger bite forces than herbivorous theropods among Ornithomimosauria and Therizinosauria, relative to body mass and absolutely. Increased bite forces in oviraptorid oviraptorosaurians compared to the earliest diverging oviraptorosaurian result from expanded muscular space and different cranial geometry, not changes in muscular arrangement. Estimated optimal and maximum possible gapes are much smaller than published estimates for carnivorous theropods, being more similar to herbivorous therizinosaurian theropod *Erlikosaurus* and modern birds. Restrictive gape and high bite force may represent adaptation towards exploiting tough vegetation, suggesting cranial function and dietary habits differed between oviraptorids and other herbivorous theropods. Differences in the relative strength of jaw adductor muscles between co-occurring oviraptorids may be a factor in niche partitioning, alongside body size.

Diet of the toothed and long-snouted longipterygid birds (Avialae: Enantiornithes) determined with reference to quantitative analysis of extant bird dietary proxies

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Birds are key indicator species in extant ecosystems, so we logically expect that Mesozoic birds are key to reconstructing Mesozoic ecosystems. However, many facets of Mesozoic bird ecology, particularly diet, remain speculative. One group of particular interest is the bizarre toothed and long-snouted longipterygid birds. Longipterygidae is the most well-understood family of enantiornithine birds, the dominant birds of the Cretaceous period. However, as with most Mesozoic birds, hypotheses of their diet are qualitative. To improve our understanding of this family, we investigated four dietary proxies in extant birds (body mass, claw morphometrics, jaw mechanical advantage, and jaw strength via finite element analysis) to determine diagnostic traits of avians with a given diet. We then investigated these proxies in longipterygids as well, and found all members of the family but *Shengjingornis* (whose diet remains inconclusive) most likely to be invertivores or generalist feeders, and all but *Longipteryx* unlikely to be raptorial. These findings are consistent with prior hypotheses that Mesozoic birds occupied low trophic levels. This study provides a 20% increase in known fossil bird diets, triples the number of known enantiornithine diets, and serves as an important first step in quantitatively investigating the origins of trophic diversity in living birds.

An estimate of the deepest branches of the tree of life from ancient vertically-evolving genes

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Core gene phylogenies provide a window into early evolution, but different data and analytical methods have yielded substantially different views of the tree of life. Previous work using core genes has typically supported a long branch separating domains. Recently, a broader set of non-ribosomal genes suggested that Archaea may be less divergent from Bacteria. Resolving this debate is key to determining the diversity of the archaeal and bacterial domains, the shape and age of the tree of life, and our understanding of the early course of evolution. Here we investigate the evolutionary history of the markers key to the debate. We show estimates of a reduced Archaea–Bacteria (AB) branch length result from inter-domain gene transfers and hidden paralogy in the expanded marker gene set. Analysis of a range of markers from 700 taxa reveals that current methods likely underestimate the deepest branch due to saturation and model inadequacy; best-performing phylogenetic markers, regardless of their function, support longer inter-domain branches. Phylogenies inferred from these markers support a long AB branch, recover DPANN at the base of the Archaea, and place CPR as the sister group to the Chloroflexota and provide insight into the metabolism of the last universal common ancestor.

A new marrellomorph arthropod from southern Ontario and the potential for soft tissue preservation on late Ordovician open marine shelves

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Post-Cambrian open marine Lagerstätten are rare and widely dispersed, producing a patchy picture of the diversity and biogeography of non-mineralized marine organisms, and challenging our understanding of the fate of Cambrian groups. We report new soft-bodied fossils, including a marrellomorph arthropod, fragmentary carapaces and macroalgae from the late Ordovician (Katian) Upper Member of the Kirkfield Formation near Brechin, Ontario, Canada. The unmineralized elements are associated with an exceptionally preserved shelly biota which was entombed rapidly in storm deposits that smothered the shallow, carbonate-dominated shelf. The marrellomorph is remarkable for its ornate, curving cephalic spines and pair of hypertrophied appendages, suggesting a slow-moving, benthic lifestyle. Re-evaluation of marrellomorph phylogeny using new data favours an arachnomorph affinity, but internal relationships are robust to differing outgroup selection. Clades Marrellida and Acercostraca are recovered, but the monophyly of Marrellomorpha is uncertain. The new taxon is recovered as sister to the Devonian Mimetaster and, as the second youngest-known marrellid, bridges an important gap in the evolution of this

clade. Taken together, the Kirkfield biota represents a rare window into Ordovician open marine shelf environments in Laurentia, representing an important point of comparison with contemporaneous Lagerstätten from other palaeocontinents, with great potential for further discoveries.

Assessing the impact of climate change on the structural integrity of benthic foraminifera during the Palaeocene Eocene Thermal Maximum – implications for future climate change

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Benthic foraminifera are a group of calcifying marine organisms whose morphology is affected during periods of environmental change. This may lead to the production of weakened forms, leaving these organisms more susceptible to breakage through predation or exposure to wave action. Finite element analysis (FEA) is a mathematical technique that allows us to assess structural integrity in biological organisms. Here we used simple finite element models to assess how the morphology and structural integrity of benthic foraminifera is affected during periods of climate change and focused on the creation of simple adjustable 3D geometric models, based on 2D images. The reliability of these models was evaluated by comparing results to biologically accurate 3D models generated from computed tomography scans. The results showed that the simple models were capable of distinguishing differences in mechanical robustness. These simple models were then altered in alignment with morphological changes observed in the fossil record of the Palaeocene Eocene Thermal Maximum (PETM). The results show that species-specific morphological changes that occurred across the PETM led to a weakening of structural integrity suggesting that, under future climate change, certain species of benthic foraminifera may produce mechanically weaker tests, making it harder to withstand physical pressures.

An early Cambrian window into mechanisms for phosphatization of labile soft tissues

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Phosphatization has the potential to preserve labile soft tissues in exquisite detail, providing a wealth of otherwise unavailable information. However, previous studies and laboratory experiments suggest that the process is highly biased, ultimately affecting our view on the fossil record. The scarcity of phosphatized fossils at any given locality prevents a comprehensive synthesis of the relationship between depositional environment and taxon-

specific anatomy/composition giving rise to phosphatized tissues. Here we explore the lower Cambrian Sirius Passet Lagerstätte (North Greenland) where phosphatized fossils are abundant. The work is based on both qualitative and quantitative (phosphatized n>700) data. The depositional environment is characterized by frequent depositional events with dense accumulations of fossils (on average ~77 specimens per 1,000 cm^3) and organic fragments, and occasional microbial mats. There is a strong bias both between and within taxa, explained by size, diet and anatomy. Organisms with high phosphorus content are favoured (*e.g.* large muscle volume, carnivorous diet). Muscle phosphatization is generally less frequent in small specimens (juveniles?) and species. Muscles phosphatize more readily in the axial region and near phosphorous-rich tissues (*e.g.* gut diverticula and ganglia). Gut diverticula phosphatize more frequently than the gut tract. Closed local environments, exemplified by enrolled arthropods, favour extensive phosphatization.

How soft-bodied fossils from the Lower Devonian of southern Belgium can help to decipher the early stages of vertebrate evolution

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The evolutionary history of vertebrates began, at the latest, during the early Cambrian with the first occurrence of elongated and laterally flattened soft-bodied organisms known as chordates, possessing a notochord but devoid of backbone and jaw. Vertebrates subsequently underwent major anatomical changes, such as the acquisition of a vertebral column, development of jaws, and adaptations to terrestrial life. Early chordate and early vertebrate fossils provide the only direct evidence of the origin of vertebrates and on how their distinctive body plan evolved. Unfortunately, the fossil record of early chordates and part of the early vertebrates is extremely scarce as these organisms mostly consist of decay-prone soft parts that are usually degraded and lost prior to fossilization, making the interpretation of their anatomy highly challenging. Recently, new mysterious soft-bodied fossils have been discovered in the Lower Devonian of southern Belgium. We studied the visible and hidden anatomy of the fossils, as well as their chemistry, using state-of-the-art imaging and spectroscopy techniques. We undoubtedly identify some specimens as euphaneropids, a group of early jawless vertebrates. The other fossils display a mosaic of characters that make their identification between early chordates and early vertebrates difficult.

Analysis of skeleton space reveals early unique excursions in the evolution of spiralian hard parts

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Among bilaterians, spiralians have the oldest recognizable hard parts, first appearing in the first ~10 million years of the Cambrian. Spiralians can therefore provide key insights into anatomical changes at deep divergences between phyla. We approach this from the perspective of 'skeleton space', characters that describe the construction and spatial relationships of animal hard parts. Skeletons are central to many hypotheses related to

the Cambrian explosion, and these characters are ideal for describing variation among groups with divergent body plans, as they assume nothing about homology. We analysed a new dataset including ancient and living spiralians, using ordination to quantify skeletal variation. Our results show that skeletal traits of major living groups (*e.g.* bivalves and brachiopods) were established by the Cambrian, and have remained relatively conservative since. In contrast, several early lineages showed much greater versatility and explored regions of skeleton-space that are entirely unoccupied by living spiralians, exemplified by tommotiids and 'halwaxiids'. Nevertheless, total skeletal disparity of Cambrian spiralians was lower than today. The Cambrian was a time of great evolutionary versatility, with lineages crossing large portions of trait-space during an initial expansion of skeletons that gave rise to the even greater disparity of established body plans in living animals.

Charniodiscus and *Arborea* are separate genera within the Arboreomorpha: using the holotype of *C. concentricus* to resolve a taphonomic/taxonomic tangle

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Charniodiscus is one of the most iconic and first described of the Ediacaran frondose taxa. Since the diagnosis of the holotype of *C. concentricus* in 1958, the scarcity and poor preservation of unequivocal specimens have resulted in genus-level taxonomic uncertainty. Since the recent reinterpretation of *C. concentricus* as a multifoliate frond, other *Charniodiscus* species – all of which are bifoliate – have been left in taxonomic limbo, with most authors comparing them to the clade Arboreomorpha and also the Rangeomorpha. Reconsideration of the taphonomy of the holotype of *C. concentricus* has revealed that the frond is bifoliate as first described, and also that the frondose portion was broadly conical rather than planar as previously inferred. The conical frond of *Charniodiscus* is thus morphologically quite different from all other frondose taxa within the Arboreomorpha. Our emendation of the generic diagnosis of *Charniodiscus* to encompass bifoliate arboreomorphs with conical fronds without a backing sheet distinguishes *Charniodiscus* from more planar leaf-like arboreomorphs such as *Arborea*, which has a distinctive backing sheet. Additionally, we find no evidence of rangeomorph-type fractal branching in *Charniodiscus*.

Radiodont oral cones from the Fezouata Biota (Early Ordovician, Morocco)

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The Fezouata Shale Formation is an important Burgess-Shale-type Lagerstätte from the Early Ordovician of Morocco. It preserves a rich diversity of arthropod remains, including radiodonts, an emblematic early Palaeozoic order. Most radiodonts possess a circular arrangement of spiney plates surrounding the mouth, usually in a triradial or tetraradial organization. These oral cones are typically not as common in the fossil record as frontal appendages. Two almost complete but isolated radiodont oral cones have been found in the Fezouata Biota. The larger oral cone specimen shows a unique morphology of only 24 plates, in tetraradial arrangement and bearing prominent nodes on just two of the larger plates. There is also the smallest oral cone ever found in the fossil record so far, with a more typical 28 plates in tetraradial arrangement. Other radiodonts from the Fezouata Shale include several hurdiids known only from appendages as well as the nearly two-metre-long suspension feeding *Aegirocassis benmoulae*, but neither oral cone

can be attributed to these taxa with any certainty. Based on recent phylogenetic analyses, oral cone morphologies show several convergences within Radiodonta, highlighting the complexity of the evolutionary history of the group.

An exceptionally diverse Early Devonian flora from the Lochkovian of South Africa

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The late Silurian to earliest Devonian times are pivotal in the evolution of early terrestrial ecosystems. Palaeontological evidence from this time is however very scarce and is as yet largely restricted to palaeotropical environments. Recently, in the course of an extensive and ongoing survey of the Devonian of South Africa, a rich and diversified Lower Devonian flora has been discovered. The newly found early plant-bearing lenses from the Baviaanskloof Formation at Impofu Dam in the Eastern Cape Province of South Africa provide evidence for one of the most diverse Late Silurian to Early Devonian assemblages known to date. The only previously known high-latitude floras from this time interval are those from the Paraná Basin of Brasil and Argentina, with a single plant species, *Dutoitia pulchra*, having been reported from southern Africa. The Mpofu Dam flora is comprised of up to twenty taxa including several species of the genus *Cooksonia*, gametophytes and several yet-unresolved specimens, though most plants could be related to existing taxa. Biostratigraphic constraints on the dating of the Baviaanskloof Formation are provided by this flora, which represents the oldest known from Africa.

Radial Porosity Profiles: a new quantitative histological method for studying dynamics of diametric limb bone growth

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In fossil tetrapods, limb bone histology is considered the most reliable information source not only for inferring skeletal maturity – a crucial assessment in palaeobiological and evolutionary studies – but also for evaluating the growth dynamics within the ontogenetic window represented by the primary bone cortex. Primary cortical vascularity has a complex relationship with bone growth and functional maturation which makes it an information-rich histocharacter for reconstructing growth dynamics in the context of various developmental strategies along the precocial–altricial spectrum. Driven by this

concept, we developed a new quantitative osteohistological parameter, called the radial porosity profile (RPP), which captures the relative primary cortical porosity changes in limb bones as trajectories. We built a proof-of-concept RPP dataset on extant birds, then added fossil paravian dinosaurs, and performed a set of trajectory-grouping analyses to identify potential RPP categories and evaluate them in the context of our ontogeny – developmental strategy working hypothesis. Our results reveal the analytical power of RPPs for studying growth dynamics, including unexpected candidates for osteohistological correlates of growth and functional development of limb bones. The diverse potential applications of RPPs pave the way for new research directions in the evolution of locomotor ontogeny.

Gone fishing: using the soft-tissue taxa to explore the fidelity of the early Palaeozoic fossil record of vertebrates

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Understanding the origin and evolution of vertebrates, one of the major transitional events, is heavily dependent on the fossil record of the non-biomineralizing, 'soft-tissue' taxa. However, this record is understandably patchy and incomplete. Even within Lagerstätten that preserve soft-tissues, non-biomineralized vertebrates are exceptionally rare, limited to only a small handful of sites. Taphonomic factors undoubtedly limit our understanding of this clade during this period, but the variability in preservation of different coeval sites suggests taphonomy may also mask unrecognized ecological or evolutionary constraints on these organisms. To distinguish biology from taphonomy, we use an array of biotic and abiotic traits, including lithography, preservation style, faunal composition, depositional environment and palaeo-location, to categorize the 14 known Lagerstätten beds that preserve soft-tissue vertebrate-lineage fossils between the Ordovician and Devonian periods. We then compared them to coeval Lagerstätten that have thus far failed to yield similar vertebrates. By using multivariate ordination, and other analytical techniques, we are able to test whether the gaps seen in the soft-tissue fossil record are a reflection of geological or taphonomic biases, or if the absence of these taxa is due to evolutionary drivers, potentially identifying ghost lineages which may uncover previously cryptic histories.

Exceptionally preserved soft tissues of *Vampyronassa rhodanica* provide new insights on the evolution and palaeoecology of vampyroteuthids

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The soft tissues of coleoid cephalopods record key evolutionary adaptations though are rarely preserved in the fossil record. This prevents meaningful comparative analyses between extant and fossil forms, and the development of a relative timescale for morphological innovations. However, unique 3D soft tissue preservation of *Vampyronassa* (Vampyromorpha, Incertae sedis) from the Jurassic Lagerstätten of La Voulte sur Rhone (Ardéche, France) provides unparalleled opportunities for the observation of these tissues in the supposed oldest-known relative of extant *Vampyroteuthis infernalis*. Synchrotron microtomography and reconstruction of *Vampyronassa* allowed, for the first time, a

high-resolution re-examination of external and internal morphology, and a comparison with other fossil and extant species, including *Vampyroteuthis*. The new data obtained demonstrate that key *Vampyroteuthis* characters, such as sucker attachments, were already present in Jurassic taxa. Nonetheless, compared with the detrivorous extant forms, many characters in *Vampyronassa* indicate a pelagic predatorial lifestyle. The contrast in trophic niches between the two taxa is consistent with the hypothesis suggesting a habitat shift towards a deep-sea environment prior to the Oligocene.

Completeness patterns of the Palaeozoic chondrichthyan fossil record

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The chondrichthyans (cartilaginous fishes) are a successful group of predominantly predatory fishes that originated and first diversified in the Palaeozoic. Their early fossil record is poor because their mostly cartilaginous skeletons are rarely well preserved and this, in turn, has restricted the data available for estimates of their evolutionary history. Here we quantify the quality of the Palaeozoic chondrichthyan fossil record by using a variation of the skeletal completeness metric (SCM), an approach that calculates how complete the skeletons of individuals are compared to their theoretical complete skeleton. We compiled a database of 804 chondrichthyan species from museum collection visits and literature. Temporal completeness patterns show major peaks in the Serpukhovian, Moscovian, Gzhelian-Asselian and Wordian, and lows in the Silurian and the Tournaisian–Visean. Chondrichthyans show a significantly lower completeness distribution than any published tetrapod group but increase highly when isolated tooth-, scale- and fin spine-based taxa are excluded. Environmental influences favour completeness of chondrichthyans from freshwater deposits in the Lower Devonian, the Devonian–Carboniferous boundary and the early Permian, while marine environments yield more complete skeletons throughout the Carboniferous and late Permian. Our results reveal weak spatial biases influencing the Palaeozoic chondrichthyan fossil record but strong environmental and temporal biases.

A juvenile rhynchosaur specimen from the Otter Sandstones of Southern England (Anisian, Middle Triassic)

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Rhynchosaurs were key herbivores of the Triassic. Here we report a juvenile rhynchosaur from the Otter Sandstone (Middle Triassic) of Devon, UK, that provides unexpected information on development and heterochrony of rhynchosaurs, and especially on a major change in dentition through ontogeny. The juvenile rhynchosaur exhibits a single row of proportionally large dentition occupying the entire margin of the tooth-bearing element unlike adult rhynchosaurs. The dentition and tooth-bearing elements exhibit no wear or tooth replacement cycle as seen in adults. Major morphological differences in the lower jaws also suggest that the juvenile jaws may have experienced different biomechanics and therefore behaved differently than the adult jaw, indicating the possibility of an ontogenetic dietary shift contributing to the success of rhynchosaurs. Further, whereas the rhynchosaurs skull generally shows evidence of a peramorphic shift in shape through the Triassic, we note a paedomorphic shift in the dentition of the dentary, from multiple tooth rows to reduced numbers of tooth rows.

Quantifying conodont crystals: controls of biomineralization in early vertebrates

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The emergence of mineralized skeletons in vertebrates is one of the most impactful events in the history of life. Conodonts are the first of this clade to have evolved tooth-like structures known as elements and provide a unique insight into these early stages of biomineralization. We can use crystal properties such as size, shape and orientation to quantify an organism's control on biomineralization by evaluating the relative organization of multiple crystals. A better alignment of these crystals c-axes would be beneficial as it would reduce episodes of breakage during feeding via better dispersal of stress throughout the material. We hypothesize that more derived conodonts will have a higher degree of organization in the alignment of crystals due to feeding adaptations. Here we test this with the application of electron backscatter diffraction (EBSD) to directly compare these crystal properties *in situ*, across multiple taxa, in order to compare crystal texture through time. We propose a new method of quantifying and comparing crystal organization using three phylogenetically distinct conodont taxa; two simple cone-like elements *Proconodontus muelleri*, *Panderodus equicostatus* and one complex blade like element of *Wurmiella excavata*. This novel approach proposes a new measure of skeletal adaptation in early vertebrates.

The morphological disparity of Fungi

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Fungi are the second-most diverse multicellular kingdom of life, represented by an estimated 5.1 million species. However, beyond the coarse categorization of species by the complexity of their form, the distribution of morphological variety across the fungal tree of life is poorly understood. Here we address this by sampling fungal morphological diversity with discrete characters and using these data to construct the first fungal morphospace. Of the main fungal phyla, the Basidiomycota and Ascomycota present the greatest morphological variation and organismal complexity. However, this superiority is limited to supracellular anatomy, as the subcellular disparity and complexity of both is comparable to that of other fungal phyla. As such, complexity only correlates with disparity at the supracellular level. Reconstructed ancestors bridge the gaps between the areas of morphospace occupied by fungal phyla, indicating that the clumpy occupation of extant fungal morphospace is a vestige of the extinction of phylogenetic intermediates, echoing the historical structure of metazoan morphospace. The tempo with which both kingdoms of life explore new areas of morphospace is also comparable, as both gradually expand their phenotypic ranges through time. These commonalities hint at a general model for the evolution of complex multicellular organisms.

Understanding the diversification dynamics of the Permo–Triassic archosauromorph radiation using occurrence-based Bayesian approaches

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The archosauromorph radiation started during the Triassic and was one of the most spectacular adaptive radiations in Earth history, giving rise to diverse stem and crown archosaur taxa, dominating the Mesozoic land and skies for >150 Ma; it provides an outstanding opportunity to test hypotheses regarding the process of adaptive radiation. Given a patchy fossil record, distant extant relatives and long ghost lineages, methods based on phylogenetic topologies are subject to a high degree of inference. We thus employ the Bayesian occurrence-based approach PyRate to better understand the diversification dynamics of archosauromorphs, using a dataset of first and last occurrences and body size proxy data from the Late Permian–Early Jurassic. Using a fossilized birth death model, we find evidence for a peak in net diversification in the latest Permian, indicating initial radiation directly concurrent with extinctions. This flatlines in the Late Triassic, indicating slowdown following niche-filling. Pseudosuchians peaked in diversification in the Ladinian and Carnian but suffered major Late Triassic extinction parallel to saurischian expansion. These results indicate a niche-related 'early burst' of diversification, initially potentially morphologically cryptic. We also find a negative correlation between body size and extinction (positive with longevity), indicating rapid evolutionary turnover among smaller-bodied taxa.

New information on the archosaurs from the Late Triassic fissure fills locality of Pant-y-ffynnon, Wales

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The Late Triassic to Early Jurassic fissure fill localities of the Bristol Channel area preserve a diverse fauna of mostly small-bodied vertebrates, which has provided important insights into the early evolution of major tetrapod groups such as mammaliaforms, rhynchocephalians, crocodylomorphs and dinosaurs. The Late Triassic site at Pant-y-ffynnon in Wales yields a particularly rich, but poorly understood assemblage of archosaurs, including the recently named theropod dinosaur *Pendraig milnerae*, the cursorial crocodylomorph *Terrestrisuchus gracilis*, the small sauropodomorph *Pantydraco caducus*, and the enigmatic pseudosuchian *Aenigmaspina pantyffonnensis*. Ongoing research has revealed several new insights into this fauna. *Pendraig* is identified as a small-sized non-coelophysid coelophysoid dinosaur. A revision of *Aenigmaspina*, characterized by unique, bifurcating osteoderms and conspicuously T-shaped neural spines on the cervical and anterior dorsal vertebrae, recovers

this genus as the sister taxon of Erpetosuchidae + Aetosauriformes in a new phylogenetic analysis. Finally, CT-scanning has elucidated the braincase anatomy of *Terrestrisuchus gracilis*, highlighting several features likely plesiomorphic to Crocodylomorpha, such as a quadrate that is not fused to the braincase. Together, these studies reveal the significance of the fissure fills fauna for our understanding of early archosaur evolution and diversity.

Comparative morphology of the passerine carpometacarpus: implications for interpreting the fossil record of crown Passeriformes

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The major crown bird subclade Passeriformes (passerines) comprises >6,000 extant species, making up over half of extant avian diversity. However, despite constituting one of the most diverse clades of living vertebrates, limited work has targeted passerine comparative anatomy on a broad phylogenetic scale. As such, many components of the passerine skeleton are understudied, thus hindering interpretation of the passerine fossil record. Isolated carpometacarpi are preserved relatively frequently, with numerous passerine carpometacarpi known from the Cenozoic. Here we present a detailed analysis of the passerine carpometacarpus. We generated a dataset including >130 extant taxa, sampling >70% of passerine family-level diversity, to identify morphological synapomorphies for major passerine subclades. We compiled >50 phylogenetically informative characters that were optimized across a robust phylogenomic scaffold derived from recent studies. Our results show high levels of homoplasy within the passerine carpometacarpus. We ran a phylogenetic analysis on Oligocene passerine carpometacarpi, placing several key carpometacarpus fossils within the crown Tyranni and crown Passeri subclades, facilitating additional calibration points in future divergence time and biogeographic analyses. This work provides a starting point for large-scale comparative analyses of the passerine skeleton, and reveals a substantial degree of previously unrecognized morphological variation among Passeriformes.

Multivariate dental topographic metrics demonstrate the dietary breadth and specialisms of conodonts

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Conodonts have one of the best fossil records of any organism and their evolutionary significance is well recognized. Despite their abundance in Palaeozoic and early Mesozoic marine ecosystems, their role in those communities is poorly constrained. Here we present the first quantitative large-scale analysis of conodont dietary range and specialisms. Using multivariate dental topographic metrics we analysed the 3D morphology of food processing P_1 elements in 48 species sampled from across the diversity of morphologically complex conodonts. This homology-free methodology allows direct statistical comparison with

analogous feeding tools of extant mammals and grasshoppers, providing robust inference of conodont diets. This reveals that conodonts have a dietary breadth comparable to both mammals and grasshoppers, ranging from taxa specialized in consumption of soft prey, through to species with tooth morphologies adapted for optimal processing of tougher cuticularized foodstuffs. Comparison of our results with qualitative morphological traits indicates that none accurately predicts diet, highlighting the need for quantitative analyses. Further application of this method to the abundant fossil record of conodonts, occupying a range of primary consumer niches through time, will facilitate investigation of ecosystem evolution and functioning across perturbation events.

Origins of the echinozoan body plan

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Echinozoans are the group of animals that includes echinoids (sea urchins) and holothurians (sea cucumbers). Echinozoans exhibit a range of body plans, from the soft-bodied vermiform holothurians, to the multi-plated globular echinoids. The clade is first recognized in the fossil record during the Ordovician period coinciding with the Great Ordovician Biodiversification Event and, despite the highly distinct body plans of modern representatives, the morphology of their earliest representatives is poorly characterized. We carried out micro-CT scanning of key early echinozoan fossils to clarify the morphological transitions that took place during the establishment of their unique body plans. We then constructed a character matrix encompassing numerous Palaeozoic echinozoans, along with outgroups, in order to understand the inter-relationships of echinozoan classes, and their phylogenetic relationships to other eleutherozoans. Finally, to better understand the genomic underpinning of echinozoan bodyplans and their association to events of genomic novelty, we carried out analyses of gene content from genomes and transcriptomes of extant echinozoans, and analysed the expression of key genes involved in the development of their modern body plans. This study sheds light on the origin of the echinozoan body plans from palaeontological, genomic and developmental perspectives.

The impact of mass extinctions on the morphological disparity of vertebrates

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Mass extinctions have had a major effect on the disparity of vertebrates throughout the Phanerozoic. Vertebrate clades that survive extinction events have a complex profile of disparity through time. Here we summarize the shape of total, pre-, and post-extinction disparity profiles using the centre of gravity (CG) metric. Clades surviving a mass extinction show a characteristic top-heavy pre-extinction and bottom-heavy post-extinction profile. This indicates that post-extinction (eco-) morphological recovery is distinct from early morphospace expansion of a clade. This pattern is similar for marine and non-marine, and amniote and non-amniote clades. In the majority of the clades that pass

through extinction events, disparity as the sum of variances and sum of ranges is reduced, whereas the pairwise distance remains largely unaffected. This indicates a selective removal of the marginal or morphologically similar taxa in morphospace. Hence, major mass extinctions are demonstrated to have been selective in the (eco-)morphological niches they affect in clades that survive these extinction events.

talks

Priapulid trace fossils from the late Ediacaran of Namibia

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Latest Ediacaran to earliest Cambrian trace fossils preserve evidence for the early evolution of metazoan complexity and behaviours, as well as the onset of critical geobiological changes that continued into the Palaeozoic (the 'agronomic revolution'). Here we present an unusual suite of trace fossils from the late Ediacaran Nasep-Huns transition (Nama Group, Namibia) potentially referable to *Archaeichnium haughtoni* Glaessner 1963, and which bear strong resemblance to priapulid burrows from the lower Cambrian Haidar Formation of Sweden. Of particular note are the two distinct surface patterns present on this material, exhibiting both distal longitudinal striations consistent with scalidophoran probiscides, and transversely-annulated proximal sections reminiscent of priapulid caudal anatomy. Furthermore, these traces appear to dip below the sediment surface and re-emerge consistent with the directions of motion, similar to modern priapulid burrows produced under experimental conditions. Attribution of these traces to priapulids would thus represent among the oldest records of crown-group Ecdysozoa, pushing their first appearance beneath the base of the Cambrian. Furthermore, this finding would illustrate that complex bioturbative – and perhaps predatory – animal behaviours evolved prior to the Ediacaran–Cambrian boundary, and may have played a prominent role in structuring benthic communities over the Ediacaran–Cambrian transition.

Cambrian stem group chaetognaths dominated the top of early pelagic food chains

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The Cambrian Explosion saw the advent of diverse animal life, the radiation of phyla. The convergent evolution of carnivory during the Cambrian may have been partly responsible for this event by shaping evolutionary arms races and adding higher levels to the food chain. Chaetognath grasping spines appear in the earliest Cambrian (Fortunian) as one of the first nektonic predators, which later became dominated by stem and crown euarthropods. Here we show a diversity of unique fossils from Sirius Passet, North

Greenland that can be attributed to the chaetognath stem group based on the presence of lateral fins, a distinct head and internal jaw structures along with a uniquely preserved ventral ganglion. The ventral ganglion is a unique feature of the chaetognaths and helps firmly establish the affinities of these taxa to this phylum along with *Amiskwia*. These new Sirius Passet taxa are markedly different from extant chaetognaths, however, as they possess a complex sensory apparatus (antennae and camera eyes) and, for one species, extremely large body size (up to 30 cm). As such, the relatively minute chaetognaths that today live as secondary consumers represent but a limited fraction of their past diversity as complex Cambrian predators higher in the food chain.

Abstracts of poster presentations

* indicates a poster eligible for the Council Poster Prize.
Underlined author denotes designated presenter.

posters

Palaeontology as a possible therapeutic tool: the fossils of the Hospital La Fe (Valencia, Spain)

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The palaeontological heritage contained in ornamental rocks constitutes a widely used resource in the dissemination of palaeontology. Thus, these resources can be useful in the hospital context, from both didactic and therapeutic perspectives, since a hospital stay carries negative repercussions on children's health conditions such as anxiety or stress. In this sense, this work aims to use the palaeontological and geological heritage of the Eocene marine rocks present in the walls of the Hospital Universitari i Politècnic La Fe, in Valencia, to develop a mobile application. This would serve as a recreational and therapeutic resource for hospitalized children with the main objective of improving their stay. For this, 15 fossil taxa present in these rocks have been selected, reconstructed in 3D and integrated into the application by means of augmented reality and virtual reality techniques. The project has been completed with a fossil route and a palaeontological collection to facilitate the location and interpretation of the fossil types found in the hospital. Given the current COVID-19 situation, the application has not been tested onsite, but we hope the new resources here presented will serve to improve the quality of life of patients during their hospital stays.

The ones that got away: X-ray imaging provides insight into the anatomy and evolution of exceptional early teleost fish fossils

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Teleost fishes comprise more than half of all living vertebrate species. However, despite their overwhelming modern success, their early evolution – particularly of taxa outside of the living radiation – is extremely poorly understood. Numerous well-preserved fossil assemblages are associated with the teleost stem, but these are typically studied in isolation, rarely integrated into larger phylogenies, and are incompletely known. Consequently, the early teleost radiation lacks a stable phylogenetic foundation, undermining attempts to understand macroevolutionary patterns. Pholidophorids are a typical example: these form a diverse, paraphyletic assemblage of herring-like actinopterygians spanning the late Triassic to the late Jurassic. Here, we present the first CT and synchrotron-based

descriptions of this elusive group, including previously unseen internal anatomy, such as the braincase and inner ear. Furthermore, we introduce the morphology of a potentially new taxon, reinvestigate existing taxa, and begin compiling a more comprehensive phylogeny, incorporating a broader range of stem teleosts than any previous study. With a robust phylogenetic hypothesis in place, we can at last pursue unanswered questions regarding speciation, diversification, and functional innovation on the teleost stem, and better understand the origins of this immensely successful group.

New plant mesofossil assemblages from the Lower Devonian (Lochkovian) of the Anglo-Welsh Basin, UK

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The near continuous fluvial sequence of the Anglo-Welsh Basin is rich with plant macrofossils, mesofossils and spores; however, they can be difficult to reconcile due to preservational biases. Sometimes plants are preserved as exceptional, albeit fragmentary, mesofossils which, whilst offering their own challenges, go some way towards harmonising the spore and macrofossil records. Two major charcoalified Konservat-Lagerstätte are already well documented from the Siluro-Devonian of the Anglo-Welsh Basin. Here we present two new early Lochkovian mesofossil sites in the Welsh Borderlands, the M50 and Ammons Hill. The former horizon consigns a kaleidoscope of plant mesofossils, including *in situ* spores, sterile axes and coprolites. The latter yields abundant nematophytes, including Pachytheca and fragmentary Prototaxites, but interestingly lacks plant remains. The preservation in these assemblages is not exceptional, although they have excellent potential for elucidating the parent plants of many contemporary dispersed spore species, unpicking phylogenetic affinities through morphological (*e.g.* axial anatomy) and TEM (spore wall architecture) analyses, and exploring the palaeoecologies of some of the plants. Finally, this assemblage lends support to the idea that wildfire-derived plant mesofossil assemblages occur reasonably often in this basin and hints that a wealth of information waits to be recovered.

Did increasing atmospheric oxygen challenge early invertebrates?

Etienne Baratchart and Emma U. Hammarlund

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During the history of life, a rise in atmospheric oxygen is assumed to favour biodiversification events, like the Cambrian Explosion and the Great Ordovician Biodiversification event. However, recent studies have suggested that invertebrates might have had difficulties coping with high oxygen levels at first, as they would have needed to maintain a certain level of hypoxia for cell stemness and tissue regeneration. We hypothesize that the massive oxygen rise happening from the Ordovician to the Devonian challenged invertebrates with limited capacities to shield their stem cells from oxic conditions. In order to test this hypothesis, we adopted a computational modelling approach in order to quantify extinction-speciation rates in several invertebrate phyla of interest. We showed that during the Devonian, mollusca, brachiopoda, arthropoda, corals and sponges suffered massive extinctions that temporally correlate with oxygen increase.

In order to investigate the reasons for these extinctions, we discuss the morphological differences between groups that adapted to these new conditions versus those that went extinct. In identifying eco-morphological features that changed within these phyla and how these changes relate to adaptations to oxygen level rising, we suggest how hypoxia-dependent tissues may have been involved in such extinctions.

The ecological importance of Ediacaran stems

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The Ediacaran-aged Avalonian Assemblage of Newfoundland, Canada (~565 million years old) hosts some of the oldest known multicellular life. Preserved as *in situ* census communities, spatial analyses can be utilized to better understand these unique assemblages. In this study, random labelling analyses (RLA) were used to investigate how morphological characteristics and taxonomic affinities impact the spatial distribution of taxa on the Lower Mistaken Point (LMP) surface. LMP is particularly well suited for these analyses because there are two abundant rangeomorph taxa – *Beothukis* and *Culmofrons* – which share many similar branching characters, but *Culmofrons* has a stem while *Beothukis* does not. Fossil specimens present on the surface were categorized according to their morphology (*i.e.* stem or not) and by their broad taxonomy (*i.e.* rangeomorph or not). In general, the spatial distribution of those morphologically- and taxonomically-defined was similar in all situations examined. However, small-scale differences are evident in the distribution of stemmed and non-stemmed rangeomorphs on the LMP surface; it is more likely that a stemmed rangeomorph individual will be located near to another stemmed individual rather than a non-stemmed individual. This suggests different ecological processes are operating on stemmed *vs* non-stemmed rangeomorphs, and demonstrates an underlying importance to broad morphological traits.

Two new artiopodans from the lower Cambrian Sirius Passet Lagerstätte (North Greenland) and their phylogenetic implications

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Artiopoda is a diverse and important group of Palaeozoic euarthropods yet to be fully understood. Here we describe two new non-trilobite artiopodans from the Lower Cambrian Sirius Passet Lagerstätte, North Greenland. New taxon 1 is a large species with an ovoid outline, a broad, domed cephalon, followed by fifteen trunk tergites and a small pygidium. New taxon 2 has an unusual obovate outline with narrow cephalon and eighteen preserved tergites. Preliminary cladistic analyses recover New taxon 1 as the sister-taxon to *Squamacula*, a genus found in the Chengjiang and Emu Bay Shale biotas which has previously been recovered as the sister to all other artiopodans. New taxon 1 is

shown to be distinct because the anterior trunk tergites bear articulating half-rings and the pleural tips and genae are rounded. Posteriorly, half-rings are absent, and the pleura form short spines. New taxon 2 is recovered as the sister-taxon to *Australimicola* from the Emu Bay Shale although their relation to the major artiopodan groups remains elusive. Strongly procurved anterior tergites which flank a small cephalon less than half the width of the trunk differentiates New taxon 2 from *Australimicola*. Preliminary results question support for Protosutura, while tentative cheloniellid links are found.

Relative head size evolution in Mesozoic archosauromorphs: morphological uniqueness of hypercarnivorous erythrosuchids

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Erythrosuchids were large, terrestrial and quadrupedal non-archosaurian archosauromorphs that likely occupied hypercarnivorous niches in the Early and early-Middle Triassic. They exhibit large, subrectangular heads that are superficially similar to the large heads of theropod dinosaurs (*e.g.* tyrannosaurs). Disproportionately large heads relative to body size in unrelated archosauromorphs have thus been deemed as convergent adaptations for hypercarnivory. However, there have been few investigations on whether erythrosuchid and theropod heads are indeed disproportionately large and on other possible drivers behind relative head size, such as phylogeny and locomotory mode. Here we investigate relative head sizes of Mesozoic archosauromorphs to examine possible intrinsic and extrinsic drivers and to reconstruct archosauromorph relative head size evolution to assess if hypercarnivorous clades are morphologically convergent. We find that phylogeny is a stronger driver behind relative head size than diet or locomotory mode. Moreover, head size scales with positive allometry in non-archosaurian archosauromorphs and scales isometrically in theropods. Ancestral skull:body-size ratio reconstructions reveal the ancestral erythrosuchid had a disproportionately large head and the ancestral theropod had a proportionately sized head. Relative head sizes of erythrosuchids and theropods are therefore not morphologically convergent, with the former clade exhibiting a bauplan unique to terrestrial Mesozoic carnivores.

Variable cynodont brain morphology: a case of natural or modeller bias?

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Mammalian brains are the complex culmination of biological experimentation over millions of years, with distinct pulses in brain development associated with improved olfaction (sense of smell), tactile sensitivity from body hair and neuromuscular coordination

of limbs. CT-scanned skulls of mammal ancestors, non-mammalian cynodonts, provides evidence of morphological changes, either from rarely preserved fossilized brains or more commonly, digital reconstructions of the endocranial cavity. Using the most prolifically discovered cynodont, *Thrinaxodon liorhinus*, from the Triassic of South Africa, digital endocasts reveal its brain morphology and comparison with later cynodonts helps to piece together the story of mammalian brain evolution towards modern counterparts, such as the South American opossum *Monodelphis domestica*. Furthermore, through reconstructing brains for a plethora of *Thrinaxodon* specimens, 3D models can highlight the morphological variation within a species, both during the life cycle (ontogeny) and between individuals of the same age (intraspecific). Whether this variation is natural or originates from bias in the reconstruction process was also tested to assess the reliability of 3D digital reconstruction techniques and therefore the inferences that can be made about cognitive and sensory capabilities, alongside behavioural patterns.

Dark data: bringing early Eocene fish of the Natural History Museum, London, into the light

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The early Cenozoic is a key window into the nature and operation of warm worlds, with community and ecosystem responses of bony fish and sharks holding insights for present and future marine impacts of global warming. Fossil fish have been collected from the UK's early Eocene (Ypresian, 56–47.8Ma) London Clay Formation for nearly two centuries, with much research confined to taxonomic monographs over 50 years old. Fossil records for bony fish and shark populations can be reconstructed from various body fossils: otoliths, teeth, scales, denticles and/or skeletal remains. Studied individually, each provides a proxy for taxonomic, ecological and functional diversity (with individual biases), but combined they are a powerful tool to assess ancient fish communities. However, a lack of body fossil record integration coupled with poor representation of fossil fish in online databases and published literature means the full potential of proxies is not harnessed. Therefore, early Palaeogene dark data from the Natural History Museum, London (NHMUK), is vital for bridging this collections *versus* published data gap. Here we present preliminary findings assessing species diversity and richness obtained from 8,224 otoliths housed within NHMUK collections compared to the combined fish/shark proxy datasets for the early Eocene of the UK.

Size bias in plant taphonomy: exploring the variability of fragment sizes in the fern Weichselia reticulata

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Weichselia reticulata is a relatively abundant fossil fern in fluvial, lacustrine and coastal Early Cretaceous plant associations. Its worldwide distribution makes it an ideal plant

to study taphonomic biases across different depositional environments and geographic locations. In this study, the preservation type and the size of 3,338 *Weichselia reticulata* fragments from 25 Early Cretaceous fossil sites are compared. The results show that charred remains are the most frequent preservation type, suggesting that *Weichselia reticulata* grew in fire-prone habitats. The size of charred remains is smaller and more homogeneous than the size of other preservation types, such as impressions. This is probably due to the fragmentation of the fern fronds while burning and to the initial abrasion and attrition produced by the transport of the fragile burnt remains. Additionally, the sizes of charred fragments vary depending on the depositional environment: smaller and more homogeneous sizes are observed in fluvial settings, whereas lacustrine remains are more variable in size. This suggests that biostratinomic processes are the main cause for size differences within charred remains. Moreover, the size differences observed between calm and energetic fluvial systems provide valuable insight into the distance the remains might have travelled from production to final deposition.

Uncovering the true diversity of the Wealden iguanodontians

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The iguanodontians were a diverse and widespread group of ornithopod dinosaurs including some very well known taxa, yet their taxonomic history is convoluted. Initial isolated finds assigned to *Iguanodon* by Gideon Mantell would not be considered valid for the erection of a new genus today. Further nineteenth century finds from the Wealden Group of the UK were often assigned to *Iguanodon* with little appraisal, resulting in it becoming something of a 'wastebasket taxon'. Valanginian deposits in the UK display a lack of iguanodontian diversity when compared to contemporaneous formations in North America. The historic lumping of specimens together into 'hypodigms' masks true diversity and causes some specimens to be overlooked. The relatively fragmentary nature and often poor preservation of these specimens further exacerbates confusion around their relationships. These issues have led to a full review of the Valanginian material at the Natural History Museum in London. Holotype material and the referred specimens of all genera have been critically reassessed for autapomorphies and shared features resulting in new definitions being produced. *Hypselospinus* has been suppressed, *Barilium* and *Kukufeldia* remain valid, *Sellacoxa* has been revived, and a single new taxon has been recognized, indicating the diversity of the Wealden is greater than previously thought.

Ontogeny of *Hypsilophodon foxii* (Dinosauria: Ornithischia) from the Hypsilophodon Bed (Wessex Formation, Isle of Wight, UK)

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Hypsilophodon foxii is a small bipedal ornithischian dinosaur from the Early Cretaceous of the Wessex Formation (Wealden Group, UK). The species is among one of the most well-studied and well-sampled British dinosaurs, with dozens of specimens being found from the 'Hypsilophodon Bed', a kilometre-long exposure along the southwest coast of the Isle of Wight. Here we examine the long bone histology of six *Hypsilophodon* individuals

from a range of size classes. We find that the *Hypsilophodon* specimens sectioned primarily exhibit fibrolamellar bone, indicating relatively fast growth rates. Slower growing parallel-fibred bone is also present in specimens of a range of sizes, although in smaller individuals this deposition is limited to the innermost cortex. All specimens lack an external fundamental system at the periphery, which suggests that even the largest individuals were still growing at death. However, the absence of this feature is also similar to that in other small ornithopods. The specimens investigated seem to include a mix of juvenile and sub-adult individuals.

The fossil record: friend or fraud? Placing realistic limits on the origins of clades

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It has often been suggested that the fossil record of a clade is not necessarily a reliable guide to its true antiquity. Here, however, we show that under all reasonable diversification scenarios (*i.e.* those with significant extinction rates) the fossil record must start soon after the origin of the clade, because of the so-called 'push of the past', unless the overall record is extremely sparse. Moreover, even if a clade were to diversify relatively slowly, examination of the nature of the early record shows that when more than a handful of old fossils are known, strong limits are placed on the probable time of its origin. For these reasons, scenarios when a fossil record commences abruptly with a reasonable number of fossils cannot be reconciled with a much deeper origin of the clade in question without invoking a similarly abrupt change in fossilization potential. Positing such a change would require evidence external to the fossil record itself. Molecular clocks have been invoked as one source of such evidence: we will discuss to what extent they can be considered to be truly independent of the fossil record.

Phylogenetic imputation helps bridge extinct and extant cetaceans in body size evolution analyses

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Cetaceans are a group with remarkable variation in body size, spanning five orders of magnitude. Thus, it poses as an interesting group to explore what mechanisms (biotic and abiotic) drove such variation. However, given that most of the diversity in this group is extinct, incorporating information on fossil species into macroevolutionary analyses becomes imperative. After compiling a large dataset of measurements of extant and extinct species of cetacea, we used phylogenetic imputation approaches to estimate total length for the typically fragmentary data available for almost all fossil species. This approach allowed us to not only estimate total length for specimens with any available measurements, but also to incorporate intraspecific variation for species with more than one measured specimen. We show that the calculated normalized root mean standardized error is comparable to ecological studies using only extant data, indicating that the broader temporal and taxonomic scales used here do not impact the quality of the estimates. Sensitivity analyses showed that the estimates of total length are closely correlated to the

empirical values after removing 10, 20 and 50% of all species. Our results show that phylogenetic imputation can help improve the coverage of morphological datasets and could be applied to other clades.

Tetrapod skeletal remains from the terminal Famennian of East Greenland

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The Hangenberg extinction at the Devonian–Carboniferous (D–C) boundary marks the beginning of a hiatus in tetrapod body fossils for around 20 million years into the Carboniferous, colloquially referred to as 'Romer's Gap'. Although it is now suspected that this gap is due to sampling bias, fossils from this period are scarce and so our understanding of the evolution of early tetrapods across the D–C boundary is poor. Here we present the preliminary description of a tetrapod lower jaw ramus, shoulder girdle and suspensorium from the Stensiö Bjerg Formation, a terminal Famennian deposit in East Greenland. These specimens have been scanned using propagation phase-contrast synchrotron microtomography (PPC-SRμCT) at ESRF in France, and have been segmented using the 3D modelling software Materialise Mimics 19.0. Analysis of the three elements suggests that they belong to a single individual and although there are broad similarities with elements from other Greenland tetrapods, some key distinctive features deem that the new elements represent a new taxon. This will be the fifth taxon among the Devonian tetrapods of Greenland, and also the most derived tetrapod of the group.

The origin of placental mammals according to the fossil record

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Recent molecular clock analyses have suggested that placental mammals originated in the mid to late Cretaceous, before the Cretaceous–Palaeogene (K–Pg) mass extinction. However, there are no unequivocal fossils of placental mammals from the Cretaceous to support this. Definitive fossils of placental mammals only appear after the K–Pg boundary. Here we present an updated version of the Bayesian Brownian Bridge model and apply it to placental mammals to estimate the age of origin. The model now estimates the extinction age of an extinct clade alongside its root, allowing the inclusion of more families and fossils into the analysis. The model works well with clades that have poor fossil records, such as the early placental mammals, and does not require a phylogeny, thereby mitigating the lingering uncertainty over the branching pattern at the root of the placental tree of life. Our results support a Cretaceous origin for placental mammals, with several families suggested to have originated in the Cretaceous despite no Cretaceous fossils. The clade then experienced a rapid radiation in the 20 million years following the K–Pg mass extinction. The Bayesian Brownian Bridge model can help reconcile palaeontological estimates with molecular estimates when investigating the origin of clades.

Preliminary phylogenetic tree of Cricetodontini (Rodentia, Mammalia)

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The extinct tribe Cricetodontini includes Eurasian and North African rodents from the Oligocene to the Pleistocene. This group comprises four cricetid genera extensively used in biostratigraphic studies of the Miocene: *Cricetodon*, *Hispanomys*, *Byzantinia* and *Ruscinomys*. Several proposals on the phylogenetical relationships between their species are found, but the evaluation of these is complicated by difficulties in taxonomical assignment of some of them. Here we present a preliminary phylogenetic tree where we have included the latest records of these genera. In this tree, we have included 59 species and 103 dental characters. These data were collected from fossils and photographs of the type series and literature. The tree was performed using TNT and R (ape and paleotree packages). Consensus tree shows two main clades being *C. kasapligili* and *C. versteegi* their basal taxa. The first clade is composed of eastern species of *Cricetodon* and the second one includes species of the other studied genera. Inside clade two, *Cricetodon* species are disposed paraphyletically, but some interesting groups can be seen (Anatolian *Cricetodon* are grouped together, as the European ones). Basal species of *Hispanomys* form a clade and *Hispanomys-Byzantinia* clade include the remaining species of these two genera together with *Ruscinomys*.

Morphological evolution of the cave bear (*Ursus spelaeus*) lower molars: coordinated size and shape changes through the Scladina Cave chronostratigraphy

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Out of all extinct megafaunal mammals of the Quaternary, the cave bear *Ursus spelaeus* is one of the most represented in the fossil record. This species has been found to exhibit morphological adaptations to a variety of environments over both spatial and temporal scales. Here we employ geometric morphometrics and phenotypic trajectory analysis to explore temporal morphological variation across the entire lower molar tooth row of *Ursus spelaeus* from the infilling of Scladina Cave, Belgium. We found that molar tooth size increases from Marine Isotope Stage (MIS) 5 – MIS 3, with cusp position varying temporally in relation to a larger talonid grinding platform in later time periods. Phenotypic trajectory analyses further show parallel evolutionary trajectories in the shape changes of the first and second molar, but not in the third molar. These shape changes are related to a relative enlargement of the molar grinding platform, with the divergent pattern of m3 suggesting lower constraints on this tooth leading to greater responses to environmental changes. The need to cope with harder fibrous plant material present in the palaeoenvironment potentially constrained morphological evolution of the cave bear until its disappearance throughout Europe.

Not a jaguar after all: affinities and morphology of *Panthera gombaszoegensis*

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Panthera gombaszoegensis is a fossil pantherine from the Pleistocene of Eurasia. Due to dental similarities with the jaguar (*Panthera onca*), it was considered to be the closest ancestor to the modern jaguar and was even sometimes considered as a subspecies of jaguar. Our knowledge of this taxa is, however, limited by the scarcity of cranial remains, which has made it difficult to properly assess the phylogenetic affinities and possible ecological role of this taxon. We describe a new cranium from Belgium and computed morphometric analyses on the cranium and dentition of extinct and extant pantherines. While the lower dentition of *P. gombaszoegensis* is indeed similar to that of *P. onca*, those similarities are not recovered on other parts of the skull. Some cranial traits of *P. gombaszoegensis* resemble those of other pantherines, especially larger species such as the tiger *P. tigris*. Some similarities with generalist taxa such as *P. tigris*, *P. leo* or *P. pardus* in the skull of *P. gombaszoegensis* suggest a generalist diet, adapted to a wide prey spectrum. The first ever phylogenetic assessment of the phylogenetic position *P. gombaszoegensis* places this taxon closer to *P. tigris* than to *P. onca*, which considerably simplifies the biogeographic history of pantherines.

Evaluating approaches to discretizing continuous morphological phylogenetic character data

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Morphological phylogenetics uses two types of phenotypic character – discrete and continuous. Discrete characters can be qualitative or quantitative, and are prevalent in the literature. Continuous characters are routinely discretized, but the effects of this process on phylogenetic estimation are little explored. Here we evaluate different approaches to the discretization of continuous characters using data from four empirical studies. We apply a systematic gap coding approach to convert continuous characters to quantitative discrete ones. The latter range from two to nine character states, which we analyse to assess their homoplasy relative to an independent molecular topology. Discretizing continuous characters increases levels of homoplasy. Discretized characters with fewer states (<6) show more variance in homoplasy than those with many states (>6). In a separate analysis, comparing quantitative continuous characters with qualitative discrete ones demonstrates that the latter are less homoplastic, but more variable. In conclusion, we show that discretized continuous characters exhibit higher homoplasy than raw continuous characters, which in turn exhibit higher homoplasy than qualitative discrete characters. We recommend phylogeneticists incorporate qualitative discrete and raw continuous characters in their analyses. When discretization of continuous data is required, aim for at least five levels of objectively defined discrete character states.

Locomotion in legged whales: muscle moment arms in transitional archaeocetes

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Among tetrapods, secondary specialization for aquatic life is a common evolutionary occurrence. The evolution of whales from terrestrial ancestors is an iconic instance of this evolutionary transition. Aquatic specialization in stem cetaceans (Archaeoceti) is relatively well preserved, providing a fascinating opportunity to explore the dynamics of the evolution of locomotion across a land–water transition. We produced 3D models of the hindlimbs of five archaeocete species spanning the transition, as well as two extant artiodactyls. By reconstructing the likely muscle placements for each species, we were able to compare the moment arms of hindlimb muscles around the pelvis. Muscle moment arms describe the distance from the line of action of a force to the joint axis and are a determining factor in the degree of torque produced about a joint. By modelling the moment arms of the hindlimb muscles through the hip joint's range of motion, we can draw cautious functional inferences. Comparing moment arms between species showed changes across the land-water transition comparable with previously-reported changes in muscle mass in extant semi-aquatic mustelids, linked with increasing femoral abduction to aid aquatic propulsion. This suggests that certain functional patterns may be common in secondarily aquatic mammals.

3D reconstruction reveals that the extinct giant shark *Otodus megalodon* was a highly migratory super predator

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Based on an exceptionally preserved fossil specimen, we create the first 3D model of the extinct shark *Otodus megalodon*, revealing unprecedented swimming and prey intake abilities. We first used fossils to reconstruct the axial skeleton and added tissue based on a full-body scan of the great white shark (*Carcharodon carcharias*), a modern analogue. Our model allowed us to estimate length, mass, cruising speed, stomach volume, gape size and daily energy requirements, which were used in probabilistic models of prey encounter rates to infer feeding ecology. Our results indicate that *O. megalodon* would have been able to attain, on average, fast cruising speeds, suggesting it was highly migratory. Although small cetaceans might have been captured daily and provided calories beyond its energetic demands, prey the size of modern apex predators (*e.g.* the killer whale) could have been devoured entirely and found frequently enough to provide excess energy to sustain prolonged migrations without further feeding. We propose that adult *O. megalodon* may have

preferred feeding upon large prey to minimize competition with smaller, more agile sharks, and fuel transoceanic migrations. As such, the extinction of this highly mobile, cosmopolitan super-predator likely had large impacts on global nutrient transfer and trophic food webs.

Salt gland, paranasal sinus system and upper respiratory tract evolution in thalattosuchian crocodylomorphs

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Thalattosuchians were a predominately marine clade of Mesozoic crocodylomorphs, which include the semi-aquatic teleosauroids and obligately pelagic metriorhynchids. While recent advances in CT scanning have provided new details of thalattosuchian endocranial anatomy, their rostral craniofacial anatomy has often been neglected. Herein we investigate the evolution of the salt glands, paranasal sinus system and the nasopharyngeal ducts in Thalattosuchia by reconstructing the internal anatomy in CT scans of ten thalattosuchian skulls from across the clade. We found that all thalattosuchians exhibit dorsal or dorsolateral nasal cavity expansions that we identify as salt gland osteological correlates. The largest expansions occur in the basal metriorhynchoid *Eoneustes gaudryi* and metriorhynchids. Thalattosuchians had exceptionally reduced paranasal sinus systems, solely comprising the antorbital sinus. In basal taxa the antorbital sinus is partially located medial to an external antorbital fenestra, broadly communicating with the dorsal alveolar canal. In metriorhynchids, the antorbital sinus is more extensive and possibly had an active function associated with a hypothesized accessory suborbital diverticulum. The nasopharyngeal ducts in metriorhynchids are dorsoventrally enlarged and possibly enabled stronger ventilation. The sequence of marine craniofacial adaptations shows a stepwise pattern predating the major skeletal adaptations, suggesting they occurred early in the thalattosuchian marine transition.

Growth and development of the earliest vertebrate skeletons

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Paraconodonts are among the earliest vertebrates in the Cambrian fossil record and are known entirely through their disarticulated, tooth-like fossils. The interpretation of paraconodont elements has relied on analysis of growth pattern, but whereas coniform elements grew through basal internal accretion of lamellae, the more structurally complex westergaardodinids are more problematic. Without understanding the growth of these

elements, their anatomical homology, function and phylogenetic position remain uncertain. We examined *Westergaardodina* elements preserved as small carbonaceous fossils from the Deadwood Formation, Saskatchewan, Canada using transmitted light to reveal exceptional preservation of their internal structures. We imaged further specimens from the Alum Shale Formation, Sweden, using oil immersion and tomographic microscopy, which allowed for segmentation of the internal element structure in three dimensions for the first time. Our results have revealed a structural homology between coniform elements and *Westergaardodina*, which both develop from an initial small, conical 'protoelement'. Unlike coniform elements, *Westergaardodina* employs a greater lateral extension of lamellae to form additional projections. However, some forms of *Westergaardodina* appear divergent in their internal structure, and incorporate two additional u-shaped denticles during morphogenesis, resulting in apparent truncations within the structure. This demonstrates a high disparity in vertebrate skeletal development much earlier than previously thought.

Hierarchical spatial data subdivision methods family – «HespDiv» – is coming to garnish the toolkit of numerical palaeontologists

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We propose a new hierarchical spatial data subdivision (HespDiv) methods family, under development in R language, that is designed to investigate the spatial structure of palaeontological records. HespDiv is a machine learning data exploration methods family which, similar to the decision tree method (such as CART), recursively performs binary partitions of data in order to produce their hierarchical classification. The main distinctions are that in HespDiv partitions are made along spatial gradients and partition criteria are manually defined by a researcher. HespDiv should be particularly useful when studying spatial structure of an emergent aspect of palaeontological data (*e.g.* spatial models of macroecology, macroevolution, species distribution, *etc.*). The preliminary tests of the prototype HespDiv version with simulated and real palaeontological data demonstrate its promising capabilities to delineate boundaries of biotic palaeoprovinces based on spatial changes in Pielou entropy index values of regional fossil taxa assemblages.

Phanerozoic parasitism and marine metazoan diversity: dilution versus amplification

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Growing evidence suggests that biodiversity mediates parasite prevalence. We have compiled the first global database on occurrences and prevalence of marine parasitism throughout the Phanerozoic and assess the relationship with biodiversity to test if there is support for amplification or dilution of parasitism at the macroevolutionary scale. Median prevalence values by era are 5% for the Palaeozoic, 4% for the Mesozoic, and a significant increase to

10% for the Cenozoic. We calculated period-level shareholder quorum sub-sampled (SQS) estimates of mean sampled diversity, three-timer (3T) origination rates, and 3T extinction rates for the most abundant host clades in the Paleobiology Database to compare to both occurrences of parasitism and the more informative parasite prevalence values. Generalized linear models (GLMs) of parasite occurrences and SQS diversity measures support both the amplification (all taxa pooled, crinoids and blastoids, and molluscs) and dilution hypotheses (arthropods, cnidarians, and bivalves). GLMs of prevalence and SQS diversity measures support the amplification hypothesis (all taxa pooled and molluscs). Though likely scale-dependent, parasitism has increased through the Phanerozoic and clear patterns primarily support the amplification of parasitism with biodiversity in the history of life.

New insight of the Early Cretaceous Pinaceae diversity from Belgium

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The Belgian Wealden facies deposits (Barremian–Albian, 125.0–100.5 Ma) have delivered hundreds of exceptionally well-preserved, yet isolated, pinaceous ovulate cones. A total of 10 species has been described in Belgium, representing about 33% of the known fossil cone species of this period worldwide. Research in the collections built up at the end of the nineteenth century by C. Bommer has led to the rediscovery of unstudied material. This has been complemented by recent excavations in the Wealden facies, which provided new coniferous fossils. In a previous study, we showed that species delimitation is inconsistent, with some species actually incorporating clearly distinct populations that should be separated taxonomically. The use of morphometry as well as micro-CT imaging of nineteenth century collections led to the description of new morphotypes and the highlighting of new anatomical features such as scale dehiscence, cone shape and scale form. In the long term, the objective is to propose new characters to be included in the phylogeny of fossil Pinaceae. By using morphological descriptions and quantitative protocols, we dust off the diversity and ecological importance of ovulate cone species described in the twentieth century and shed a new light on the shape of their Cretaceous radiation.

Neoichnology of amphibious arthropods: implications for the colonisation of land

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The colonization of land was a major evolutionary event and trace fossils produced by arthropods represent some of the earliest evidence for this event. Neoichnology, the study of the traces of extant organisms, provides a vital tool for better understanding trace fossils. We conducted neoichnological experiments to test hypotheses regarding producers and palaeoenvironmental conditions of trace fossils recording the colonization of land. Our experiments comprised two protocols: exposed and submerged silty mud. We utilized five arthropods: from fully aquatic ostracods to amphibious horseshoe crabs, shore crabs and scarlet hermit crabs, and largely terrestrial sea slaters. Our results show how substrate, producer, behaviour and their interactions affect arthropod trace morphology. The different arthropods were observed performing locomotory, resting and feeding behaviours,

which all resulted in different traces, and this was influenced by the substrate conditions and their preference for living in and out of water. In general, trace depth increased with arthropod mass and on exposed compared to submerged substrates. In the majority of cases, comparisons with selected trace fossils support previous hypotheses as to their producers. This research will help to more accurately define the colonization of land.

New material of the pinnipedimorph *Pacificotaria hadromma*, shedding new light on an enigmatic key taxon in pinniped evolutionary history

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The pinnipedimorph fauna of the upper Burdigalian (lower Miocene) Astoria Formation of Oregon, USA is remarkably diverse, having yielded (type) specimens of early non-pinniped pinnipedimorphs, desmatophocids and early odobenids. One non-pinniped pinnipedimorph, *Pacificotaria hadromma*, is little understood, known from one cranium from the Iron Mountain Bed (IMB) of the Astoria Formation. In the present study, a new partial cranium, mandibles and a few postcranial bones are described, also from the IMB, and identified as *P. hadromma*. The lack of fusion of the epiphyses of the postcranial bones suggests that the specimen represents a subadult or juvenile individual. The newly described mandible shows that *P. hadromma* had an exceptionally developed gonion, suggesting a strongly developed m. pterygoideus medialis and, hence, a powerful bite. In conjunction, the unique dentition (bulbous, conical upper postcanines versus gracile, multicuspate lower postcanines) suggests a unique adaptation to feeding and niche partitioning which allowed coexistence with other pinnipedimorphs along the Miocene coast of the northwest Pacific. The new specimen allows more robust phylogenetic analyses of the species, returning *P. hadromma* as a taxon that is closely related to Pinnarctidion and one of the latest branching stem-pinnipedimorphs.

Does evolutionary allometry predict static allometry in fossil bryozoan species?

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Allometry, the study of biological scaling, is vital to understanding the mechanisms underlying phenotypic evolution. Empirical and theoretical studies on allometry over evolutionary timescales based on fossils are limited for solitary organisms and non-existent for colonial organisms. Here we use six Pleistocene-to-Recent New Zealand species of the bryozoan *Microporella* to investigate size covariation between feeding modules and (i) orifices (openings for the feeding organ), (ii) ovicells (brooding structures), and (iii) avicularia (defensive polymorphs) within populations, species and across species. We hypothesize that traits bearing directly on reproduction (ovicells) and developmentally more tied to the module bearing it (orifices) are more evolutionarily constrained than traits that are developmentally more independent (avicularia). Preliminary results show that, with a few exceptions, the different traits are similarly constrained with the slopes of static allometry in the targeted species predicted by the evolutionary allometry estimated from >80 *Microporella* species worldwide. We also observe variation in slopes/intercept of static allometries in the same species across time that cannot be attributed to palaeoclimate, in contrast with previous work on another species from the same assemblage. Our study

demonstrates the importance of understanding population level and temporal variation in grasping the potential drivers of long-term evolutionary change.

'Comatulid crinoids' on the morning news: preliminary observations and implications of a new Bathonian (Middle Jurassic) Lagerstätte in Wiltshire, UK

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A new UK Bathonian (Middle Jurassic) Lagerstätte has revealed one of the most important Jurassic echinoderm localities in the world. Excavation of the site has produced large numbers (thousands) of exceptionally preserved articulated echinoderms including at least 18 species, belonging to all five extant echinoderm classes. Other significant fossils include plants and Radiolaria, the latter being rarely seen in UK onshore Jurassic rocks. The fossils are preserved in indurated packstone horizons (at least two) within a unit of interbedded buff siltstones and dark grey unlithified mudstones that vary rapidly in thickness and lateral extent. The well-preserved echinoderm fossils are preserved in various orientations, indicating brief transportation prior to rapid burial (obrution). Other shelly faunas are more disarticulated and suggest greater residency within the environment and greater transportation prior to burial. The echinoderm fossils are dominated by the true comatulid crinoid *Palaeocomaster* sp., represented by over 3,000 individuals, and the stalked crinoid *Isocrinus* sp. This is the earliest incidence of true comatulid crinoids dominating a marine environment. It is significant as "comatulid meadows", important areas of biomass and diversity in several modern soft sea floor ecosystems (such as at continental shelf margins), are unknown in the fossil record before the Cretaceous.

Armoured penis worms of North Greenland: a new palaeoscolecid (Ecdysozoa) from the Sirius Passet Lagerstätte, Cambrian Stage 3

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Palaeoscolecids are fossil ecdysozoan worms of uncertain affinity, known from the Cambrian to Silurian. While superficially priapulid-like, with an annulated trunk and spine-bearing

introvert, their armour of phosphatic sclerites is unique among ecdysozoan worms. Evidence from ecdysozoan worms and fossil panarthropods suggests that the ancestor of Ecdysozoa was a priapulid-like worm. In this context, palaeoscolecids have been suggested to represent the vermiform ancestor of panarthropods, but despite recent discoveries of panarthropod-like morphology in the palaeoscolecid introvert, sclerites and trunk, phylogenetic analyses consistently resolve them as stem-group priapulids. Improved understanding of palaeoscolecids is therefore important for understanding the early evolution of Ecdysozoa as a whole. Here we describe a new palaeoscolecid from the Sirius Passet Lagerstätte, North Greenland, Cambrian Stage 3 (*c.* 518 Ma). It differs significantly from the previously described palaeoscolecids of Sirius Passet in its high length-to-width ratio, more lightly armed introvert and double paired posterior hooks, more closely resembling the palaeoscolecids known from the contemporaneous Chengjiang Biota. We present evidence for the widespread preservation of the ventral nerve cord among Sirius Passet palaeoscolecids alongside new details of previously described taxa and discuss these results in the context of their importance for understanding the deep evolutionary history of Ecdysozoa.

A multidisciplinary approach to untangle life history and growth mode in brachiopods: the case of *Calloria inconspicua* (Sowerby, 1846)

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We integrated different methodologies to achieve a sclerochronological study of the brachiopod species *C. inconspicua* from a coeval population collected in Otago Harbour (New Zealand). In our analysis, we reconstruct the life history and ontogenetic age based merely on morphological features of the valves. By examining the shell shape and the external morphologies of growth lines, we highlight quasi-regular cycles of accretion in most individuals, despite their different significant sizes and, thus, disparate ontogenetic ages. Furthermore, we measured the stable isotope ($\delta^{18}O$ and $\delta^{13}C$) on the main direction of accretion to verify if a seasonal signal is recorded in the fibrous layer and the extent of its correlation to morphological markers of age. Comparing the amplitude of $\delta^{18}O$ measured in the shells and the seasonal seawater temperature recorded at the study locality provides clues about the robustness and weaknesses to account for in this type of survey. The identification of common growth patterns in a modern population of *C. inconspicua* remarkably places the brachiopods among the seasonal archives of past climate.

Abandoning ship: Court Jester and Red Queen sex in digital organisms

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What drives the maintenance of sexual reproduction in eukaryotes is a key question in evolutionary biology. Modelling and empirical studies investigating this seemingly disadvantageous reproductive method are widespread. To date there are no definitive answers. Sex originated prior to the last eukaryote common ancestor (LECA), and the timescale since this innovation, coupled with the diversity of sexual traits and ecologies in living organisms, makes it hard to identify mechanisms underlying its origin then maintenance. Here we use the eco-evolutionary model REvoSim to assess how Red Queen, Court Jester and pluralistic conditions impact the prevalence of sex over macroevolutionary

timescales in a single digital ecosystem. Our results indicate that antagonistic relationships (pathogens/predators), high rates of abiotic change and limited environmental resources all elicit higher proclivity of sex in evolutionary agents sharing traits of LECA. Increased sex also helps organisms evade faster-evolving antagonists. Pluralistic investigations show increased sexual breeding in response to antagonists and dynamic abiotic environments. We argue that abandon-ship mechanisms allow sexual lifecycles to break down maladapted epistatic relationships in stressful conditions. Our findings support multiple mechanisms driving sex within early eukaryotes. We highlight the need to investigate abandon-ship dynamics further in living systems experiencing stress from multiple ecological sources.

Cope-Depéret rule in perissodactyls: passive artefact or active trend?

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The Cope-Depéret rule is an iconic 'rule' of macroevolution, whereby lineages tend to become larger over evolutionary time. Since its proposal in the 1880s, many attempts have been made to test the validity of this rule, but often without the appropriate phylogenetic comparative basis. Further, possible drivers for the rule are debated, whether there might be active directional selection for fitness benefits, or passive diffusion from a boundary condition giving an artificial appearance of a driven trend. Here we explore the Cope-Deperét rule in the classic test case, the perissodactyls. We show that the rule holds true, with body mass increase being a driven trend, as shown by the skewness test, ancestor-descendant test and minimum test. The Cope-Deperét rule is also present at different taxonomic levels within Perissodactyla (order and family levels), further confirming it is a driven trend across the clade. In horses, several evolutionary rate and regime shifts coincided with ecological and environmental changes, particularly the dietary transition from browsing to grazing, and the climatic cooling trend of the Neogene.

Realizing the potential of treeshrews in palaeodietary analysis using dental microwear texture analysis

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Dietary reconstructions are fundamental to understanding organisms' ecological interactions, responses to environmental change and their roles in ecosystems. Modern treeshrews provide a powerful model for understanding basal primate and therian mammal dietary ecology due to their highly conserved 'primitive' molar morphology and anatomical similarity to early mammals. Unfortunately, dietary data, in the form of stomach and scat analyses, is available for only a handful of treeshrew species, and is insufficient to realize their potential as palaeodietary analogues. To address this issue we have conducted the first dental microwear texture analysis (DMTA) of treeshrew diets. The limited published dietary data, combined with recent analysis of dental topography, suggests that tree shrew species differ in the proportions of insects, fruit and leaves making up their diet. Microwear texture tracks these differences and allows us to make robust dietary inferences in species for which we lack dietary data. These results, and the multivariate microwear texture-diet framework they provide, indicate that DMTA is sensitive enough to record subtle dietary differences that allow detailed analysis of dietary transitions and niche partitioning in extinct 'insectivorous' mammals.

Muscular moments in a quadrupedally launching ornithocheiraean pterosaur model

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As the first and largest known flying vertebrates, pterosaurs are important for understanding the limits of flight. Launch is the locomotory phase which most constrains the ability to fly. This is especially true of larger animals as the launch impulse their muscles can generate scales at a lower rate than mass increases. One hypothesis for how pterosaurs circumvented this problem is the use of a quadrupedal launch. To test this hypothesis, we have created a musculoskeletal model of a representative ornithocheiraean pterosaur including 27 pectoral and 12 pelvic muscles. Using launch poses proposed in the literature we created a kinematic profile of the quadrupedal launch. Using the maximum isometric force of each muscle from birds and crocodiles we determined the muscle moments throughout the launch for averaged, avian and crocodilian scaled moments. We found that much of the moment generating capacity throughout the launch occurs at the glenoid; the only exception being the flexors of the elbow in the crocodilian model which account for 40% of all flexion. Humeral adductors had the greatest leverage on the quadrupedal launch with the m. pectoralis accounting for a minimum of 30% of the total moment generating capacity in the glenoid.

posters

Testing hypotheses of heterostracan feeding using computational fluid dynamics(CFD)

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The ecological context of early vertebrate evolution has been characterized as a shift from passive to more active feeding modes. This evolutionary scenario has been based largely on poorly constrained inferences of the feeding ecology of extinct stem-gnathostomes, among which heterostracans are the earliest. Heterostracans possessed a dentition of rod-like oral plates with rows of forward-facing denticles, previously interpreted as an adaption for suspension feeding. We test this hypothesis by applying computational fluid dynamics (CFD). We simulate water flow around 2D models consisting of rows of denticles both forward-facing and reversed, to assess whether these orientations are hydrodynamically linked to suspension feeding through the creation of flow disturbances and recirculation patterns. All tested models, independent of denticle orientation, show similar flow, velocity and vorticity patterns. Recirculation patterns, highest velocity and vorticity develop directly on top of the denticles and in spaces between the denticles, whereas the flow above the denticles remains undisturbed. Therefore, we reject the hypothesis that the forward-facing denticle orientation is an adaption for flow disturbance linked to suspension feeding. The denticles only occur on the lateral sides of the distal tip of the oral plates and might have instead prevented material from lodging between the plates.

Ancient life in moving fluids: using computer flow simulations to reconstruct the palaeoecology of the first animal communities

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The Ediacaran biota (~571–539 Ma) represents the first radiation of complex macroscopic life on Earth. This period ushered in an extraordinary diversity of benthic forms, including the first animals. The Ediacaran–Cambrian transition, the biotic turnover that corresponds with the emergence of animal-dominated ecosystems, remains poorly understood in part due to uncertainties surrounding the palaeoecology of Ediacaran organisms, most of which lack modern analogues. In recent years, computational fluid dynamics (CFD) has emerged as a powerful tool to aid functional inference in these enigmatic organisms, enabling rigorous hypothesis-testing relating to feeding in individual Ediacaran taxa. Here we applied CFD for the first time to Ediacaran multi-organismal arrays. We used R to simulate virtual communities based on *in situ* fossil beds from the Avalon assemblage (~571–560 Ma), recreating Earth's oldest Ediacaran communities using 3D computer modelling software. We then carried out CFD simulations for different virtual communities from this assemblage. Results from these analyses allow us to elucidate the impact of community structure and composition on vertical mixing. Ultimately, assessing how these patterns changed through time will shed light on the evolution of ecosystem engineering during the Ediacaran and its role in the emergence of the modern marine biosphere.

Sub-micrometre 2D–3D investigation of the hydrothermal mineralization of Earth's oldest stromatolites (~3.5 Ga)

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Palaeoarchaean stromatolites are among the oldest compelling evidence for life. Here we present advanced 2D–3D reconstructions of the morphology, mineralogy, trace element geochemistry and taphonomy of permineralized stromatolites from the lowermost ~3.5 Ga North Pole Chert, Dresser Formation, Pilbara, Western Australia. These stromatolites comprise syndepositional silica and baryte, and recent iron oxides. Rare earth element compositions suggest marine deposition; this contrasts with younger Dresser stromatolites, which are interpreted to have developed around hot springs. The intimate association of stromatolites with chert–baryte veins and strong Eu anomalies in chert denote pervasive, syndepositional hydrothermal activity, promoting exceptionally high-fidelity microstructural preservation. Although no primary kerogen is preserved, numerous 2D–3D

morphological characteristics are consistent with a biogenic origin. Phototrophic growth is evidenced by non-isopachous laminations with crestal thickening, fine-scale undulatory laminations, ragged and laminoid fenestrae, and sub-vertical fabric elements resembling microbial palisade structure. 3D reconstructions using laboratory and synchrotron approaches highlight the utility of tomography for non-destructive, high-resolution analyses of fossil microbialites. The correlated micro-analytical strategy used cements the Dresser stromatolites as the oldest convincing microbial fossils and could be applied to samples returned from Mars, where extracting large amounts of geochemical information from small amounts of potentially fossiliferous materials will be essential.

A second 'Great American Biotic Interchange' signals the Anthropocene impact of humans

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Analysis of historical records of neobiotic species introduced to the ten ecoregions of the conterminous USA since 1700 CE has identified three theoretical biostratigraphic intervals in 1948-52, 1964-67 and 1979-82 in which seven or more ecoregions might be correlated using first occurrences of neobiota with a known biostratigraphic record. Thirty-four introduced aquatic taxa are identified as having potential to produce high-resolution biostratigraphies that would identify anthropogenically-modified sedimentary deposits and help characterize the Anthropocene in North America. Two accelerations of introductions occur, centred on 1873 and 1949, coinciding with shifts in anthropogenic land-use. Post-WWII economic development in the Neotropics, Indo-Malay and Afrotropic biogeographic realms resulted in increased translocation of neobiota from these regions to North America. Neobiota from the Neotropic realm underwent the greatest relative increase of North American introduced taxa from 8.7% pre-1949 to 17.5% at present. Thus, a second Great American Biotic Interchange may be recognizable, the biostratigraphic record of which may be predicted from the historical records of species translocations and tested through field-based studies. Demonstration of the real-world stratigraphic signature of neobiotic introductions predicted from historical records allows interconnected webs of correlation to be defined that facilitate inter-regional and inter-continental correlation of widely distributed recent sedimentary deposits.

Tabelliscolex (Cricocosmiidae: Palaeoscolecidomorpha) from the early Cambrian Chengjiang biota, and the evolution of seriation in Ecdysozoa

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Cricocosmiidae is a clade of palaeoscolecid-like worms from the Chengjiang biota, China (Cambrian Stage 3). In contrast to palaeoscolecids *sensu stricto*, which exhibit tessellating micro-plate trunk ornamentation, cricocosmiids possess larger, serially repeated sets of

trunk sclerites bearing resemblance to lobopodian trunk sclerites (*e.g. Microdictyon* spp.). Cricocosmiidae were therefore proposed as stem-group Panarthropoda in some studies but are recovered as stem-group Priapulida in most phylogenetic analyses. The affinity of cricoscosmiids within Ecdysozoa is therefore of much interest, as is testing the homology of these seriated structures. We report four new specimens of the rare cricocosmiid *Tabelliscolex hexagonus*, yielding new details of the ventral trunk projections, sclerites and proboscis. New data confirm *T. hexagonus* possessed paired ventral trunk projections in a consistent seriated pattern, which is also reported from new material of *Cricocosmia jinningensis* (Cricocosmiidae) and *Mafangscolex yunnanensis* (Palaeoscolecida *sensu stricto*). Even when the seriated sclerites and ventral projections of cricocosmiids are coded as homologous with the seriated trunk sclerites and paired appendages, respectively, of lobopodian panarthropods, our tree searches indicate they are convergent. Cricocosmiidae is nested within a monophyletic "Palaeoscolecida *sensu lato*" clade (Palaeoscolecidomorpha nov.) in stem-group Priapulida. Our study indicates that morphological seriation has independent origins in Scalidophora and Panarthropoda.

The role of habitat density, migration and developmental mode in avian skull evolution

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One of the most famous examples of adaptive radiation is that of the Galapagos finches' skull morphology correlating with feeding ecology. Yet increasingly studies are questioning the strength of this correlation between feeding ecology and morphology in relation to the neornithine radiation. We aim to test the influence of habitat density, migration and developmental mode in shaping avian skull evolution. We utilized a sample of high-density 3D geometric morphometric data for 354 extant species for flexible phylogenetic regressions in the mvMORPH R package and we estimated evolutionary rates. Our results showed that there is a significant relationship between shape and both habitat density and migration categories ($P<0.001$), but not between shape and developmental mode ($P=0.096$). Birds in open habitats evolve ~3 times more slowly than those in dense or semi-open habitats. Precocial birds evolve ~3 times faster than semi-precocial birds and ~4 times faster than altricial birds. Migratory birds evolve faster (1.64×10^{-7}) than sedentary or partially migratory birds (7.07×10^{-8} and 1.06×10^{-7} respectively). These patterns demonstrate that habitat density and migration help shape the tempo and mode of avian phenotypic evolution, and that skull evolution in birds is not simply a reflection of feeding ecology.

Biostratigraphy and sequence stratigraphy of the Jurassic–Cretaceous transition in the Canadian High Arctic, inferred from palynomorphs and macrofauna

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The Rollrock Section in Arctic Canada offers one of the best-exposed, most continuous high-latitude sedimentary and palaeontological archives of the Jurassic–Cretaceous transition. Nine out of 15 macrofossil horizons correlate to Pan-Boreal zonal schemes for

the Tithonian–Berriasian interval. Dinoflagellate cyst assemblages from 200 samples, taken at intervals of 1.5 m or greater over a 560 m succession, conform to seven Oxfordian to early Valanginian biozones. Statistical analysis of the same assemblages reveals long-term trends as well as short-term, cyclic shifts in community structure, driven by dinoflagellate palaeoecology. In particular, abundances of proximochorate and chorate dinocysts are utilized as proxies. While the former prefer proximal, high-energy, nutrient-rich settings, the latter dominate in distal, low-energy, nutrient-depleted environments. They thus can be linked to regressive and transgressive systems tracts, respectively, and are useful to infer fourth-order sequence stratigraphy. Altogether, the studied succession spans two entire and two partial third-order transgressive-regressive sequences, and its upper portion is subdivided into ten fourth-order sequences. Integrating the results from macrofossil and palynological analysis, a greatly improved stratigraphy is now available for the Jurassic–Cretaceous boundary interval in Arctic Canada, and will be used in subsequent studies to reconstruct the palaeoenvironmental dynamics at high latitudes in greater detail.

A new view on Tuzoia based on soft tissues from the Burgess Shale

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Cambrian 'bivalved arthropods' are characterized by a cephalothoracic carapace. Carapaces are hard structures that appear preserved even in Burgess-Shale type deposits with low abundance of soft body fossils. Multiple species of 'bivalved arthropods' are currently known mostly from their carapaces, including the highly abundant *Isoxys* and *Tuzoia*. While our understanding of *Isoxys* has greatly improved in the last decade, this is not the case for *Tuzoia*. *Tuzoia* has been known since 1912 and represents one of the most widespread arthropod species, with at least a dozen species recognized worldwide. Yet only the presence of eyes and antennae have been recognized since. Here we reveal further details of the soft anatomy of *Tuzoia* from the Marble Canyon site of the Burgess Shale. *Tuzoia* has *c*. 11 pairs of thoracic limbs up to the telson. The legs are robust, heptapodomerous and bear spinose endites. The body ends in one pair of large paddle-shaped caudal rami. Details on the head have not been recovered, but the presence of antennae or raptorial appendages cannot be confidently confirmed. We discuss potential affinities to *Isoxys*, but also highlight important ties to hymenocarines, challenging our understanding of the position of 'bivalved arthropods' in early arthropod evolution.

Locomotion of the enigmatic giant kangaroo *Protemnodon*: information from limb proportions

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Kangaroos (Marsupialia; Diprotodontia; Macropodoidea) are well known for their bipedal hopping, but many smaller ones primarily employ quadrupedal bounding for their fast gait. Optimum body mass for hopping is 50 kg, with a limit predicted at 160 kg due to potential tendon strain. Extant kangaroos range in body mass from 500 g to 70 kg; however, in the Pleistocene a variety of "giant" kangaroos approached this hopping size limit. Here we examine large species of the enigmatic Pleistocene kangaroo *Protemnodon* (*P. anak* ~166 kg, *P. brehus* ~131 kg). To assess their locomotion we investigated the

association between limb proportions and locomotor mode across Macropodoidea. We applied multivariate analysis to a dataset of linear limb measurements from 60 extant and extinct species. Using 14 'osteological indices' we assessed how postcranial morphology relates to primary locomotor mode. We found that hopping and quadrupedally bounding kangaroos have different morphologies; large *Protemnodon* species occupy a vacant area of morphospace – they have short feet like the quadrupeds but retain the long tibiae typical of hoppers, and have uniquely robust forelimbs. *Protemnodon* represents an extinct ecomorph with an anatomy indicative of a significantly greater amount of quadrupedal locomotion than in modern large kangaroos.

Diversity partitioning in Phanerozoic reef building communities

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Biodiversity can be partitioned into three hierarchical concepts: alpha diversity assesses within-habitat diversity, beta diversity looks at the compositional variation between assemblages, and gamma diversity assesses richness within the entire observed system. Unweighted by-list sampling standardization of tropical reef builders, and other Phanerozoic marine invertebrates, reveal important differences in their diversity trajectories. Reefs, defined as laterally confined structures built by the growth and/or metabolic activity of sessile benthic organisms in an aquatic environment, are ecologically important ecosystems. Alpha diversity for both systems increases over time, indicating increasing habitat complexity, but in almost all instances, reef builders comprise of more genera than other marine organisms. Gamma diversity trajectories show differing pathways – generic richness in reefs has declined over time, whereas the rest of the invertebrate taxa have an exponential increase. This result is an important deviation from earlier studies which discovered that reefs and the rest of the marine taxa share congruent extinction patterns. Reef beta diversity declines significantly over time, while other invertebrates show no temporal trend. Reef beta decline may be attributed to the increasing dominance of corals as reef builders. Diversity partitioning of reef builders provides empirical support for the statement that reefs are "cradles of biodiversity".

Changes in the body size of burrowing decapods in response to Anthropocene warming

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Anthropogenic activities are the direct cause of increasing global surface temperatures, and are predicted to have significant effects on marine ecosystems. This study tests the prediction that the body size of marine animals will shrink in response to warming, focusing on burrowing decapods. Bioturbation of the sea floor causes significant changes to sediment biogeochemistry, and burrowing decapods from the infraorders Axiidea and Gebiidea produce some of the deepest and most complex burrows in the marine environment. Dimensions of 751 specimens of Callianassidae and Upogebiidae collected over the past 200 years, and 260 specimens of their burrows collected since 1977, were measured to analyse size changes through the Anthropocene. Significant reductions in size with increasing sea surface temperature anomalies and global atmospheric CO_2 were recorded in the Callianassidae, supporting the prediction of shrinking body size and

showing that it has already started. Upogebiidae, in contrast, showed either no response or a body size increase. Reasons for these differences are discussed. Continued declines in burrow size and surface area will have detrimental effects on nutrient cycling and productivity. Fossil crustacean burrows (*Thalassinoides*) record similar size reduction during past warming events, indicating similar responses and consequences for marine ecosystems past, present and future.

The clam before the storm – what bivalves can tell us about climate change

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Previous studies into the effect of climate change on the growth of organisms have made broad generalisations across disparate species. This study is the first in-depth look at how multiple aspects of climate change will affect the growth of families within one class: Bivalvia. Bivalve growth patterns are sensitive to environmental conditions and combinations of stressors act in an additive or dampening manner. Previous studies are contradictory, making identifying overall trends challenging. This study uses meta-analysis of current literature to examine how bivalve growth rates respond to increased temperature, acidification, lowered salinity, hypoxia and combinations. Different families of bivalves do not respond in the same degree to individual stressors and combinations of stressors. The effects on growth are significant, but the magnitude and direction of those effects are not predictable at the family level. Climate change will affect different families disproportionally. The effect-size can be used to predict an extinction threat level for each family. Using data from the fossil record, extinction rate for each family can be calculated across the end-Cretaceous mass extinction. Generalised linear modelling can then predict whether vulnerability to climate change is correlated with extinction rate, when adjusted for phylogenetic and spatial signal.

Revision of the Early Jurassic ichthyosaurian *Temnodontosaurus zetlandicus*

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Parvipelvia is a major clade of ichthyosaurians that appeared during the Late Triassic and rapidly diversified into a disparate assemblage of morphologies during the Early Jurassic. However, the inter-relationships of early parvipelvians are unclear and many genera are loosely diagnosed, such as *Temnodontosaurus*, an ecologically important genus from the Early Jurassic of Western Europe. One taxon concentrates many taxonomic issues: *Temnodontosaurus acutirostris*, to which *'Ichthyosaurus' zetlandicus* is currently assigned. We redescribe the holotype of *'Ichthyosaurus' zetlandicus* (CAMSM J35176) as well as a new specimen attributable to this taxon (MNHNL TU885), from the Toarcian of Luxembourg. We find that *Temnodontosaurus zetlandicus* is a valid species that can be referred to *Temnodontosaurus*, sharing a number of morphological traits with *Temnodontosaurus nuertinguensis* and *Temnodontosaurus trigonodon*, despite having a distinct cranial architecture. Our phylogenetic analyses under implied weighting maximum parsimony and Bayesian inference support the integration of *T. zetlandicus* in *Temnodontosaurus*. The species currently referred to as *Temnodontosaurus* are relatively

well clustered within Early Jurassic parvipelvians. However, the genus still appears polyphyletic, notably due to the stronger affinity of *Temnodontosaurus azerguensis* with leptonectids. This highlights, more than ever, the need of a thorough reinvestigation of the taxonomic content of *Temnodontosaurus* and early parvipelvians relationships.

Evolving ecology and morphology of Neogene planktonic foraminifera

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Planktonic foraminifera are marine microorganisms that have the most complete fossil record of the Cenozoic era. As such, they are widely employed for generating palaeoceanographic proxy data and for addressing evolutionary questions at the species level. In this work we use a high-resolution direct sampling approach to investigate the paired morphological and ecological evolution of a group of enigmatic clavate planktonic foraminifera; the *Globigerinella* and *Beella* lineages. This high-resolution analysis has allowed the speciation of *G. siphonifera*, *G. calida*, *G. adamsi* and *B. megastoma* and the extinction of *G. praesiphonifera* to be studied in detail. Paired individual-level morphometric and geochemical data have allowed for investigation into the relationships between chamber size, body size and increasing ocean depth habitat through time.

True colours or red herrings? Appropriate colour maps for finite element analysis to enhance interpretation and accessibility

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Accessibility is a key aspect for the presentation of research data. New data on the palaeobiology of extinct organisms are routinely obtained with computational techniques, such as finite element analysis (FEA). FEA is used to calculate stress and deformation in skeletal objects when subjected to external load forces. Results are displayed using false-colour contour plots in which colour information is used to convey the underlying biomechanical data. The rainbow colour map is nearly exclusively used in these contour plots. However, numerous studies in other disciplines have shown the rainbow colour map to be problematic due to uneven colour representation and its inaccessibility for those with colour-vision deficiencies. Here different colour maps were tested for their accuracy in representing the underlying stress values of FEA models. Differences in stress magnitudes (ΔS) and colour values (ΔE) of the FEA models were compared and their correlation was used as a measure of the accuracy. The results demonstrate that the rainbow colour map is not well suited to represent the underlying stress distribution of FEA models. However, the performance of other colour maps varied with the tested scenarios and stress types. It is therefore recommended to use different colour maps for specific stress types.

The Triassic thylacocephalans from Slovenia: implications for their evolution and diversification

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Thylacocephala is an enigmatic fossil euarthropod ingroup, often associated with Pancrustacea. Despite the remaining questions on their anatomy, thylacocephalans are characterized by key anatomical features: a folded shield enveloping most of the body, hypertrophied compound eyes, three pairs of raptorial appendages, a trunk made of eight to 22 segments bearing appendages, and eight pairs of gills. Known from at least the Silurian to the Cretaceous, it was during the Triassic that thylacocephalans were the most taxonomically diversified. Unknown until recently in the fossil record of Slovenia, many specimens of thylacocephalans have now been collected from various localities in the Julian and Kamnik-Savinja Alps. Dating back from the Anisian up to the Carnian, these localities display well-diversified thylacocephalan assemblages. Taxa already known from the Middle and Late triassic of Austria and Italy (*Microcaris* Pinna, 1974; *Atropicaris* Arduini and Brasca, 1984) have been recorded while new morphologies have also been identified. The new morphologies present typical characters of Jurassic representatives, especially a posterior notch and posterior spines. These new findings provide important insight into the diversity and geographic distribution of thylacocephalans during the Triassic but also into the morphological evolution of this puzzling group.

posters

A new lobopodian from the middle Cambrian of Utah – did swimming body flaps convergently evolve in stem-group arthropods?

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Arthropods are ubiquitous in all habitats on our planet today and yet the origin of this mega-diverse phylum remains poorly known. It is widely thought that the segmented, articulated and extensively sclerotized body of arthropods evolved from the annulated vermiform body of a lobopodian ancestor *c.* 540 Ma. This anatomical transformation included the evolution of the sclerotized and articulated arthropod appendage from an annulated non-jointed limb. However, this scenario is complicated by the presence of different kinds of body flaps in addition to/replacement of walking limbs in many stem-group arthropods. We describe a new flap-bearing lobopodian from the Drumian strata of Utah. It is known from an incomplete specimen displaying a faintly annulated body, eight pairs of swimming flaps, and digestive glands. Extensions of the body cavity into the body flaps suggest that they are modified lobopods, like the ventral body flaps of radiodonts and possibly *Kerygmachela*. Yet, parsimony and Bayesian inference phylogenetic analyses suggest that lobopod-derived body flaps have evolved convergently in those taxa, most certainly accompanying a shift towards a predominantly swimming predatory lifestyle. Our results caution against describing the origin of arthropods as a linear sequence of acquisition of arthropod traits.

One hundred and ten million year record of elasmobranch egg capsules from methane seeps

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Elasmobranch egg capsules are rare in the fossil record. They include Palaeozoic and Mesozoic spirally coiled capsules of the *Palaeoxyris* group found mainly in freshwater deposits, occasional occurrences of chimaeroid egg capsules (*Chimaerotheca*) ranging back to the Triassic, and rare skate egg capsule specimens (*Rajitheca*) from the Oligocene of central Europe. All these records represent internal or external moulds, many are flattened, and a capsule wall has never been reported. Here we report a small diversity of new elasmobranch egg capsules from fossil methane seep sites in New Zealand (Miocene), Japan (Santonian), California, USA and the Canadian Arctic (both Albian). Many of these capsules are associated with tube worms, as are previously-described catshark egg capsules from a Late Eocene seep in Washington State, USA (*Scyliorhinotheca goederti*), and modern catshark and skate egg capsules from several deep-water seep sites in the modern Eastern Mediterranean. This indicates that methane seep ecosystems have served as nurseries for predatory elasmobranch fishes for at least 110 million years. The fossil capsules are preserved three-dimensionally and some show mineralized remnants of organic capsule walls, now replaced by carbonates resulting from the anaerobic oxidation of methane biogeochemical process.

New specimens of *Bunaia woodwardi* Clarke 1919, (Eucheliceratа) and its putative Vicissicaudata affinities

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The Eucheliceratа are a successful clade of arthropods including Xiphosura, Chasmataspidida, Eurypterida and Arachnida as well as the paraphyletic 'synziphosurines'. Here we describe new material assigned to the Silurian 'synziphosurine' *Bunaia woodwardi* that exhibits previously unknown features of its ventral anatomy, such as five pairs of biramous appendages in the prosoma and a pre-telson segment bearing a possibly membranous and bilateral process. A similar structure is also present in undescribed 'synziphosurines' from the early Ordovician Fezouata Biota, while several other Cambrian and Ordovician taxa bear an anal pouch (*Habelia optata*) or variably modified post-ventral appendages (Vicissicaudata) in their posterior trunk region. Phylogenetic analyses and anatomical comparisons of these processes (*i.e.* the anal pouch, post-ventral appendages and 'synziphosurines' post ventral process) allow us to propose the hypothesis that all

share a homologous appendicular origin, which we consider as the apomorphic state for a monophyletic clade formed by Euchelicerata and Vicissicaudata. The clade Artiopoda, formed by Euchelicerata, Vicissicaudata and Trilobitomorpha, has already been retrieved in several phylogenetic analyses, and our new findings on the 'synziphosurines' elucidate the possible relationships within the clade, supporting a sister-group position of Vicissicaudata with respect to Euchelicerata.

Classic early Late Cretaceous marine reptiles from the Hibernian Greensand (Cenomanian–Early Santonian) of SW Antrim and the Belfast hill and glen country, Northern Ireland, UK

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The early Late Cretaceous was a period of heightened global terrestrial and oceanographic change, with marine reptile ecosystems undergoing profound restructuring epitomized by the final disappearance of platypterygiine ichthyosaurs, decline of large pliosaurs, and increasing dominance of mosasauroids, marine turtles, and xenopsarian plesiosaurs. However, despite recent attention and globally extensive reptile-bearing marine sediments from this period, the detail of this transition in marine reptile evolution remains poorly understood. Here, limited, yet distinctive, dental and post-cranial remains from the Hibernian Greensand Group of Southern Antrim, UK are described for the first time. Material accords to the platypterygiine-pliosaurid-elasmosaurid peri-Tethyan marine reptile association recognized across the European Archipelago from Britain to European Russia and supports recent hypotheses on the survival of brachauchenine pliosaurs beyond the Middle Turonian. While adding to an already diverse fish and chondrichthyan fauna from the Hibernian Greensand, they collectively represent the only significant set of remains of early Late Cretaceous marine reptiles so far described anywhere in the British Isles outside of England. With marine reptile remains now coming from every major Mesozoic marine unit in Northern Ireland, it implies regional rarity to be caused by collecting biases and the effects of regional geology.

The consequences of Oligo-Miocene climatic changes on the morphology and ecology of the large benthic foraminifera *Heterostegina costata* and their implications for the modern day

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Climate change has multifaceted consequences for marine organisms. Individuals must adapt, or suffer the effects of changing environmental and ecological pressures. Foraminifera have been shown to adapt and evolve rapidly in response to climate change. However, the precise morphological alterations in response to climate dynamism are poorly understood. In addition, past studies have not assessed how climate affects foraminifera productivity. Here it is shown, from the Oligo-Miocene stratigraphy of Malta (27.8–7.2 Ma), that foraminifera adapt dramatically to environmental change. The test modifications of *Heterostegina costata* in particular closely reflect changes in the environment as a result of climatic dynamism. It was found that the test diameter of *H. costata* decreased as sea surface temperatures increased leading up to the mid-Miocene Climatic Optimum, and

increased when temperatures cooled following the mid-Miocene Climatic Transition (MCT). Furthermore, *H. costata* dominates during the Mi-1 cooling event and following the MCT, demonstrating that climate drives morphological and ecological response in this species. This study demonstrates that palaeoclimatic changes reduced the health and productivity of producer-level benthic foraminifera. Understanding the basal effects of climate change is pertinent for marine conservation. Conserving the health of producers will significantly improve the longevity of organisms at higher trophic levels.

Hydrodynamics of the rangeomorph Ediacaran organism *Pectinifrons abyssalis*

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Late Ediacaran fossil surfaces at Mistaken Point (~574–564 Ma) preserve some of the oldest complex macroscopic communities, and are dominated by 'fractal' rangeomorph organisms whose relationships to extant animal groups are unknown. Among the least well-understood of these is *Pectinifrons abyssalis* – a fence-like organism consisting of a curved basal pedicle rod and two upright rows of rangeomorph fronds. Like other rangeomorphs *Pectinifrons* is widely believed to have been a sessile osmotroph, feeding via the direct absorption of dissolved organic compounds; however this model has yet to be objectively tested. In this project we used computational fluid dynamics (CFD) modelling to examine simulated flow patterns around *Pectinifrons* under a range of realistic palaeoenvironmental conditions. The patterns were compared both with those computed for other Ediacaran organisms, and with a range of potential modern analogues. These data allowed us to critically assess the palaeobiology of *Pectinifrons*, including the establishment of likely feeding mode, as well as to examine a range of potential interactions with co-occurring rangeomorph organisms. Ultimately this work sheds new light on a little-studied Ediacaran organism, and tests the hypothesis that *Pectinifrons* formed part of a unique biocoenosis that disappeared prior to the base of the Cambrian.

Silurian ostracods were pioneer colonists of estuaries

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Ostracod crustaceans occupy an exceptional range of modern aquatic environments and are invaluable palaeoenvironmental indicators in the fossil record. However, pre-Carboniferous records of supposed marginal marine and non-marine ostracods are poorly documented and the timing of their marine to non-marine transition has proven elusive. Here we reassess

the early environmental history of ostracods from new late Silurian finds in northern Vietnam. Two low diversity but distinct ostracod assemblages are associated with estuarine deposits of the Si Ka Formation. This occurrence is consistent with previous incidental reports of ostracods occupying marginal and brackish settings through the late Silurian and Devonian. We show that ostracods were pioneering the occupation of marginal marine and estuarine settings 60 million years before the Carboniferous, and that ostracods were a component of the early phase of transition from marine to non-marine environments.

Enigma variations: characteristics and likely origin of the problematic surface texture *Arumberia*, as recognized from an exceptional bedding plane exposure and the global record

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Arumberia is a surface texture that consists of parallel, sub-parallel or radiating lines. It has been interpreted as the impression of a metazoan, a 'vendobiont', a sedimentary structure formed on a substrate with or without a microbial mat covering, or a non-actualistic microbial community. Here we contribute new insights into the origin of *Arumberia*, resulting from the discovery of the largest contiguous occurrence of the texture reported to date. We compare the features of *Arumberia* at this locality with 38 other records, revealing four defining characteristics: the three-dimensional morphology of exposed *Arumberia* lines records fully preserved cords within clay laminae; lines may transition laterally into reticulated patterns; characteristic *Arumberia* lines can become modified by desiccation on emergent substrates prior to interment; and *Arumberia* are streamlined with palaeoflow in successions showing evidence of unidirectional currents, but are organized parallel to ripple crests where strata were sculpted by oscillatory flows. The most reliable examples are stratigraphically restricted to a 40 Ma interval straddling the Ediacaran–Cambrian boundary. Together these characteristics suggest that *Arumberia* records the remains of extinct, sessile filamentous organisms that occupied shallow water and emergent environments across the globe at the dawn of the Phanerozoic Eon.

How do you solve a problem like Marsupialia? Compensating for the limitations of the Gondwanan mammal fossil record

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Throughout the geological past, many mammalian groups have proliferated and diversified across South America, Antarctica and Australasia. However, the spatial bias of the Gondwanan fossil record has obscured our understanding of notable biogeographical narratives, including the dispersal events that resulted in the present-day distributions of marsupial groups across the three continents. We propose that by modelling the ecological niche of modern mammalian clades, and projecting said niches onto palaeoenvironmental reconstructions, we can predict the habitat suitability and dispersal patterns of these groups in Gondwana across deep time. Applying such a process to extant marsupial orders, we find that during the Cenozoic, only some groups (including the microbiotheres, which live today only in Chile and Argentina) were able to travel freely between South America and

Australasia via Antarctica. Our results elucidate the historical biogeography of an iconic and charismatic clade, as well as acting as important groundwork for future analyses.

Intraspecific variation on tail morphology in a new titanosaur (Dinosauria, Sauropoda) from Lo Hueco (Late Cretaceous, Spain)

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Lo Hueco is a multi-taxa bonebed from the upper Campanian–lower Maastrichtian of Spain, which includes several partial titanosaurian skeletons, mostly articulated or with low dispersion. This remarkable sample is key to understanding the phylogeny of Ibero-Armorican titanosaurs. *Lohuecotitan pandafilandi* was the first established taxon at the Lo Hueco site; however, the presence of two to three additional lithostrotian forms is being considered. The intraspecific variation in the taxa represented by more than one individual is being analysed through the detailed description of several morphological characters. HUE-EC-02 and HUE-EC-03 seem to belong to the same taxon, and the comparison of their tail morphology identifies variable features: morphology of the condyle; prezygapophyseal processes; orientation of the anterior articular face; and development of the vertebral laminae and fossae (*e.g.* prsl, pocdf). The orientation of the neural spine and prezygapophyseal processes, the anteroposterior length of the posterior condyle and the morphology of the ventral hollow is less variable. Higher degree of variability is observed in the anterior section of the tail. The suture between the neural arch and centrum is still visible in HUE-EC-02, suggesting that the present variation could be related to ontogeny.

A new specimen of *Petalodus* from the Mississippian of County Kerry, Ireland

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Petalodontiforms are a clade of cartilaginous fish from the Palaeozoic. With the exception of rare body specimens, they are known mostly from disarticulated teeth. This is true for *Petalodus*, which is one of the most common genera. Petalodontiform teeth are distinct as they possess large petal-shaped crowns with deep roots. A new specimen of petalodontiform (TCD.31087) is reported from a disused coastal quarry at Doon Point, near Ballybunion in Kerry. The quarry section reveals a series of interbedded limestones and shales from the Corgrig Lodge Formation and are late Viséan in age. TCD.31087 is a fragile specimen, so it was scanned using micro-computed tomography. Resultant CT-slices were rendered in SPIERS, producing 3D models from which the anatomical characters were described. The crowns of the teeth are petal-shaped and labio-lingually flattened, with concave lingual surfaces. There are cristae at the base of the crowns, with the crown-base over twice the width of the roots. TCD.31087 is identified as *Petalodus* cf. *ohioensis*. The relative completeness of the specimen allows for tooth variation within *Petalodus* to be assessed. It was found that the teeth were heterodont and some were part of a tooth replacement whorl.

Re-exploring the exceptionally preserved fossils of the Tonian Svanbergfjellet Formation of Svalbard to understand the rise of eukaryotes

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The diversification of complex eukaryotic life during the Neoproterozoic Era is one of the greatest geobiological transitions in our planet's history. The Tonian (1,000–720 Ma) Svanbergfjellet Formation, Svalbard, provides an exceptional view into this nascent eukaryotic world with the preservation of entirely soft-bodied microfossils including examples of the oldest green algae. Despite their importance, Svanbergfjellet microfossils have not been studied in depth since the early 2000s. We present microfossil data from new samples taken in a high-resolution stratigraphic framework (sampling at ~5–10 cm intervals) at two localities in northeastern Spitsbergen: De Geerbukta, where the fossils were originally discovered, and Freken, a new site in southern Lomfjorden. Over 1,000 microfossils are documented from mudstone strata bracketed by stromatolitic bioherms of the informal algal dolomite member. New palaeoenvironmental data, including detailed mineralogy and a Re-Os age constraint, provide context for emerging eukaryote biodiversity. Diversity and preservation quality vary markedly between samples, but the newly documented microfossils are highlighted by an exceptionally preserved population of the possible chlorococcolean alga *Palaeastrum*.

posters

Assessing the adequacy of morphological models used in phylogenetic palaeontology

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Accurate phylogenetic trees are essential for understanding how species have diversified through time. Within Bayesian phylogenetics a major step in producing a tree is in choosing an appropriate model of character evolution. If a model is chosen that does not provide a good fit to the data, the inference can produce erroneous results. The Mk family of models are commonly used in palaeontology, as they can be applied to discrete morphological traits, allowing for the incorporation of fossils. However, it is not known whether the simple Mk model provides a sufficiently good fit to morphology. Model selection can be applied to find the best available model from a pre-defined group, but this approach cannot tell you whether existing models accurately capture the complex processes that generated your data. Model adequacy, which tests the absolute fit of available models, offers a more robust way of confirming that you have chosen an appropriate model. We performed a series of model adequacy tests using posterior prediction simulations. Taking morphological matrices of fossil tetrapods we simulate data to assess how well the current popular Mk model performs. We highlight ways in which existing models both succeed and fail to capture the complexity of morphology.

Panderodus from the Waukesha Lagerstätte of Wisconsin, USA: a primitive macrophagous vertebrate predator

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Oxford University Museum of Natural History, UK

The earliest predatory vertebrates known are the conodonts, found almost entirely from their teeth-like feeding elements scattered through rocks, 500 million years old. Despite their long history, only 12 specimens are known that preserve soft parts of the animal's body, and among those there is a single specimen representing the most primitive conodonts. It was first described in the 1980s, but now modern imaging techniques have revealed a wealth of new information: soft supports for a revised feeding apparatus, similar to those in hagfish; buried muscles; and a 'flat fish'-like body shape. Together, these new observations allow a unique insight to the anatomy and evolution of the first vertebrate predators and their role in the nektonic ecology of Cambrian–Silurian oceans.

A new Early Cambrian vetulicolian fauna from Sirius Passet, Greenland

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Deuterostomia comprises two reciprocally monophyletic groups: Ambulacraria (echinoderms and hemichordates) and Chordata (cephalochordates, tunicates and vertebrates), with major phylogenetic debates concerning their monophyly or paraphyly and the inclusion of additional phyla (xenacoelomophs) in Deuterostomia. Cambrian fossils, with their mosaic anatomies, have the potential to help resolve these phylogenetic disputes. However, a paucity of clear homologies uniting some extinct groups to living clades means that their affinities remain controversial. Vetulicolians, with their distinctive bipartite bodyplan, rank among the most enigmatic of these putative deuterostomes. Controversies persist around aspects of their anatomy, mode of life and, consequently, phylogenetic placement. We describe a new Vetulicolian fauna from the Early Cambrian Sirius Passet biota of Greenland which sheds light on the anatomy, taxonomy and plausible affinities of vetulicolians. We present new phylogenetically informative data on the mouthpart anatomy of *Ooedigera*, the only previously described Sirius Passet genus. In addition, we reveal several previously undocumented morphotypes, potentially rivalling the diversity of the Chengjiang Lagerstätte. These novel forms extend the envelope of vetulicolian disparity to include diminutive elongated and oar-like bodyplans. At the same time, the occurrence of didazoonids and Vetulicola-like morphotypes in Sirius Passet points to a biogeographical continuity with other early Cambrian Lagerstätten.

Multiple phyla, one time resolution? Similar time averaging in benthic foraminifera, mollusc, echinoid, crustacean and otolith fossil assemblages

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Time averaging is a fundamental aspect of fossil assemblages, constraining temporal resolution of palaeoecological, palaeoenvironmental and geochronological inferences. However, quantitative estimates of the duration of time averaging are still lacking for many

higher taxa, limiting our understanding of the factors controlling it. Here we compare post-mortem age structure across five different phyla of major skeletal carbonate producers based on individually dated specimens sampled from a sediment core from the northern Adriatic Sea. We used amino-acid and radiocarbon methods to date bivalve shells, foraminiferal tests, tests and isolated plates of irregular and regular echinoids, crab claws and fish otoliths. In spite of different skeletal architecture, mineralogy and life habit, all species showed comparable, millennial time averaging varying from ~1,800 to ~3,600 years (interquartile age ranges), while their median ages differ by up to ~3,700 years. Our results suggest that remains of echinoids and crustaceans – two groups with multi-elemental skeletons often assumed to have low preservation potential – can still undergo extensive age mixing comparable to that of the co-occurring mollusc shells. The timing of hardpart production and extrinsic sedimentary or taphonomic factors can thus be more important than intrinsic skeletal durability in determining temporal resolution of multi-taxic fossil assemblages.

Rapid redox variations in a Lower Jurassic black shale: a palaeontological and geochemical perspective

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The Toarcian oceanic anoxic event (T-OAE) occurred in the Lower Jurassic (~183 Ma) and is associated with the deposition of black shales across much of Europe, including in the Cleveland Basin (Yorkshire, UK). Despite extensive geochemical evidence for severe oxygen depletion in the Toarcian Mulgrave Shale Member, the presence of thin 'pavements' of bivalves (predominantly *Pseudomytiloides dubius*) indicates that oxygen levels were more dynamic than low-resolution geochemistry suggests. This dynamism is further implied by the presence of a thin black shale unit (the Lower Sulphur Band – LSB), in an otherwise oxygenated shale unit stratigraphically below the Mulgrave Shale. Here we present the results of an ongoing, high-resolution, combined geochemical-palynological-macropalaeontological study of the LSB and bivalve pavements. We document the occurrence of bioturbation (*Chondrites*) closely associated with the deposition of the LSB, the presence of a mixed marine-terrestrial palynofacies, and consider the implications of both of these palaeobiological observations for geochemical studies of condensed black shale intervals. Our study of the LSB, in particular, highlights the sensitivity of this Jurassic marine system to changes in the exogenic carbon cycle, and carries implications for the future trajectory of modern marine systems exposed to anthropogenic oxygen depletion.

Functional morphology of the Ediacaran organism *Tribrachidium heraldicum* revealed by computational fluid dynamics

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The latest Ediacaran (~575–539 Ma) directly precedes the Cambrian and has long been thought to consist of simple ecosystems dominated by organisms feeding via osmotrophy

(*i.e.* direct absorption of dissolved organic compounds). However, recent studies have demonstrated higher ecosystem complexity and a broader range of feeding modes than previously appreciated. Among the most bizarre and historically confounding species is the tri-radially symmetrical organism *Tribrachidium heraldicum*. Rahman *et al.* (2015) used a 3D *Tribrachidium* model generated from CT scanning to simulate water flow around the organism, finding flow patterns suggesting suspension feeding rather than osmotrophy. Here we expand on this research using 3D CAD models including important morphology missing from earlier models. Using a more accurate model of *Tribrachidium*, we replicate Rahman *et al.*'s original study for validation. In addition, we investigate the effects of specific features as possible controls on fluid flow patterns using a range of null models. Lastly, the results are compared to potential modern analogues thought to feed similarly. The results of this work provide further insight into the palaeobiology and functional morphology of an iconic Ediacaran organism and highlight the potential role played by suspension feeding in structuring late Ediacaran benthic communities.

New Cambrian fossils from Utah illuminate the early evolution of nervous and sensory systems in ctenophores

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Ctenophores, or comb jellies, are a group of predatory, mainly holopelagic macroinvertebrates, whose controversial phylogenetic position has prompted several competing evolutionary scenarios regarding the origin of animal body plans. Molecular clock estimates predict that the living diversity of ctenophores has a relatively late origin, but their gelatinous bodies typically exclude them from the conventional fossil record. Here we describe two new ctenophores from the Cambrian Marjum Formation of Utah, which illuminate the early evolution of nervous and sensory features in the phylum. *Thalassostaphylos elegans* is reconstructed as having 16 comb rows, a well-developed oral skirt and an apical organ with ciliated polar fields. *Ctenorhabdotus campanelliformis* features *c.* 24 comb rows, a well-developed oral skirt and a prominent apical organ enclosed in a skeletonized capsule. *C. campanelliformis* preserves neurological tissues as carbonaceous films concentrated around the apical organ and ciliated furrows, which connect to a transverse circumoral nerve ring via longitudinal giant axons. The presence of interconnected aboral and oral nerve centres deviates from the neurological organization of living ctenophores, but resembles certain cnidarians. Our findings demonstrate substantial complexity in the nervous system of Cambrian ctenophores, and refine our understanding of the evolution of the ctenophore crown group.

Rapid early growth in a Cambrian apex predator

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Radiodonts, Palaeozoic stem-group euarthropods comprising *Anomalocaris* and relatives, include some of the largest predators known from Cambrian seas. Our understanding of the diversity and disparate ecological niches this group occupied has increased

greatly over recent years; however, with the exception of a single juvenile *Lyrarapax*, the growth dynamics of radiodonts have remained unexplored. Here we report the first quantitative data on the ontogeny of a radiodont, using hundreds of frontal appendages of the Chengjiang amplectobeluid *Amplectobelua symbrachiata*. Linear measurements of appendage length and height display a mulitmodal distribution. An expectation-maximization algorithm resolved this as three overlapping normal distributions – interpreted as representing three distinct instars separated by two growth increments of 300% and 150% respectively. Comparison with growth data of body parts in other euarthropods demonstrates that the first growth increment in *A. symbrachiata* is exceptionally large. This large growth increment early in the life history of *A. symbrachiata* demonstrates sophisticated growth dynamics in the euarthropod lower stem. It may reflect a need to grow quickly to feed on larger prey, to avoid predation, or the fluctuating conditions in the Chengjiang at the time.

Phyologenetics and systematics of the subfamilies Cheirurinae and Deiphoninae: shedding light on the root relationships

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Cheiruridae was one of the most diverse families of trilobites during the Ordovician with 453 species assigned. Within Cheiruridae, eight subfamilies (Acanthoparyphinae, Cheirurinae, Cyrtometopinae, Deiphoninae, Eccoptochilinae, Heliomerinae, Pilekiinae and Sphaerexochinae) have been historically recognized. Although some subfamiles have been subjected to phylogenetic analysis, no broader analyses involving different subfamilies have been performed. In a first step to clarify the evolution of Cheuiruridae, we performed a phylogenetic analysis of the subfamilies Cheirurinae, Deiphoninae and Cyrtometopinae, which have historically been defined by putative synapomorphies (*e.g.* anteroposterior constriction of the thoracic pleura, pleural furrow morphology, pygidial morphology) that differentiate them from the rest of Cheiruridae. Ordovician species were selected for analysis, prioritizing older species in order to improve the resolution of basal nodes. Parsimony analyses were performed in T.N.T., under equal weight and implied weights, using the heuristic "Traditional Search" under tree bisection-reconnection (TBR) branch swapping with 100 replicates x 100 iterations. The preliminary result indicates that Cheirurinae and Deiphoninae are monophyletic. 'Cyrtometopines' have been resolved as a paraphyletic grade rooted at the base of Deiphoninae. The new phylogenetic framework permits the construction of hypothesis about the early evolution of Cheiruridae and provides new information about trilobites in the Ordovician radiation.

Pterosaurs evolved a muscular wing-body junction that provided advanced aerodynamic smoothing, sophisticated wing root control and wing force generation

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Pterosaurs were the first flying vertebrates, but details of their flight anatomy and performance remain unclear. Using laser-stimulated fluorescence, we observe direct evidence of a wing root fairing in a pterosaur for the first time. This feature smooths out the wing-body junction and reduces drag, as in many modern aircraft and flying animals. The pterosaur wing root fairing was composed uniquely of muscle, rather than fur or feathers as in bats and birds. Pterosaurs appear to have used their muscular fairing to access additional flight performance benefits through sophisticated wing base control and contributions to wing elevation and/or anterior wing motion during the flight stroke. This study demonstrates how new instrumentation can help to fill gaps in our knowledge of pterosaur flight anatomy and evolution.

The ecomorphological and functional innovation of bizarre claws among early-branching maniraptorans

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Maniraptora, meaning 'hand snatchers', was originally named after the mobile wrist and hand, yet their hands had a much wider range of functions. Late-branching members, like birds, generally have hands forming the wings or pre-wing forelimbs. In early-branching clades, alvarezsauroids have hands with a stout and pickaxe-like, single functional finger, while therizinosaurs have elongate fingers with slender and sickle-like manual claws. These were not 'grasping' hands, but their functions have been elusive. Two-dimensional morphospace analysis and finite element analysis (FEA) have been conducted on therizinosaurian manual unguals. Here we further provide a more broadly sampled, three-dimensional shape analysis on claws among early-branching maniraptorans. We simulate three key functions of their claws – namely digging, piercing and pulling – in FEA, comparing their biomechanical performance to non-maniraptorans and mammals. We compare our results using the 'intervals' method (a quantitative method comparing FE simulation results among taxa) and develop a method called functional-space analysis (FSA). In FSA, the biomechanical performance of each claw is quantitatively displayed and compared. Our analyses reveal surprising functional divergence among early-branching maniraptorans, and diverse evolutionary paths leading to various functions and morphologies: the claws of later alvarezsauroids are well suited to all functions, whereas the function of therizinosaurids claws remains puzzling.

Functional optimisation and trade-offs in the lower jaws of Crurotarsi

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Crocodilian jaw morphology is a clear example of the relationship between form and function. However, the ecological diversity of modern crurotarsans is vastly outstripped by their extinct relatives which included active terrestrial forms, herbivores and fully marine species. These lifestyles may have imposed different functional demands, but their effects on jaw morphology remain largely unquantified. Here we combine elliptical Fourier analysis with functional testing to build a performance landscape of theoretical jaw shapes to investigate the drivers of morphological evolution in crurotarsans. Our sample of 242 crurotarsan jaws generally occupy the most optimal regions of theoretical morphospace for rotational efficiency, resistance to Von Mises stress, hydrodynamic efficiency or a trade-off between multiple functions, though some seemingly viable shapes remain unrealized. Jaw speed is optimized only in a narrow region of morphospace whereas many shapes possess optimal jaw strength, which may manifest as a minimum boundary for most taxa. Shape variation shows little phylogenetic signal and functional convergence towards distinct ecological roles is common. Jaw morphology of aquatic taxa is constrained by hydrodynamics, whereas terrestrial taxa are free of this restriction. Diet also plays a crucial role in determining jaw shape, largely dictated by the importance of rotational efficiency in feeding.

Notes on a composite ammonite panel at the Maputo Zoo with a review of ammonite faunas reported from Mozambique

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The Maputo Zoo, founded by the *Zoological Association of Mozambique* in 1929, once exhibited a wide array of fauna and flora, but now only cares for five animal species displayed in a degraded setting as a result of civil war and post-independence (after 1975) nation building challenges. One interesting feature that has survived relatively unscathed near the zoo entrance is a decorative composite panel of ammonites, petrified wood and minerals, believed to have been created by amateur geologist/palaeontologist members of the *Zoological Association* and put on display by the early 1970s, intended to complement the zoological motif. The ammonite *Deiradoceras* spp. comprises the majority of the specimens present on the panel; *Mortoniceras*, *Tropaeum* and the nautiloid *Cymatoceras* are also present. These fossils are likely from early Cretaceous (Aptian-Albian) exposures of the Maputo Formation in southernmost Mozambique. The quality of the ammonite specimens and the historical nature of the panel at the Zoo warrant ongoing discussions related to conservation and preservation efforts. A literature review revealed sparse Late Jurassic (Kimmeridgian–Tithonian) but diverse Cretaceous ammonite faunas reported from Mozambique; a biostratigraphic framework of these ammonite faunas containing over 100 species was developed and an abridged version is presented.

A practical comparison of sample and population density estimates using fossil maps, Damuth's law, Taylor's law and density mass allometry

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Damuth's law relates population density to body mass, and Taylor's law states that the variance of the population densities is a power-law function of the mean population density. Density mass allometry affirms that the mean population density of a set of populations is a power-law function of mean individual body mass. We use solid geometric models to estimate the original body mass (/kg) of invertebrates, which is assumed to follow a normal distribution. We then infer their population densities using nomographs based on these laws and measurements. Population density (n/km^2) is compared to the sample densities, estimated from outcrop maps of fossiliferous beds. The sample density estimates are scaled upwards to be compared directly with the nomographs. Results show hypothesized population density, based on morphometrics, differs significantly from the estimated sample density. More fossil maps yield further sample densities to be evaluated against hypothesized population densities using a t-test. The test statistics show, at 99.8% confidence, that the sample density differs from hypothesized population density for all the mapped fossils. Furthermore, our provisional conclusion is that the sample density is greater than the population density due to taphonomic complexities, *e.g.* preferential preservation, mineralogy, and structure.

Diversification declines in major dinosaurian clades are not because of edge effects or incomplete fossil sampling

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Signatures of catastrophic mass extinctions have long been reported to be obscured by the edge effect where taxonomic diversity appears to decline gradually. Similarly, models of diversification based on splitting of branches on a phylogenetic tree might also be affected by under-sampling of divergences towards the edge. The implication is that long-term declines in diversification recovered from such models – *e.g.* in dinosaurs – may be artefacts of unsampled divergences. However, this effect has never been explicitly tested in a phylogenetic model framework – *i.e.* whether phylogenetic nodes (speciation events) close to the edge are under-sampled and if diversification declines are artefacts of such under-sampling. Here we test whether dinosaur species in temporal proximity to the Cretaceous–Palaeogene mass extinction event are associated with fewer nodes than expected, and whether this under-sampling can account for the diversification decline. We find on the contrary that edge taxa have higher numbers of nodes than expected and that accounting for this offset does not affect the diversification decline. We demonstrate that the observed diversification declines in the three major dinosaurian clades in the Late Cretaceous are not artefacts of the edge effect.

Evidence of hatching on dinosaur eggs from the Campanian–Maastrichtian of the Villalba de la Sierra Formation (Central Spain)

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The Poyos site (Guadalajara, Spain) has provided valuable oological remains including isolated eggshell fragments, multiple isolated complete eggs and several egg clutches. Although these remains so far cannot be assigned to a specific ootaxon, it is clearly distinct to those found on other Campanian–Maastrichtian Iberian sites, such as *Megaloolithus siruguei* from Portilla (also from the Villalba de la Sierra Formation) or Pinyes (Tremp Formation), and more closely resembles some specimens from Villeveyrac–Valmagne (Villeveyrac Basin, France) and Auca Mahuevo (Anacleto Formation, Argentina). Most complete eggs from Poyos are preserved in three dimensions with little to no horizontal deformation, as the eggshell is highly cracked, but most fragments retain their original position. Some specimens explored via CT scanning revealed a concentration of disorganized eggshell fragments at the lower part (related to the strata) of the egg fill and a 'hatch ring' at the top of the eggshell. Since eggs and clutches in similar conditions have been found on other sites from *e.g.* Romania, these findings serve as evidence for both the interpretation of their parents' reproductive biology and the taphonomy of the eggs and clutches.

Translating 2D enamel patterns of herbivore mammals into numerical descriptors

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Herbivore enamel configuration is regarded as an adaptation with sound ecological and evolutionary effects. It is no surprise that the systematics of many fossil mammal species strongly rely on the dentition morphology. Consequently, their two-dimensional representations are commonly portrayed in the literature and vastly outnumber other sources of available morphological data such as three-dimensional models. A series of numerical descriptors have been previously proposed for parametrizing tooth topology in 2D (*e.g.* indentation index, fractal dimensionality, *etc.*). All have in common that enamel complexity is described in the form of a single value per specimen and to record complex occlusal patterns and small variations within a specimen's topology. We propose a novel method to quantify three different parameters describing enamel topology: orientation, thickness and anisotropy. This multichannel approach uses two-dimensional images as a reference and free software, ImageJ, for analysis. The ability to record changes in topology was investigated using a dataset comprised of tooth samples of macro and microherbivore taxa with dentitions ranging from brachydont to hypsodont. This economical and relatively easy-to-use method is potentially useful for monitoring interspecific, intraspecific or ontogenetic tooth variations of a wide array of mammalian herbivores with conspicuous wear facets and exposed enamel borders.

Climatic conditions during interglacial and glacial phases in Argentine pampas based on stable isotope analysis of fossil mammals

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Profound climatic changes, related to the alternation of glacial and interglacial periods, took place during the Pleistocene. We have evaluated the variability of mean annual precipitation (MAP) and mean annual temperature (MAT) in the Argentine Pampas (La Pampa and Buenos Aires Provinces) during three phases: Last Interglacial (LIG, ~125,000 calBP); Last Glacial Maximum (LGM, 28,170–19,849 calBP) and post-Last Glacial Maximum (post-LGM, 17,281–11,500 calBP). The estimation of these parameters was based on tooth enamel $\delta^{13}C$ and $\delta^{18}O$ isotopic data of equids and cervids from nine fossil sites. During the LIG, we calculated a MAT of 15.9°C but MAP could not be estimated. In the LGM, a MAT of 14.8°C and a MAP of 552 mm were calculated. During the post-LGM, we calculated a MAT value range from 14.6 to 17.0°C and MAP from 480 to 1,229 mm. Variability of post-LGM localities parameters may be due to the alternation of warm (*e.g.* Bølling-Allerød) and cold (*e.g.* Younger Dryas) events. Changes identified seem to be controlled by alterations in atmospheric circulation. Thanks to current atmospheric circulation models and the estimated MAT and MAP of each phase, we propose differential atmospheric scenarios that explain such climatic changes across the Late Pleistocene.

Dyrosaurids have a unique postcranial anatomy

*Isaure Scavezzoni and Valentin Fischer
Université de Liège, Belgium

Dyrosauridae is a family of neosuchian crocodyliformes known from both terrestrial and aquatic environments across the Cretaceous–Palaeogene transition. The postcranium of dyrosaurids comprises astonishing features such as their vertebra with hypapohyses and tall neural spines, their well-developed pelvic girdles, and stout limbs, *etc*. However, their postcranial anatomy has long been overlooked, obscuring both their locomotive adaptations and the magnitude of their disparity. From this point of view, we thoroughly analysed the entire anatomy of the key dyrosaurids *Congosaurus bequaerti* and *Hyposaurus natator*, along with other extant (Crocodylia) and extinct Crocodyliformes (Thalattosuchia). In parallel, we also produced a comprehensive dataset of 187 traits on 27 taxa, largely covering the cranium and postcranium of exemplar crocodyliforms. These data were analysed following principal coordinate analysis (PCoA) to envision the morphospace occupation of Dyrosauridae, Thalattosuchia and Crocodylia. Our data report that Dyrosauridae displays a unique postcranial architecture, considerably contrasting with that of Crocodylia,

but in some ways not totally dissimilar from that of Thalattosuchia. Consequently, extant crocodylians might not represent a good functional analogue for extinct crocodyliformes. Furthermore, phylogenetic and disparity analyses would benefit from the employment of more postcranial data.

A freshwater bivalve superfamily Deccanoidea nov., from the Saurashtra Deccan intertrappean, western India: an example of vicariance palaeobiogeography

*Nishi Shah and Satish Patel
The Maharaja Sayajirao University of Baroda, India

The Deccan large igneous province (DLIP) of India marks geological, biogeographical, climatic and extinction events on the rapidly migrating Indian plate over the Reunion hotspot across the Cretaceous–Palaeogene. The waning phase of the DLIP is characterized by intermittent lava flows emanating into fossiliferous intertrappean rocks, chiefly of continental realm. The Saurashtra Peninsula, western part of the Indian plate, comprises thick, grey to rusty brown fossiliferous sandy/muddy shale studded with fresh water bivalve shells (mussels) of the order Unionida. These are fragile and disarticulated in preservation, mostly occurring as moulds or casts and occasionally calcified; the fissility of the shale obstructs their complete retrieval. High-resolution photography and X-radiography revealed various morphological features which enabled specimens to be distinguished, suggesting new stocks of Unionida. A new superfamily level category Deccanoidea nov. is proposed; morphological and morphometric analysis led to further subdivision which includes family Deccanoidae nov. and subfamilies Deccanoinae nov. (two genera, four species) and Chotiloinae nov. (one genus, three species). After the break-up from Gondwanaland and subsequent separation from Madagascar, the Indian plate exhibited island biogeogeography with a volcano-prone environment which might have led to isolation-forced localized radiation in fresh water bivalves suggesting evidence of vicariance palaeobiogeography.

Unravelling complex taphonomy and depositional histories in tropical cave deposits

*Holly E. Smith
Griffith University, Australia

In tropical regions such as Southeast Asia, complex infilling and depositional histories of cave deposits have made it difficult to ascertain the provenance of vertebrate remains within, and the taphonomic factors that influence them. These natural mixing processes may result in preservation bias amongst karst fossil assemblages and so there must be careful taphonomic consideration of temporal mixing before any meaningful palaeoecological interpretations are attempted. Here a multi-method contextual taphonomic approach is used to establish a more robust reconstruction of complex sedimentary cave evolution in three sites in the Padang Highlands of Sumatra, Indonesia. Integrating rapid neutron tomographic imaging and micromorphology has provided detailed evidence that is key to reconstructing the complex taphonomic history of Southeast Asian cave fossils, the depositional history of the deposits in which they are cemented and the diagenesis of the sediments in which they are held. Replicating this new approach may derive new insights into the archaeology and natural history of tropical cave sites around the world that could establish the provenance of important artefacts and rewrite the narrative of hominin and palaeofaunal biodiversity.

Dipnoan diversity in the early Pennsylvanian of Scotland: new lungfish from the Lower Coal Measures of North Lanarkshire

Timothy R. Smithson[1], Francis M. Elliott[2] and Thomas J. Challands[3]
[1]*University of Cambridge UK*
[2]*Scottish Universities Environmental Research Centre, UK*
[3]*University of Edinburgh, UK*

During the past one hundred and fifty years only two lungfish have been recorded in the Scottish Coal Measures: *Ctenodus* and *Sagenodus*. Here we describe a suite of new lungfish specimens collected from sites in the Scottish Central Coalfield that represent at least four taxa: *Sagenodus*; *Conchopoma*; and two new forms. They are part of an extensive vertebrate fauna recently discovered in the colliery waste from mining the Upper and Lower Drumgray Coal. These coals lie within the Communis Zone and are of Langsettian age. The specimens are much smaller than those found previously in the Scottish Coal Measures and represent fish between 60 and 360 mm long. The basihyal tooth plates of *Conchopoma* are the first record of this genus in the Pennsylvanian of Europe. One of the new taxa has a heterodont dentition not previously described from the Pennsylvanian. All the new material is preserved in thin, laminated shales suggesting a small lake environment rather than the typical coal swamp. These new discoveries demonstrate that Pennsylvanian lungfish were more diverse than previously realized and add to the growing evidence that the rate of lungfish evolution did not decline significantly after the Devonian, but remained high throughout the Carboniferous.

Scaling and multifractal nature of palaeontological and geological dynamics: implications of the extreme variability for the detection and testing of cyclic processes

Andrej Spiridonov[1] and Shaun Lovejoy[2]
[1]*Vilnius University, Lithuania*
[2]*McGill University, Canada*

Numerous spectral analysis-based studies claimed the presence of long-term cyclicities in macroevolution. Similarly, there is a resurgence of claims that Earth system dynamics proxies are characterized by deca-million scale cycles of differing period lengths, which presumably are produced by coupled Earth-life synchronized 'pulses'. The fluctuation analysis of palaeontological and geochemical time series revealed the presence of ubiquitous scaling, and of strong intermittency ('anomalous' extremes) – the characteristics of multifractal processes. Analysis of the 'spikiness' and probability distributions and intermittency of palaeotemperatures, origination and extinction rates and biodiversity show that they are strongly non-Gaussian. However – significantly for the interpretation of the spectrum – we also find that they are also spiky and strongly non-Gaussian in the Fourier domain. While these spectral peaks are highly statistically significant with respect to Gaussian null hypotheses, they are on the contrary common features of multifractal, scaling processes. Our results show how this strongly non-Gaussian variability may easily produce spurious but highly significant results in Fourier spectra of palaeorecords. This finding forces us to rethink our basic assumptions about the use of popular null models in the search for grand cycles in the evolution of Earth and life.

Recurrence plots – a new tool for the non-parametric and model free analysis of dynamics of taxon rank abundance distributions

Robertas Stankevič and Andrej Spiridonov
Vilnius University, Lithuania

Taxon rank abundance distributions (RADs) reveal relative contributions of coexisting species or higher taxa in their local or regional scale communities. The shapes of RADs reflect patterns of dominance and also complexity of palaeocommunity structures. They could be used for gaining insights into mechanisms of assembly and interspecific dynamics in studied ecosystems. The temporal changes in RADs are usually revealed by fitting different empirical or theoretical models. However, sometimes many models produce a poor fit or fail to converge due to non-standard shapes of underlying distributions. We propose that RADs could be compared directly in temporal (stratigraphic) sequences using various distance metrics, and the revealed distances matrices could be converted to the recurrence plots which reveal temporal structures of similarity between samples. By applying this approach to a range of stratigraphic series of Silurian palaeocommunities we revealed a high potential for this tool to find previously undetected significant state shifts in long-term palaeocommunity dynamics.

Widespread palaeobiogeographical signals of the Silurian encrinurid trilobites of Japan

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[3]*Keele University, UK*
[4]*Nagoya University Museum, Japan*
[5]*Kumamoto University, Japan*

Encrinurid trilobites are geographically widespread in the Silurian strata of Japan, occurring in all three of its lower Palaeozoic terranes. Previously, revision of other Japanese trilobite groups has extended the palaeobiogeographical ranges of several taxa but has not signalled a consistent palaeogeographical affinity. Here we present a revision of all previously described encrinurids from Japan (~10 species). These show strong biogeographical links between all three Japanese terranes, as well as with the Australian segment of East Gondwana, Indochina, and the North China palaeo-plate, as well as weaker biogeographical links with the South China palaeo-plate, Sibumasu, Laurentia and possibly Baltica. These biogeographical signatures partly overlap those of Illaenid and Scutelluid trilobites, but more broadly represent a pan-tropical signal, whereby climate was a significant control on trilobite distribution.

Ultrastructure and *in situ* chemical characterization of intracellular granules of embryo-like fossils from the early Ediacaran Weng'an biota

*Weichen Sun[1,2], Zongjun Yin[1], Pengju Liu[3], Philip C. J. Donoghue[4], Jinhua Li[5] and Maoyan Zhu[1]

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[4]*University of Bristol, UK*
[5]*Innovation Academy for Earth Science, China*

Embryo-like fossils from the early Ediacaran Weng'an biota provide an exceptional window into the period of Earth history in which molecular clocks estimate when the fundamental animal lineages to have diverged. However, their diversity and biological affinities have proven difficult to constrain due to the simple geometry of their multicellular fossil organisms. Subcellular structures preserved in these embryo-like fossils might help to understand their cytology, biology and diversity, but the potential of these structures has not been fully realized because of an absence of microscale physical and chemical investigations that we have now remedied. Three types of subcellular structure occur: small and spheroidal granules in embryoids with equal cell division pattern; large, spheroidal or polygonal granules in embryoids exhibiting unequal and asynchronous cell division; and small membrane-bounded spheroidal granules. These three types may be rationalized to a single taphonomic pathway of preferential mineralization of the cell cytoplasm, preserving an external mould of subcellular granules. The distinction between these subcellular structures together with different cell division patterns reveal a cryptic diversity of the Weng'an embryo-like fossils which have been attributed into the morphological *Megasphaera*.

Timing, tempo, and mode in pongine evolution

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University of Bristol, UK

Though pongines first occurred during the Middle Miocene, the exact timing of their origin is unknown. This is because fossils spanning the transition of early apes to pongines have not yet been discovered. When qualitative methods are insufficient for inferring the origin of clades, quantitative methods must also be applied, such as computational macroevolutionary analysis (CMA). Previously, CMA could not be performed on pongines due to phylogenetic uncertainties. However, recent studies have resolved these issues, thus creating a robust pongine phylogeny. As such, our study represents the first application of CMA to pongines and early hominids. Alongside a time-calibrated version of the pongine phylogeny resolved to species-level, we present evolutionary rate estimations for each pongine taxon. These were calculated using first divergence dates and tooth dimensions (mesiodistal and buccolingual lengths) of taxa, gathered from the literature. Combining the results of our analysis with climate data, we suggest that the ancestor to Ponginae entered South Asia before 13 Ma, adaptively radiating soon after. We also find that pongines tend towards slow evolution and are generally sensitive to climate change. The topological accuracy of our phylogeny is corroborated by the presence of three divergence periods, each coinciding with climate change events.

Locating the BACE of the Cambrian: global correlation of the Ediacaran–Cambrian boundary

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The emergence and diversification of animals during the Cambrian is one of the most significant evolutionary events in Earth's history. However, the sequence of events leading to the origin of 'modern' ecosystems and the exact temporal relationship between Ediacaran and Cambrian faunas are uncertain, as identification of the Ediacaran–Cambrian boundary and global correlation through this interval remains problematic. The base of the Cambrian has been the source of constant conjecture due to the drawbacks of *Treptichnus pedum* and the lack of secondary markers at the GSSP. Because of this we suggest that the GSSP be redefined elsewhere, in a new section that contains secondary markers that permit global correlation. We propose the nadir of the BAsal Cambrian carbon isotope Excursion (BACE) as the favoured candidate to define the base of the Cambrian. It is essential however, that the BACE be complemented with secondary markers, such as the protoconodont *Protohertzina* and *Treptichnus pedum*. These taxa provide essential biostratigraphic control on the BACE and increase potential for effective global correlation. We also recommend that an Auxiliary boundary Stratotype Section and Point (ASSP) be simultaneously established in order to incorporate additional markers that will aid global correlation of the Ediacaran–Cambrian boundary.

posters

3D reconstructions reveal the leaf arrangement of Rhynie chert lycopsid *Asteroxylon mackiei*, one of the earliest examples of leaves in land plants

Holly-Anne Turner and Alexander J. Hetherington

University of Edinburgh, UK

The leaves of extant plants are produced in the shoot apical meristem in a regular pattern known as phyllotaxis. When phyllotaxis first evolved in plants and whether the earliest leaves developed in a similar arrangement to any living species is currently unknown. Here we investigate the phyllotaxis of the lycopsid *Asteroxylon mackiei* from the early Devonian Rhynie chert, one of the first species of land plant to possess leaves. We assessed *A. mackiei* leaf traits with a novel approach: using serial cellulose acetate peels made from Rhynie chert blocks and SPIERS software, to create the first digital reconstructions of leaf-bearing axes. These to-scale 3D models of fossil stems allowed for the measurement of quantitative phyllotactic traits including leaf shape, density on the stem and angle of divergence. The relationship between ontogeny and phyllotaxis was investigated by reconstructing mature stems, meristems and fertile regions. This analysis represents the earliest detailed investigation of phyllotaxis in the fossil record and can be used to make inferences about the evolution of phyllotaxis in land plants.

Morphometric analysis of Skiagia-plexus acritarchs: towards a meaningful evaluation of phenotypic plasticity

*Elise Wallet, Sebastian Willman and Ben J. Slater
Uppsala University, Sweden

The Cambrian evolutionary radiations are marked by spectacular biotic turnovers and the establishment of increasingly tiered food chains. At their base are primary producers, which in the Cambrian fossil record are chiefly represented by an informal category of *incertae sedis* called 'acritarchs'. The form-taxonomic subdivisions of acritarchs have been intensively used in biostratigraphy, but also in large-scale studies of phytoplankton diversity. However, both prospects are challenged by cases of taxonomic inconsistencies and over-splitting arising from the significant phenotypic plasticity evident in these microfossils. Here we apply a multivariate approach to investigate the morphological variation among the biostratigraphically significant acritarch genus *Skiagia*. Using an assemblage sourced from the Buen Formation (Cambrian Series 2, Stage 3–4) of North Greenland, our analysis showed that the current specific-level classification of *Skiagia* discretizes a continuous spectrum of morphologies, likely encompassing a mixture of various ontogenetic stages and ecophenotypes. These findings shed light on important taxonomic and biostratigraphic hurdles, and question the reliability of currently used measures of ancient phytoplankton diversity. This study demonstrates the value of using morphometric tools to explore acritarch phenotypic plasticity and its potential ontogenetic and palaeoecological drivers in Cambrian ecosystems.

An exploration of soft-tissue pyritization through experimental decay and computed tomography

*Madeleine Waskom, Sarah R. Losso and Javier Ortega-Hernández
Harvard University, USA

Pyritization represents one of the most common modes of exceptional preservation in the fossil record and has the potential to capture highly detailed morphological information of both animal and plant macrofossils. The preservation of delicate morphological detail in pyritized Palaeozoic animal macrofossils suggests that this process likely took place during early diagenesis before the loss of information by extensive decay. Despite its palaeobiological significance and a working understanding of the pyritization process, there is much that remains unresolved. Although the fossilization of soft-tissues indicates that pyritization must happen rapidly, pyritization is microbially-mediated and mineralization is typically a longer process. Experimental taphonomy can be employed to better understand the complex dynamics between the short- and long-term diagenetic process and establish a timeline for the formation of pyritized remains in the fossil record. By optimizing experimental conditions through biogeochemical methods, we followed pyritization in *Triops* using organic-poor sediment with sulfur-reducing bacteria, which recreated realistic conditions. We employed micro-computed tomography to track differences in density in the experimental vials where we could observe the precipitation of minerals and density decrease in decaying specimens providing a non-invasive and non-destructive method to investigate the timeline of pyritization and fossil formation.

Microfossils from the ~850-million-year-old Veteranen Group of Svalbard: insights into the nascent eukaryotic world

*George O. Wedlake[1], Sanaa Mughal[1], Timothy M. Gibson[2], Alexie E. G. Millikin[2], Justin V. Strauss[3], Alan D. Rooney[2], Karsten Piepjohn[4], Nicholas J. Tosca[5] and Ross P. Anderson[1]

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[5]*University of Cambridge, UK*

The emergence and diversification of complex eukaryotes marks a pivotal turning point in life's history on Earth. Molecular clocks predict the emergence of major eukaryotic clades (*e.g.* green algae) by ~1,000 Ma. However, it is difficult to test these hypotheses due to the rarity of early eukaryote fossils with sufficient morphological characters to be allied to modern groups. Here we report new early Neoproterozoic microfossils from mud- and siltstones of the ~850 Ma Veteranen Group of Svalbard. The Veteranen Group has remarkable potential for new phylogenetically informative fossil discoveries. The succession is ~4.5km thick and records prolonged deposition in marginal marine environments that may have been relatively nutrient-rich. Preliminary data from samples collected at Faksevågen (Spitsbergen) and Nordvika (Nordaustlandet) indicate a microfossil community with modest diversity. This contrasts with younger deposits from higher in the sedimentary succession, like the Svanbergfjellet Formation, which are among the most diverse Neoproterozoic assemblages worldwide. However, preservation quality is high in the Veteranen Group suggesting that the difference in diversity may reflect ecological differences between Veteranen and Svanbergfjellet environments. This study highlights the potential for Veteranen strata to yield major new fossil discoveries.

posters

The first look at cranial modularity and integration in Anomodontia

*Shane Wheatley[1], Marcello Ruta[1] and Christian F. Kammerer[2]

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Synapsida – the clade that includes mammals and their nearest extinct relatives – evolved into an astounding array of groups throughout the Permian and Triassic Periods and occupied a wide variety of niches. Despite an extensive literature on morphological integration and modularity in the skulls of crown mammals, the skulls of non-mammalian synapsids have not been subjected to comparable investigation. Here we present a 2D morphometric analysis of the skull of Anomodontia, one of the most speciose and most successful radiations of non-mammalian synapsids, and test hypotheses of cranial modularity and integration across the group. Using 23 landmarks captured on the lateral aspect of the skulls of 141 specimens representing 101 species over four models, we show that their skulls are highly integrated and modular with the presence of three separate modules, both modularity and integration remain consistent among most models. The highly integrated nature of Anomodont skulls is clearly key to the evolutionary history of Anomodonts and could be key to their success as a clade; this is also the first example of modularity within Anomodontia. This has exciting implications for the shape evolution of Synapsids and the need for further study.

Planetary-scale change to the biosphere signalled by global species translocations can be used to identify the Anthropocene

Mark Williams[1], Reinhold Leinfelder[2], Anthony D. Barnosky[3], Martin J. Head[4], Francine McCarthy[4], Alejandro Cearreta[5], Kristine L. DeLong[6], Stephen Himson[1], Rachael Holmes[1], Jens Zinke[1], Colin Waters[1], Jan Zalasiewicz[1] and Simon Turner[7]

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[7]*University College London, UK*

We examine three distinctive biostratigraphical signatures of humans associated with hunting and gathering, landscape domestication, and globalization. All three signatures have significant biostratigraphical records of regional importance that can sometimes be correlated inter-regionally and help us to understand the developing pattern of human expansion and appropriation of resources, but none has individual first or last appearances that provide a globally synchronous marker. All three signatures overlap stratigraphically, in that they are part of a continuum of change, with complex regional patterns, rather than time-limited events. However, in contrast to earlier palaeontological signals caused by humans, we find that late nineteenth and twentieth century records of species translocations can be used to build an interconnected web of palaeontological correlation with decadal or sub-decadal precision that dovetails with other stratigraphic markers of the mid-twentieth century onset of the Anthropocene. This palaeontological web is also a proxy of accelerating species extinction and of a state shift in the biosphere in the twentieth century.

Clumped isotope analysis reveals ammonite palaeoecology and latest Cretaceous climate variability in the US Gulf Coastal Plain

James D. Witts[1], Corinne E. Myers[2], Sierra V. Petersen[3], Jonathan Hoffmann[3], Jone Naujokaityte[2], Remy Rovelli[2], Matthew P. Garb[4], George Phillips[5] and Neil H. Landman[6]

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Geochemical records from well-preserved shell carbonates are used to reconstruct the palaeoecology and habitat of ammonoid cephalopods (ammonites) and the evolution of ancient marine ecosystems and climate. Carbonate clumped isotope ($\Delta 47$) analysis is a promising tool which does not rely on assumptions of ancient seawater composition that hamper 'traditional' stable isotope studies. We present a multi-taxon dataset from the Maastrichtian Owl Creek Formation, Tippah County, Mississippi. This site contains an exceptionally preserved molluscan fauna constrained by macro- and microfossil biostratigraphy to the final ~300 kyr of the Cretaceous. Fossils of three ammonite genera,

infaunal bivalves and rare nautilids were systematically collected and sampled throughout a 9 m-thick section. Preservation was assessed using the SEM preservation index (PI). Clumped isotope palaeotemperatures and $\delta^{18}O_{seawater}$ values reveal overlap in values and close agreement between all taxa. Ammonites and benthic bivalves thus secreted their shells in isotopic equilibrium with seawater of the same composition and probably lived in similar environments. We see no evidence that ammonites exhibit 'vital effects' with respect to their clumped isotope composition. These data provide new constraints on the palaeoecology of extinct cephalopod taxa and marine climate evolution in the Gulf Coastal Plain immediately prior to the end-Cretaceous mass extinction.

The unbearable uncertainty of panarthropod relationships

*Ruolin Wu, Philip C. J. Donoghue and Davide Pisani
University of Bristol, UK

Panarthropoda, the clade comprised of the phyla Onychophora, Tardigrada and Arthropoda, encompasses the largest majority of animal biodiversity. The relationships among the phyla remain contested and resolution is key to understanding the evolutionary assembly of the arthropod bodyplan on which so much of animal diversity is based. Molecular phylogenetic analyses generally support monophyly of Onychophora and Arthropoda to the exclusion of Tardigrada (the Lobopodia hypothesis) while analyses of morphological data have been interpreted to support monophyly of Tardigrada and Arthropoda to the exclusion of Onychophora (the Tactopoda hypothesis). Lobopodia is strongly supported by molecular data while support for Tactopoda is unclear. We investigated whether morphological data used to support Tactopoda can discriminate statistically from competing hypotheses within a diversity of phylogenetic inference methods. We found that morphological data cannot discriminate statistically between any of the competing hypotheses of panarthropod relationships, irrespective of the criterion used to analyse the data. Given the strong genomic evidence for the competing Lobopodian hypothesis and given that putative morphological evidence exists also for this group, we conclude that Tactopoda should be rejected in favour of the Lobopodia hypothesis.

The Palaeontological Association

Annual General Meeting

14.45

Sunday

19th December

Papers

AGM

Annual General Meeting 2021

Notification of the 2021 Annual Meeting, AGM and Annual Address

The 2021 Annual Meeting of the Palaeontological Association will be held at the University of Manchester, UK, on 18–20 December, organized by Dr Rob Sansom and colleagues. Council will inform the membership via e-mail regarding details of the AGM in due course.

AGENDA

1. Apologies for absence
2. Minutes of the 64th AGM
3. Trustees Annual Report for 2020
4. Accounts and Balance Sheet for 2020 and reappointment of financial examiner
5. Election of Council and vote of thanks to retiring members
6. Report on Council Awards
7. Annual address

DRAFT AGM MINUTES 2020

Minutes of the Annual General Meeting held on Thursday 17th December 2020. This meeting was held virtually due to the coronavirus pandemic.

1. Apologies for absence. Dr Uwe Balthasar and Dr Liam Herringshaw.

2. Minutes. The minutes of the 2019 AGM were agreed a true record by unanimous virtual poll.

3. Trustees Annual Report for 2019. The report was agreed by unanimous virtual poll.

4. Accounts and Balance Sheet for 2019. The accounts were agreed by unanimous virtual poll. The proposal to reappoint M.R. Corfield of Corfield Accountancy Ltd as the Association's independent examiner was also agreed by unanimous virtual poll.

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: Prof. T.R.A. Vandenbroucke, Dr P. Winrow, Dr B.H. Lomax, Dr G.T. Lloyd, Dr T.J. Challands, Prof. M.E. McNamara, Dr U. Balthasar and Prof. R.C.M. Warnock.

5.2 The following members were elected to serve on Council: President: Dr P.J. Orr, Vice-Presidents: Dr F.L. Gill and Prof. R.J. Butler, Treasurer: Dr M. Sakamoto, Secretary: Dr C.T.S. Little; Chair of the Editorial Board: Prof. M.A. Purnell; Editor Trustees: Prof. N.J. Butterfield and Dr S.C.R. Maidment, Newsletter Editor: Dr E. Jarochowska, Book Review Editor: Dr T. Clements, Publicity Officer: Dr S.J. Lydon, Education Officer: Ms E. Wallace, Outreach Officer: Ms Z.E. Hughes, Internet Officer: Dr R.J. Garwood, Meetings Coordinator: Dr U. Balthasar, Diversity Officer: Dr F. Saleh, Ordinary Members:, Dr T.H.P. Harvey, Dr L. Hide, Dr S. Giles and Mr R. Theodore.

5.3 Dr R. Sansom and colleagues will organize the Annual Meeting in 2021 at the University of Manchester, UK.

6. Resolution to amend the Constitution. A resolution to update the Constitution was agreed by a majority of the membership in a virtual poll (Yes 374; No: 7; Abstain: 34). The updates include: changes to the electronic voting procedure; replacing 'Editor-in-Chief' with 'Chair of the Editorial Board' to reflect operational changes to our publications team; and introducing gender-neutral terms throughout the document where appropriate.

7. Association Awards. The following awards were announced:

7.1 The Lapworth Medal was awarded to Dr A.B. Smith (Natural History Museum, London, UK).

7.2 The President's Medal was awarded to Prof. X. Xing (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China).

7.3 The Hodson Award was presented to Dr E.E. Saupe (University of Oxford, UK).

7.4 The Mary Anning Award was presented to Mrs M. Wood (South Queensferry, UK).

7.5 The Gertrude Elles Award for public engagement was presented to Dr J. Murray for The History of Life project (NUI Galway, Ireland).

7.6 Research Grants were awarded to: Dr N. Davies (University of Cambridge, UK), *Controls on bioturbation and ichnological signatures in Cambrian shelf facies of SW Baltica*; Dr K. Hickman-Lewis (Università di Bologna, Italy), *Microbial silicification in Yellowstone hot springs: a tool for interpreting the Precambrian fossil record*; Dr E. Panciroli (University of Oxford, UK), *Biomechanics and the Competitive Replacement of Tritylodontids*.

7.7 Under the Small Grants Scheme, the following awards were announced: the Whittington Award to Mr J. Hennekam (University of York, UK), *Morphological divergence of the island ruminant* Myotragus balearicus; Stan Wood awards to Dr L. Liebe Delsett (University of Oslo, Norway), *First plesiosaur from the early Cretaceous of Arctic Canada and the biogeography of marine reptiles during the J–C transition* and Dr H. Zhang (University of Bristol), *Laetoli: unchartered crossroad in elephant evolution?*; and Sylvester-Bradley awards to Ms S. Losso (Harvard University, USA), *Comparative isotopic analysis of exceptional fossils preserved through calcite from two Paleozoic Konservat-Lagerstätten*, Ms J. Órfão (University of Aveiro, Portugal *On captorhinids: is skull sculpturing a good criterion to distinguish taxa?*, and Ms V. Rossi (University College Cork, Ireland), *Taphonomy of the plumage of a Late Pleistocene Eurasian griffon vulture preserved in a pyroclastic flow from Central Italy*.

7.8 Undergraduate Research Bursaries were awarded to: Ms S. McCormack, University of Liverpool, UK, supervised by Dr K.T. Bates, *Variation in human foot bone shape: the key to understanding the evolution of hominin bipedalism* Ms M. Harbich, University of Edinburgh, UK, supervised by Dr T.J. Challands, *Environmental changes during the emergence of the modern vertebrate fauna*; Ms P. Spruce, University of Leeds, UK, supervised by Dr A.M. Dunhill, *Deep-fried calamari? The effect of Early Triassic extreme global warming on cephalopod biogeography*; Ms B. Pittard, University College London, UK, supervised by Dr P.M. Mannion, *Systematic and biogeographic affinities of the early titanosaur sauropod dinosaurs from the Early Cretaceous of the UK*; Mr T. Green, University of Leicester, UK, supervised by Prof. M.A. Purnell, *Treeshrews as dietary analogues for Paleocene mammals: testing hypotheses of diet using microwear texture analysis*; and Mr J, Rawson, University

of Bristol, UK, supervised by Prof. E.J. Rayfield, *Testing Williston's Rule: a network analysis of skull evolution across the water to land transition*.

7.9 Engagement Grants were awarded to Ms S. Chakravorti for *Museum on Wheels: when you cannot come to the museum, the museum comes to you*; Mx F. Keeley for *EvoArcade*; and Dr C. Martínez-Pérez for *The hospital's fossils: an educational resource for paediatric patients*.

7.10 The 2020 Best Paper Awards were presented to Prof. R.D.K. Thomas and colleagues for their paper '*Pelagiella exigua*, an early Cambrian stem gastropod with chaetae: lophotrochozoan heritage and conchiferan novelty' (*Palaeontology*), and to Dr J.R. Thompson and colleagues for 'Phylogenetic analysis of the Archaeocidaridae and Palaeozoic Miocidaridae (Echinodermata, Echinoidea) and the origin of crown group echinoids' (*Papers in Palaeontology*).

7.11 President's Prizes were awarded to Ms A. Cribb, Ms S. Gutarra Diaz and Mr A. Xafis.

7.12 Council Flash Talk Prizes were awarded to Dr E.M. Dunne, Mr E. Furness, Dr C. Blanco Moreno and Ms J. Reeves.

7.13 Council Poster Prizes were awarded to Ms B.J. Allen, Ms S. Gutarra Diaz, Ms P. Spruce and Ms L. Austin Sydes.

8. Annual Address. A talk entitled 'Tales from the Cambrian Explosion' was given by Prof. Rachel Wood (University of Edinburgh, UK).

Trustees Annual Report 2020

The Trustees present their report with the financial statements of the charity for the year ended 31 December 2020. 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 1 January 2015).

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 General statement about the COVID-19 pandemic: The coronavirus pandemic had a significant impact on Association activities in 2020, particularly on in-person meetings, which from March onwards either had to move online (*e.g.* Council meetings, Annual Meeting, Progressive Palaeontology, Lyme Regis Fossil Festival) or were postponed (Yorkshire Fossil Festival and many external meetings and workshops).

1.3 Grants-in-aid for meetings and workshops: The Association provided funds to support the following meetings and workshops: 18th International Nannoplankton Association Meeting (INA 18) (Dr C.T. Bolton, CEREGE, Aix-en-Provence, France); Developing a taxonomic framework for the Ediacaran Macrobiota (Dr F.S. Dunn, University of Oxford, UK) and 9th International Meeting on Taphonomy and Fossilization (TAPHOS) and 6th ICAZ Taphonomy Working Group Meeting (ICAZ-TWG) (Dr Y. Fernández-Jalvo, Museo Nacional de Ciencias Naturales, Madrid, Spain).

1.4 Public meetings: Two public online meetings were held in 2020, and the Association extends its thanks to the organizers of these meetings.

64th Annual Meeting. The Association's Annual Meeting is its flagship meeting and this year was an online event held 16th–18th December, hosted by the Oxford University Museum of Natural History. The meeting was organized by Dr J.J. Matthews and colleagues, and included a symposium entitled 'New Ideas on Old Fossils: A Symposium of Early Career Palaeontologists from Around the World'. There were 500 registrants. The Annual Address was given by Professor Rachel Wood (University of Edinburgh, UK), entitled 'Tales from the Cambrian Explosion'. President's Prizes for best 15-minute oral presentations by early-career researchers were awarded to Ms A. Cribb (University of Southern California, USA), Ms S. Gutarra Diaz (University of Bristol, UK) and Mr A. Xafis (University of Vienna, Austria). Council Flash Talk Prizes for best five-minute presentations by early-career researchers were awarded to Dr E.M. Dunne (University of Birmingham, UK), Mr E. Furness (Imperial College London, UK), Ms C. Blanco Moreno (Universidad Autónoma de Madrid, Spain) and Ms J. Reeves (University of Manchester, UK). Council Poster Prizes for best poster presentations by early-career researchers were presented to Ms B.J. Allen (University of Leeds, UK), Ms S. Gutarra Diaz (University of Bristol, UK), Ms P. Spruce (University of Leeds, UK), and Ms L. Austin Sydes (University of Manchester, UK).

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 2020 meeting was organized by Ms B.J. Allen and a team of other students at the University of Leeds, UK, and held online 11th – 13th June, with over 140 virtual delegates.

1.5 Publications: The journals *Palaeontology* and *Papers in Palaeontology* are produced by Wiley. During 2020, the following volumes were published: *Palaeontology* volume 63, comprising six issues; and *Papers in Palaeontology* volume 6, comprising four issues. As announced at the AGM in 2019, paper copies ceased to be printed following these volumes and publishing will move to online only. Council thanks Mr N. Stroud for assistance with the typesetting and production of the *Palaeontology Newsletter*.

1.6 Research Grants: A total of 22 valid applications for Palaeontological Association Research Grants were received. Three were recommended for funding in 2020, totalling £16,227, and were awarded to: Dr N. Davies (University of Cambridge, UK), 'Controls on bioturbation and ichnological signatures in Cambrian shelf facies of SW Baltica'; Dr K. Hickman-Lewis (Università di Bologna, Italy), 'Microbial silicification in Yellowstone hot springs: a tool for interpreting the Precambrian fossil record'; and Dr E. Panciroli (University of Oxford, UK) 'Biomechanics and the Competitive Replacement of Tritylodontids'.

1.7 Small Grants Scheme: The scheme received 15 valid applications. Six were recommended for funding in 2020, totalling £8,281. Small grants were awarded as follows: Mr J. Hennekam (University

of York, UK) received the Whittington Award; Dr L. Liebe Delsett (University of Oslo, Norway) and Dr H. Zhang (University of Bristol, UK) received Stan Wood Awards; Ms S. Losso (Harvard University, USA), Ms J. Órfão (University of Aveiro, Portugal) and Ms V. Rossi (University College Cork, Ireland) received Sylvester-Bradley Awards.

1.8 Undergraduate Research Bursary Scheme: The scheme attracted eight applications, of which six were recommended for funding in 2020, totalling £14,649. The awardees were as follows: Ms S. McCormack, University of Liverpool, UK, supervised by Dr K.T. Bates; Ms M. Harbich, University of Edinburgh, UK, supervised by Dr T.J. Challands; Ms P. Spruce, University of Leeds, UK, supervised by Dr A.M. Dunhill; Ms B. Pittard, University College London, UK, supervised by Dr P.D. Mannion; Mr T. Green, University of Leicester, UK, supervised by Prof. M.A. Purnell; and Mr J. Rawson, University of Bristol, UK, supervised by Prof. E.J. Rayfield.

1.9 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. Face-to-face engagement activities were prevented during 2020 by the coronavirus pandemic. The Lyme Regis Fossil Festival took place as an online event. The Public Engagement Group (PEG), consisting of the Outreach Officer, Education Officer, Publicity Officer, Executive Officer, President and Treasurer, decided on expenditure of the group budget (£19,000 for 2020), supporting recurring festival activities and Engagement Grants.

1.10 Engagement Grants: The scheme received a total of six applications in 2020, of which three were recommended for funding, totalling £16,000. These were awarded to Ms S. Chakravorti, 'Museum on Wheels: when you cannot come to the museum, the museum comes to you'; Mx F. Keely, 'EvoArcade'; and Dr C. Martínez-Pérez, 'The hospital's fossils: an educational resource for paediatric patients'.

1.11 Diversity Group: The Diversity Group (DG) continues to implement the recommendations of the Diversity Study completed by Parigen Ltd in 2018, led by the Diversity Officer. In 2020, along with the remaining members of Council, the DG revisited the Undergraduate Research Bursaries, aiming to increase the diversity of applicants. Supervisors and students applying for the first time are now eligible for one-year free Association membership. Priority is given to students from under-represented groups based on self-declared protected characteristics, and the requirement for transcripts or grades is removed. The Progressive Palaeontology meeting and the Annual Meeting were both held virtually in 2020. Progressive Palaeontology talks were pre-recorded and all presentations were available for the full duration of the conference via the Association website, increasing accessibility. Reduced registration fees, fee waivers and the removal of the need for travel and accommodation likely drove the increase in accessibility of the Annual Meeting (50.7% were not UK-based and several attendees were from countries that would not usually be represented). LGBTQ+ meet-ups were facilitated at both conferences and a symposium 'New Ideas on Old Fossils: A Symposium of Early Career Palaeontologists from Around the World' was held at the Annual Meeting, increasing visibility of researchers from regions not usually represented at Association conferences. The DG has continued to try and "internationalize" the *Palaeontology Newsletter* away from its UK-centric past. The regular columns 'Legends of Rock', 'Behind the Scenes at the Museum' and 'A Palaeontologist Abroad' covered more than 15 countries in 2020. The 'Spotlight on Diversity' section covered the lived experiences of palaeontologists who are trans, diabetic, from under-

represented regions and those who speak minority languages. Following the appointment of Dr S.C.R. Maidment in 2019, Dr E. Kustatscher has now joined the Editorial Board of the Association's journals, shifting the gender balance of the Board to 50:50. The DG requested that the handling editors seek input from at least one woman reviewer for each article sent to review. In 2017 the Association mentoring scheme was introduced to assist palaeontologists at the start of their academic careers and focused on those transitioning from postdoctoral positions to permanent jobs. In 2020 the scheme has been expanded to accommodate those transitioning from late-stage PhD to postdoctoral positions. In 2020 members of the DG led work to produce the Association's statement in support of Black colleagues, available on the Association website and published in *Newsletter* 105, and were grateful for input from external sources. The statement acknowledges the additional barriers and challenges faced by Black palaeontologists at work and in their daily lives, resulting from systemic racism.

1.12 Palaeontological Association Exceptional Lecturer scheme: Dr A.J. Hetherington was selected in a competitive process to become the Palaeontological Association Exceptional Lecturer for 2020/2021; however, due to travel restrictions, only two of the six scheduled lectures of the Innovations in Palaeontology Lecture Series were delivered within the usual timeframe (at the Geological Society of London and the University of Plymouth, UK). Both of these were delivered virtually and a recording of the latter is available on the Palaeontological Association's YouTube channel. The other four lectures by Dr Hetherington are planned during the remainder of 2021. Dr E.G. Mitchell from the University of Cambridge, UK was selected in a competitive process to be the Palaeontological Association Exceptional Lecturer for the academic year 2021–2022. To date, five institutions have registered their interest to host Dr Mitchell.

1.13 Online activities: 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]). New hosting arrangements have either been signed (Carnets Geol), or planned for 2021 (Journal of Palaeontological Techniques). The listserver 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, whilst e-mail, file hosting and internal e-mail lists have been switched to GSuite through its non-profit provision. At the end of 2020 members of the Association Facebook group numbered 2,241 and the newer Facebook page had 614 followers. The Association Twitter account had 7,389 followers.

1.14 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 Dr Andrew B. Smith (Natural History Museum, London, UK). 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 Professor Xu Xing (Institute of Vertebrate Paleontology and Paleoanthropology, China). 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 Erin E. Saupe (University of Oxford, UK). The Mary Anning

Award, for an outstanding contribution by an amateur palaeontologist, was made to Mrs Maggie Wood (South Queensferry, UK). The Gertrude Elles Award for high-quality, amateur or institutional, public engagement projects that promote palaeontology was awarded to Dr J. Murray for The History of Life project (NUI Galway, Ireland). The 2020 Best Paper Awards in *Palaeontology* and *Papers in Palaeontology* were given respectively to Prof. R.D.K. Thomas and colleagues for their paper entitled 'Pelagiella exigua, an early Cambrian stem gastropod with chaetae: lophotrochozoan heritage and conchiferan novelty', **63(4)**, 601–627; and Dr J.R. Thompson and colleagues for their paper 'Phylogenetic analysis of the Archaeocidaridae and Palaeozoic Miocidaridae (Echinodermata, Echinoidea) and the origin of crown group echinoids', **6(2)**, 217–249. Council also awards Undergraduate Prizes to outstanding students in university departments worldwide where Palaeontology is taught beyond Level 1; a total of 14 were awarded throughout the year.

1.15 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 2021 Progressive Palaeontology meeting will again take place online due to the continuing coronavirus pandemic, but the 65th Annual Meeting, to be hosted by The University of Manchester, UK in December 2021, is planned as an in-person meeting with some virtual access. In 2021 *Palaeontology* and *Papers in Palaeontology* will move to an online-only publication model. In 2021 the Association's Public Engagement Group will develop a five-year plan, to incorporate its wider public engagement work, as well as the focus on working with schools and young people. The Diversity Group will continue to implement the recommendations of the Diversity Study, removing barriers to participation and increasing access to palaeontology for under-represented groups. Upcoming surveys of the membership will aid with monitoring progress.

1.16 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 2020, the Association agreed to support a total of five palaeontological meetings, symposia or workshops worldwide (three held online hosted by UK institutions in 2020 and two in-person events in Spain and France postponed). Due to major meetings being held virtually in 2020, no applications for the Postgraduate Travel Fund were received in 2020. The Association's support enabled the worldwide dissemination of research to the benefit of the global palaeontological community.

2.2 Publications: During 2020, 292 papers were submitted to either *Palaeontology* or *Papers in Palaeontology*. Of these, 136 (47%) were considered to be within scope by the Editorial Board and 86 (29%) were subsequently accepted following peer review; a further 25 papers were still awaiting submission of a revised manuscript before a final decision could be made. A total of 96 papers were published online. The number of downloads of articles via Wiley Online Library was 41% higher in 2020 relative to 2019 for *Palaeontology* and 40% for *Papers in Palaeontology*. This represents a significant increase for both journals. The Association continues to support data archiving by sponsoring Dryad data records although we now also strongly encourage authors to use an appropriate subject-specific repository where appropriate (*e.g.* MorphoSource for image data and MorphoBank for phylogenetic data); 74% of all published papers had an associated data archive

in 2020, with the remainder including all relevant data and observations within the paper. The Association published one book in 2020, *Fossils of the Kimmeridge Clay Formation*, in two volumes, both edited by D.M. Martill and S. Etches.

2.3 Support for research: In 2020 the Association agreed to fund the research activities of 16 early-career researchers based in six countries (Ireland, Italy, Norway, Portugal, the UK and 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 2020 was the same as 2019. Compared to 2019, applications for Research Grants increased from 13 to 22, and thus the success rate decreased from 23% to 13%. The applications to the Small Grants Scheme decreased (from 22 to 15), and the success rate consequently increased from 32% to 47% (including one award that was declined). Applications to the Undergraduate Research Bursary Scheme decreased strongly in 2020 compared to 2019 (from 18 to 8) and the success rate increased to 75%.

2.4 Mentoring scheme for early career palaeontologists: In 2017 the Association established a mentoring scheme. Priority areas were identified and in the first instance the focus was on the transition from postdoctoral positions to permanent jobs. In 2020 the decision was taken to expand the scheme to late-stage PhD students and this change to the scheme was advertised in *Palaeontology Newsletter* 105. A total of 23 palaeontologists in permanent positions have offered to act as mentors and, so far, 12 early-career palaeontologists have taken part in the scheme. The Association mentoring scheme is via direct mentoring, via e-mail, video call or other forms of communication.

2.5 Outreach, education and public engagement: During 2020, the Association provided £3,000 to support the Lyme Regis Fossil Festival, an online event 24–25 October 2020. The event received 3,210 unique visitors, making 14,775 visits over the weekend and 18,709 separate page views. The average visit length was 31 minutes and six seconds (a remarkably long time in online engagement terms). The Education Officer delivered a talk and took part in a Q&A session. The online offering also showcased the 'The Palaeontological Association presents…' playlist of short, professionally-produced, YouTube videos featuring members of Council. In 2020, PEG awarded three Engagement Grants (see 1.9). The Association's Twitter and Facebook accounts continue to enable engagement with wider audiences, and rapid dissemination of news about research, events and palaeontology outside the academic world. The Association's YouTube channel (accessible at <**https://www.youtube.com/thepalaeontologicalassociation**>) hosts videos for a general audience as well as recordings of talks from the 2020 Annual Meeting and Progressive Palaeontology meeting.

3. FINANCIAL REVIEW

3.1 Reserves: As of 31st December 2020, the Association holds reserves of £858,207 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 £125,353 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 2021 totalled £983,560.

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 2020, was £315,657. Governance costs were £13,131. Total resources expended were £361,233. 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 organization (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 2020 totalled 1,206 (1,177 at end 2019). Of these, 593 were Ordinary Members, 194 Retired Members, 19 Honorary Members, 375 Student Members and 25 Institutional Members. There were 35 institutional subscribers to *Papers in Palaeontology*. Wiley also separately manages further institutional subscribers and arranges 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 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 19th December 2019 to serve as Trustees in 2020:

Prof. C. H. Wellman	President
Prof. T. R. A. Vandenbroucke	Vice President
Dr F. L. Gill	Vice President
Dr C.T.S. Little	Secretary
Dr P. Winrow	Treasurer
Dr B.H. Lomax	Chair of the Editorial Board
Prof. M. A. Purnell	Editor Trustee
Prof. N. J. Butterfield	Editor Trustee
Dr R. Garwood	Internet Officer
Dr G.T. Lloyd	Newsletter Editor
Dr T.J. Challands	Book Review Editor
Dr Z. E. Hughes	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 T. Clements	Ordinary Member
Dr S. Giles	Ordinary Member
Dr T.H.P. Harvey	Ordinary Member
Dr E.A. Hide	Ordinary Member

5.4 Professional services: The Association's Bankers are NatWest, 42 High Street, Sheffield, S1 2GE. The Association's Independent Examiner is Ms M.R. Corfield ACA ACMA, Corfield Accountancy Ltd., Myrick House, Hendomen, Montgomery, Powys, SY15 6EZ. The Association's investment portfolio is managed by Quilter Cheviot Investment Management, Senator House, 85 Queen Victoria Street, London, EC4V 4AB.

Approved by order of the Board of Trustees on 23rd June 2021.

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

Independent examiner's report to the Trustees of The Palaeontological Association ('the Charity')
I report to the charity Trustees on my examination of the accounts of the above charity for the year ended 31 December 2020 set out on pages 14 to 22.

This report is made solely to the Charity's Trustees, as a body, in accordance with Section 145 of the Charities Act 2011. My work has been undertaken so that I might state to the Charity's Trustees those matters I am required to state to them in an Independent Examiner's report and for no other purpose. To the fullest extent permitted by law, I do not accept or assume responsibility to anyone other than the Charity and the Charity's Trustees as a body, for my work or for this report.

Responsibilities and basis of report
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"). You are satisfied that the accounts of the Charity are not required by charity law to be audited and have chosen instead to have an independent examination.

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

Independent examiner's statement
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 matters have come to my attention in connection with the examination giving me cause to believe:

1. accounting records were not kept in respect of the Charity as required by section 130 of the 2011 Act; or
2. the accounts do not accord with those records; or
3. the accounts have not been prepared in accordance with the methods and principles of the Statement of Recommended practice for accounting and reporting by charities (applicable to charities preparing their accounts in accordance with the Financial Reporting Standard applicable in the UK and Republic of Ireland (FRS102)) and the 2011 Act.

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: 23rd June 2021

THE PALAEONTOLOGICAL ASSOCIATION

Statement of Financial Activities for the Year Ended 31 December 2020

	Notes	Unrestricted funds £	Designated funds £	31.12.20 Total funds £	31.12.19 Total funds £
INCOME AND ENDOWMENTS FROM					
Donations and legacies		55,214	1,866	57,080	61,571
Charitable activities					
Public Meetings		10,730	—	10,730	53,301
Publications		325,339	—	325,339	320,107
Investment income	**2**	10,640	1,574	12,214	14,743
Total		401,923	3,440	405,363	449,722
EXPENDITURE ON					
Raising funds	**3**	32,445	—	32,445	36,459
Charitable activities					
Public Meetings		17,597	—	17,597	73,364
Grants & Awards		22,100	8,516	30,616	65,494
Administration		48,052	—	48,052	51,479
Publications		219,392	—	219,392	239,820
Governance Costs		13,131	—	13,131	25,063
Total		352,717	8,516	361,233	491,679
Net gains on investments		25,466	—	25,466	94,878
NET INCOME/(EXPENDITURE)		74,672	(5,076)	69,596	52,921
Transfers between funds		183	(183)	—	—
Net movement in funds		74,855	(5,259)	69,596	52,921
RECONCILIATION OF FUNDS					
Total funds brought forward		783,352	130,612	913,964	861,043
TOTAL FUNDS CARRIED FORWARD		858,207	125,353	983,560	913,964

The notes form part of these financial statements.

THE PALAEONTOLOGICAL ASSOCIATION

Balance Sheet
At 31 December 2020

	Notes	Unrestricted funds £	Designated funds £	31.12.20 Total funds £	31.12.19 Total funds £
FIXED ASSETS					
Investments	**6**	583,371	125,353	708,724	688,995
CURRENT ASSETS					
Debtors	**7**	190,350	—	190,350	175,564
Cash at bank		101,384	—	101,384	90,743
		291,734	—	291,734	266,307
CREDITORS					
Amounts falling due within one year	**8**	(16,898)	—	(16,898)	(41,338)
NET CURRENT ASSETS		274,836	—	274,836	224,969
TOTAL ASSETS LESS CURRENT LIABILITIES		858,207	125,353	983,560	913,964
NET ASSETS		858,207	125,353	983,560	913,964
FUNDS					
Unrestricted funds	**9**			983,560	913,964
TOTAL FUNDS				983,560	913,964

The notes form part of these financial statements.

The financial statements were approved by the Board of Trustees and authorised for issue on 23rd June 2021.

THE PALAEONTOLOGICAL ASSOCIATION

Notes to the Financial Statements for the Year Ended 31 December 2020

1. ACCOUNTING POLICIES

Basis of preparing the financial statements

The financial statements 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 Charities Act 2011.

The Palaeontological Association meets the definition of a public benefit entity under FRS102. Assets and liabilities are initially recognized at historical cost or transaction value unless otherwise stated in the relevant accounting policy.

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 PALAEONTOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2020

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) meeting.

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

	31.12.20 £	31.12.19 £
Deposit account interest	123	274
Investment Income	12,091	14,469
	12,214	14,743

3. RAISING FUNDS

	31.12.20 £	31.12.19 £
Voluntary Income Costs: Administration	30,578	32,759
Investment Management Costs: Stockbroker Fees	1,867	3,700
	32,445	**36,459**

4. TRUSTEES' REMUNERATION AND BENEFITS

There were no Trustees' remuneration or other benefits for the year ended 31 December 2020 nor for the year ended 31 December 2019.

Trustees' expenses

The total travelling expenses reimbursed to 20 Members of Council (2019:19) was £3,799 (2019: £12,308).

THE PALAEONTOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2020

5. STAFF COSTS

Analysis of Staff Costs and Remuneration

	£ 2020	£ 2019
Salaries	89,956	85,753
Social Security Costs	5,998	6,467
Pension Costs	8,996	8,575
Total	104,950	100,795

The average monthly number of employees during the year was as follows:

	2020	2019
Publications	1	1
Administration	1	1
	2	2

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

	31.12.20 £	31.12.19 £
Sundry Debtors	190,350	175,564

8. CREDITORS: AMOUNTS FALLING DUE WITHIN ONE YEAR

	31.12.20 £	31.12.19 £
Trade creditors	5,475	19,734
Subscriptions in advance	11,423	21,604
	16,898	41,338

THE PALAEONTOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2020

9. MOVEMENT IN FUNDS

	At 1.1.20 £	Net movement in funds £	Transfers between funds £	At 31.12.20
Unrestricted funds				
General fund	783,352	74,672	183	858,207
Sylvester-Bradley	17,608	(3,022)	—	14,586
Jones-Fenleigh	28,376	27	—	28,403
Hodson	295	—	(183)	112
Callomon	2,433	(1,111)	—	1,322
Whittington	15,823	159	—	15,982
Stan Wood	66,077	(1,129)	—	64,948
TOTAL FUNDS	913,964	69,596	—	983,560

Net movement in funds included in the above are as follows:

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
Unrestricted funds				
General fund	401,923	(352,717)	25,466	74,672
Sylvester-Bradley	600	(3,622)	—	(3,022)
Jones-Fenleigh	27	—	—	27
Callomon	344	(1,455)	—	(1,111)
Whittington	598	(439)	—	159
Stan Wood	1,871	(3,000)	—	(1,129)
TOTAL FUNDS	405,363	(361,233)	25,466	69,596

THE PALAEONTOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2020

9. MOVEMENT IN FUNDS — *continued*…

Comparatives for movement in funds:

	At 1.1.19 £	Net movement in funds £	At 31.12.19 £
Unrestricted Funds			
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	66,960	(883)	66,077
TOTAL FUNDS	861,043	52,921	913,964

Comparative net movement in funds included in the above are as follows:

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
Unrestricted funds				
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	2,154	(3,037)	—	(883)
TOTAL FUNDS	449,722	(491,679)	94,878	52,921

THE PALAEONTOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2020

9. MOVEMENT IN FUNDS — *continued*…

	At 1.1.19 £	Net movement in funds £	Transfers between funds £	At 31.12.20
Unrestricted funds				
General fund	728,871	129,153	183	858,207
Sylvester-Bradley	21,073	(6,487)	—	14,586
Jones-Fenleigh	27,503	900	—	28,403
Hodson	294	1	(183)	112
Callomon	3,368	(2,046)	—	1,322
Whittington	12,974	3,008	—	15,982
Stan Wood	66,960	(2,012)	—	64,948
TOTAL FUNDS	861,043	122,517	—	983,560

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 £
Unrestricted funds				
General fund	843,067	(834,258)	120,344	129,153
Sylvester-Bradley	1,436	(7,923)	—	(6,487)
Jones-Fenleigh	900	—	—	900
Hodson	1	—	—	1
Callomon	709	(2,755)	—	(2,046)
Whittington	4,947	(1,939)	—	3,008
Stan Wood	4,025	(6,037)	—	(2,012)
TOTAL FUNDS	855,085	(852,912)	120,344	122,517

Transfers between funds

The transfer of £183 from the designated Hodson fund to General funds is to re-allocate a cost originally attributed to the unrestricted general fund in 2019.

THE PALAEONTOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2020

10. RELATED PARTY DISCLOSURES

There were no related party transactions for the year ended 31 December 2020.

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 2020	31st December 2019
	£	£
Realized Gain/(Loss)	(26,637)	2,803
Unrealized Gain/(Loss)	52,103	92,075
Total per Statement of Financial Activities	25,466	94,878

12. INVESTMENT PORTFOLIO 2020

See pages 21–22.

Detailed Statement of Financial Activities for the Year Ended 31 December 2020

	31.12.20 Unrestricted funds £	31.12.19 Total funds £
INCOME AND ENDOWMENTS		
Donations and legacies		
Donations	4,636	8,140
Subscriptions	52,444	53,431
	57,080	61,571
Investment income		
Deposit account interest	123	274
Investment Income	12,091	14,469
	12,214	14,743
Charitable activities		
Scientific Journals	319,314	309,605
Special Papers	298	573
Newsletter	—	80
Field Guides	5,346	9,129
Distribution	381	720
Scientific Meetings	10,730	53,301
	336,069	373,408
Total incoming resources	**405,363**	**449,722**
EXPENDITURE		
Raising donations and legacies		
Administration	30,578	32,759
Investment management costs		
Stockbroker Fees	1,867	3,700
Charitable activities		
Scientific Journals	61,721	67,050
Field Guides	11,390	25,622
Newsletters	19,540	18,990
Marketing	600	297
Publication Costs	85,769	82,544
Editorial Costs	40,372	45,317
Public Meetings & Costs	17,597	73,364
Grants & Awards	21,309	37,534
Research Grants	9,307	27,960
Administration	48,052	51,479
Consultancy	—	2,800
	315,657	432,957
Support costs		
Governance costs		
Trustees' expenses	3,799	12,308
Accountancy and legal fees	595	595
Administration	8,737	9,360
	13,131	22,263
Total resources expended	**361,233**	**491,679**
Net income before gains and losses	**44,130**	**(41,957)**
Realized recognized gains and losses		
Realized gains/(losses) on fixed asset investments	25,466	94,878
Net income	**69,596**	**52,921**

This page does not form part of the statutory financial statements.

Palaeontological Association year ended 31st December 2020.

Nominal	Holding	Cost (bought pre 2020) £	Value end 2019 £
£18,000	UK 4.75% Stock 07/03/20 GBP 100	18,145.87	18,403.00
49,685.81	COIF Charities Fixed Interest Fund	65,807.52	68,342.83
9,275	Allianz Global Investors Gmbh Index Linked Gilt E Inc GBP Dic		
9,000	Allianz Global Investors GMBH Gilt Yield I (Inc) GBP Dis		
7,200	AXA Investment Managers UK Ltd US Sht Duration High Yld		
9,730.085	M&G Securities Limited Optimal Income J GBP Dis	10,060.08	10,130.00
5,500	Royal London Unit Trust Mngrs Sterling Credit Z GBP NAV		
7,500	Royal London Unit Trust Mngrs Sterling Credit Z GBP NAV	10,474.20	10,680.00
700	Pimco Global Advisors Irl Ltd Global Inv Grade Cred	9,620.07	9,828.00
1,425	BP Ord 25c shares	5,047.35	6,720.00
600	Royal Dutch Shell B shares	4,422.42	13,473.00
600	BHP Billiton $0.5 shares	4,341.48	10,661.00
180	CRH ord EUR 0.32	4,426.82	5,476.00
1,400	Smith(DS) ord GBP 0.10	4,569.69	5,379.00
370	Halma ord GBP 0.10	3,871.71	7,829.00
350	Experian Ord 10C	2,870.79	8,932.00
200	Diageo Ord GBP 0.28	3,884.00	6,401.00
200	Persimmon Ord 10p	2,258.00	5,390.00
60	Reckitt Benckiser Group ord GBP 0.10		
70	Reckitt Benckiser Group ord GBP 0.10	5,325.75	4,290.00
30	Unilever PLC Ord GBP 0.031111		
150	Unilever PLC Ord GBP 0.031111	2,163.11	6,526.00
120	Astrazeneca Ord 25c	5,749.41	9,128.00
450	Glaxo Smithkline Ordinary 25p shares	7,083.98	8,006.00
2,500	Tesco ord GBP0.05	5,953.09	6,380.00
300	Relx Olc GBP 0.1444	4,438.20	5,717.00
300	Compass Group Plc ord GBP0.1105	5,399.53	5,670.00
641	National Grid Ord GBP 0.12431289	3,648.26	6,053.00
2,250	Barclays 25p Ord shares	4,867.00	4,042.00
1,465	HSBC Holdings Ordinary 0.5 US Dollar shares	4,534.00	8,671.00
6,000	Mercantile Investment Tst Plc(The) ord GBP0.025	10,171.60	15,720.00
300	Findlay Park Partners US Smaller Companies	4,347.16	31,034.00
2,525	Ishares S&P 500 GBP	18,161.79	61,414.00
4250	Fidelity EUR Value Ordinary 25P shares	4,059.07	11,050.00
30	Roche Hldgs Ag Genusscheine Nvp	3,335.33	7,345.00
6,600	Thesis Unit Trust Mngmt Ltd TM Crux European GBP Dis	7,140.00	14,993.00
9,000	Baillie Gifford & Co Japanese Income Growth W4 Dis	11,977.02	12,519.00
1,007	Eastspring Investments SICAV Japan Dynamic FGDY GBP	7,837.74	10,056.00
26	Veritas Funds Plc Veritas Asian D GBP Inc	8,182.27	18,585.00
900	JPMorgan Am UK Ltd Emerging Markets I Instl	5,043.10	9,351.00
650	RIT Capital Partners Ordinary £1 shares	4,903.90	13,748.00
800	BH Global Ltd ord GBP	10,226.25	12,140.00
4,400	Invesco Fund Managers Targeted Y Acc	9,770.33	9,860.00
37	Marshall Wace UCITS Funds Plc MW Tops UCITS G GBP	4,849.70	5,223.00
9,000	Charities Property Fund Income	11,043.28	11,592.00
1,021.54	COIF Charities Investment Fund Acc Units	59,678.69	192,239.12
396,865	Quilter Investors Ltd QC Global Income & Growth Fund GBP Dis		
	Total	379,689.56	688,996.95

Schedule of Investments (Note 12 to the Accounts).

Proceeds (sold in 2020) £	Cost (bought in 2020) £	Gain realised during 2020 £	Value end 2020 £	Gain unrealised during 2020 £
18,000.00		-403.00		
			70,643.28	2,300.45
11,273.19	11,227.89	45.30		
19,107.43	19,394.58	-287.15		
6,257.12	6,393.82	-136.70		
9,110.55		-1,019.45		
7,672.81	7,683.54	-10.73		
10,462.92		-217.08		
9,502.58		-325.42		
4,382.23		-2,337.77		
7,366.19		-6,106.81		
9,854.00		-807.00		
4,887.15		-588.85		
4,481.18		-897.82		
8,354.62		525.62		
9,806.13		874.13		
5,269.19		-1,131.81		
4,241.56		-1,148.44		
4,396.65	3,831.70	564.95		
5,129.43		839.43		
1,283.81	1,250.22	33.59		
6,419.03		-106.97		
9,962.52		834.52		
7,247.88		-758.12		
5,575.04		-804.96		
5,543.30		-173.70		
3,312.43		-2,357.57		
6,194.51		141.51		
1,983.59		-2,058.41		
5,709.62		-2,961.38		
11,264.95		-4,455.05		
32,157.68		1,123.68		
61,421.98		7.98		
10,958.60		-91.40		
7,672.35		327.35		
13,557.40		-1,435.60		
11,755.22		-763.78		
7,934.66		-2,121.34		
20,705.17		2,120.17		
9,389.95		38.95		
11,583.97		-2,164.03		
14,634.58		2,494.58		
9,616.01	176.48	-420.47		
5,347.37		124.37		
10,949.41		-642.59		
			211,053.23	18,814.11
	396,038.05		427,027.00	30,988.95
451,735.95	445,996.28	-26,637.28	708,723.51	52,103.51

Nominations for Council

At the AGM in December 2021, the following vacancies will occur on Council:

- Vice President
- Secretary
- Publicity Officer

Nominations received thus far are as follows:

- Vice-President: Prof. P. M. Barrett
- Secretary: Dr A. R. T. Spencer
- Publicity Officer: Dr N. Vuolo

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