The Palaeontological Association

62nd Annual Meeting

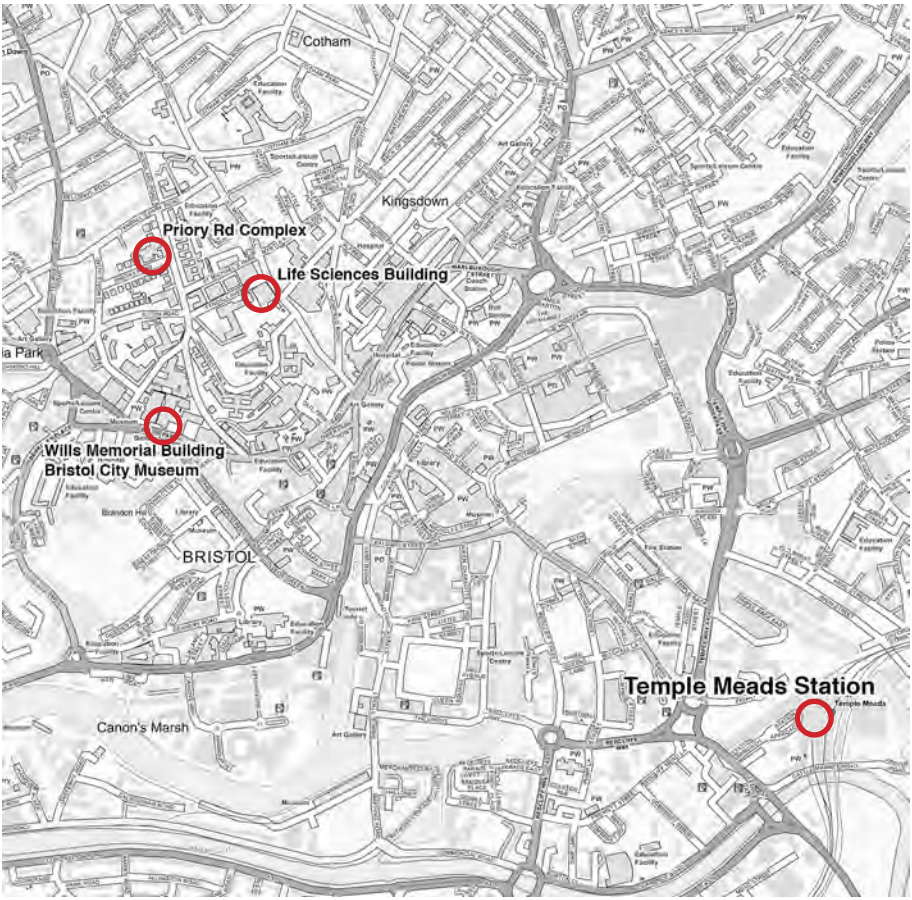
14th–17th December 2018

University of Bristol

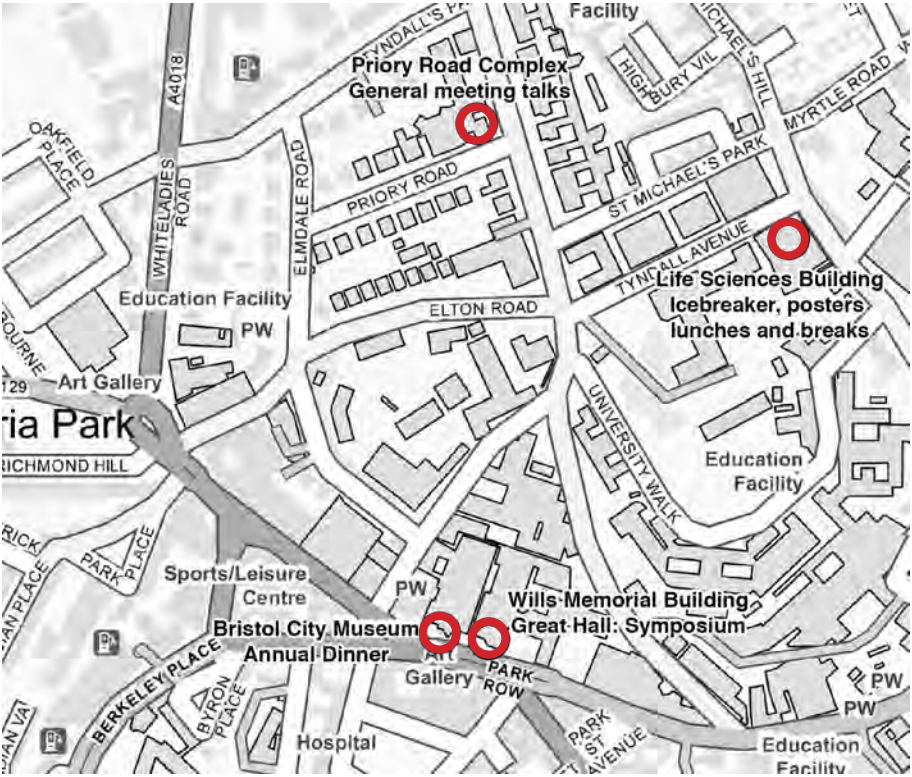
PROGRAMME, ABSTRACTS and AGM papers

MAPS

The University in the City:



The Meeting venues in the University:



The Palaeontological Association
62nd Annual Meeting
14th–17th December 2018
University of Bristol

The programme and abstracts for the 62nd Annual Meeting of the Palaeontological Association are provided after the following information and summary of the Meeting. An easy-to-navigate pocket guide to the Meeting is also available to delegates.

Venue

The Annual Meeting will take place at various locations within the University of Bristol. The Symposium will be taking place in the Great Hall in the Wills Memorial Building. The main meeting will take place at the Priory Road complex (talks) and the Life Sciences Building (posters and breaks).

Registration

Registration will be possible before and during the Symposium outside the Great Hall, Wills Memorial Building, and later in the Life Sciences Building during the icebreaker reception. During the main meeting a registration desk will be available at the Priory Road complex.

Oral Presentations

All speakers (apart from the symposium speakers) have been allocated 15 minutes. You should therefore present for only 12 minutes to allow time for questions and switching between presenters. We have a number of parallel sessions in adjacent lecture theatres so timing is very important. All lecture theatres have an AV projector linked to a large screen. All presentations not submitted to Jakob Vinther prior to the meeting must now be uploaded to the local system. During the meeting there will be a volunteer with a computer outside the lecture rooms who can upload your presentation from your USB memory stick. Please upload your presentation as soon as possible, and at least half an hour before your session.

Poster presentations

Poster boards can accommodate an A0-sized poster presented in portrait format only. Pins to affix your poster to the boards are available. Posters are displayed in the Life Sciences Building. Please put up your posters either during the icebreaker reception or in the mornings at times indicated in the detailed programme.

Travel grants to student members

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

Childcare

There are nursing rooms/baby changing facilities in the basement of the Life Sciences Building and at the Priory Road complex.

Accessibility

There is access via elevators and lifts throughout the Life Sciences and Priory Road complex. An assistive listening / hearing enhancement system is available in each venue. For more information, see <**https://www.accessable.co.uk/venues/wills-memorial-building**>, <**https://www.accessable.co.uk/venues/life-sciences-building**> and <**https://www.accessable.co.uk/venues/social-sciences-complex-priory-road-complex**>. For assistance during the meeting please speak to volunteers on the registration desk.

Bristol

Bristol was named the best place to live in Britain in 2017. Described as 'a small city that feels like a big city', Bristol boasts a wide range of cultural events, restaurants, pubs, museums and historic buildings. Go through the town and see how many Banksy paintings you can spot or take part in one of the guided tours. The Clifton Suspension Bridge is a magnificent industrial age monument based on designs by Isambard Kingdom Brunel. Stokes Croft is a great hub for music, art and counter-cultural lifestyles. See <**https://visitbristol.co.uk**> for information on events during your stay.

Sponsors

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

John Wiley & Sons

Nikon Metrology

Thermo Fisher Scientific

Nature Ecology & Evolution

Geological Society Publishing House

Cambridge University Press

The Paleontological Institute

Taylor & Francis

Time Bites

Summary of Schedule

Friday 14th December: Workshops, Symposium and Reception

The Annual Meeting will begin with a Symposium entitled "Frontiers and Advances in Dinosaur Palaeobiology" in the Great Hall, Wills Memorial Building.

Following the Symposium there will be an icebreaker reception from 19.15 to 21.00 in the Life Sciences Building.

The registration desk will open at 13.30 outside the Great Hall in the Wills Memorial Building and will be available during the reception in the Life Sciences Building.

Saturday 15th December: Conference, AGM, Annual Address and Annual Dinner

Registration will be open from 08.00 at the Priory Road complex.

The conference will start at 09.00 in the Priory Road complex. Talks will be held in triple, double and single sessions in the three lecture theatres, all of which are close to each other. 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 in the Life Sciences Building where lunch and coffee breaks will also be held. Please note that the Life Sciences Building is a five-minute walk from the lecture halls, and that lunch and refreshments are included in your registration fee. An informal LGBTQ+ gathering will be held during the Saturday lunch break (follow the rainbow trilobites).

The afternoon will have a dedicated poster session (17.00–18.45) in the Life Sciences Building where drinks will be served.

The Annual Dinner will be held in the Bristol City Museum. Doors open at 19.00. The Dinner will feature a three-course meal accompanied by drinks, an open cash bar, and the venue is ours until 01.00.

Sunday 16th December: Conference and prizes

Registration will be open from 08.00 at the Priory Road complex.

Talks will begin at 09.30 in the Priory Road complex. Coffee breaks and lunch will be served at the Life Sciences Building and posters will be on display. Talks will end by 17.15, 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.

Monday 17th December: Post-conference field-trips

Field-trip 1: Triassic–Jurassic section in Watchet, North Somerset

We will visit the classic Triassic–Jurassic section in Watchet, North Somerset. At this locality, well-preserved ammonites can be found with ammolite-quality nacre. Soft-bodied coleoids and vertebrate remains are also regularly found. This will be both a fossil-hunting trip and a chance to see some spectacular geology and Alpine folding. Please remember that as this is a site of special scientific interest (SSSI) no hammering will be permitted on the bedrock, although loose blocks can be split, of which there are plenty. Due to the tide schedule we will need to make a very early start in the morning. For lunch we will visit a local pub with a magnificent West Country cider selection and have fish and chips.

Departure time 07.00. We will leave from The Hawthorns on the corner of Woodland Road and Elton Road. Expect to return in the late afternoon/early evening.

Field-trip leaders: Benjamin Moon and Jakob Vinther.

Field-trip 2: Classic microvertebrate sites near Bristol

At the end of the Triassic the Bristol area was located in tropical lagoons surrounding limestone islands. While the classic Rhaetian bone beds were accumulating during offshore storms, cracks in the rocks of the islands were gathering skeletons of reptiles and mammals. We will visit Aust Cliff, famous Rhaetian bone bed site, Manor Farm, and Cromhall, one of the famous Bristol fissures sites. Lunch will be served in a local hostelry.

Departure time 08.30. We will leave from The Hawthorns on the corner of Woodland Road and Elton Road. Expect to return in the late afternoon/early evening.

Field-trip leaders: Mike Benton, David Whiteside and Pamela Gill.

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 meeting, run by students for students with the support of the Palaeontological Association. The Association Code of Conduct relates to the behaviour of all participants and attendees at annual events.

Behavioural expectations: It is the expectation of the Palaeontological Association that meeting attendees behave in a courteous, collegial and respectful fashion to each other, volunteers, exhibitors and meeting facility staff. Attendees should respect common sense rules for professional and personal interactions, public behaviour (including behaviour in public electronic communications), common courtesy, respect for private property and respect for intellectual property of presenters. Demeaning, abusive, discriminatory, harassing or threatening behaviour towards other attendees or towards meeting volunteers, exhibitors or facilities staff and security will not be tolerated, either in 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, please notify the meeting coordinator Dr Jakob Vinther (<**Jakob.Vinther@bristol.ac.uk**>) and/or a member of the Palaeontological Association Council in a designated leadership position: Executive Officer Dr Jo Hellawell: <**executive@palass.org**>; President Prof. Paul Smith: <**paul.smith@oum.ox.ac.uk**>; Vice-President Prof. Richard Twitchett: <**r.twitchett@nhm.ac.uk**>; or Vice-President Dr Caroline Buttler: <**Caroline.Buttler@museumwales.ac.uk**>.

Anyone experiencing or witnessing behaviour that constitutes an immediate or serious threat to public safety, or a criminal act, is expected to contact the emergency services by phoning 999. Those witnessing a potential criminal act should also take actions necessary to maintain their own personal safety.

Schedule of events and timetable of presentations

Friday 14th December

Pre-meeting workshops

09.00 – 12.30 **Bayesian phylogenetic analysis of morphological character data using RevBayes**
Rachel Warnock, Mark Puttick, Joseph O'Reilly and Holly Betts
Old Council Chamber, Wills Memorial Building

10.00 – 12.00 **3D data visualization and segmentation using Avizo**
Thomas Davies and Elizabeth Martin-Silverstone
Room 138, Life Sciences Building. Meet at the entrance of the building by the porter's lodge

10.00 – 12.30 **'Friends of the Rotten' discussion meeting**
Room 3.30, Wills Memorial Building

REGISTRATION

13.30 – 18.30 Wills Memorial Building

Symposium: *"Frontiers and Advances in Dinosaur Palaeobiology"*

Great Hall, Wills Memorial Building

14.25 – 14.30 **Welcome address**

14.30 – 14.55 **Evolution of nesting and reproductive traits in dinosaurs**
Darla K. Zelenitsky, François Therrien and Kohei Tanaka

14.55 – 15.20 **Dinosaur biomechanics: a tale of hard tissues and soft evidence?**
Karl T. Bates

15.20 – 15.45 **Approaches for understanding the evolution of weaponry in dinosaurs**
Victoria M. Arbour

15.45 – 16.00 Break

16.00 – 16.25 **Why do dinosaurs have different shaped skulls?**
Emily J. Rayfield

16.25 – 16.50 **How fossil biomolecules unveil the hidden stories of dinosaur biology**
Jasmina Wiemann

16.50 – 17.15 **The trophic habits of Mesozoic birds: data from the Jehol avifauna**
Jingmai K. O'Connor

17.15 – 17.30 Break

Public event

17.30 – 18.00 **Embryonic genesis of the dinosaur body**
Bhart-Anjan S. Bhullar

18.00 – 18.30 **The rise and fall of the dinosaurs**
Stephen L. Brusatte

18.30 – 19.00 **Tracing the evolution of major bird characteristics: recent advances and future prospects**
Xing Xu

Icebreaker Reception

19.15 – 21.00 Life Sciences Building

Saturday 15th December

Conference, Association AGM, and Annual Dinner

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

08.00 – 08.45 Poster set-up in Life Sciences Building

Session 1A (in parallel with sessions 1B and 1C)
Priory Road complex, Lecture Room A Chair: Robert Goodall

09.00 – 09.15 **Clarifying the Kukruse–Haljala stage boundary in northwest Estonia**
*Tõnn Paiste, Tõnu Meidla, Peep Männik and Jaak Nõlvak

09.15 – 09.30 **Trace fossil insights into Early Devonian terrestrial ecosystems – a case study from Gaspé, Quebec**
*Anthony P. Shillito and Neil S. Davies

09.30 – 09.45 **Body size changes in bivalve molluscs following the end-Triassic mass extinction event**
*Jed W. Atkinson and Paul B. Wignall

09.45 – 10.00 **Organically-preserved epithelia of a multicellular eukaryote from the late Neoproterozoic of Arctic Norway**
Heda Agić, Anette E.S. Högström, Małgorzata Moczydłowska, Sören Jensen, Teodoro Palacios, Guido Meinhold, Jan Ove R. Ebbestad, Wendy L. Taylor and Magne Høyberget

10.00 – 10.15 **Silurian and Devonian trilobites of Japan: 'eye witnesses' to the early geological evolution of the Japanese islands**
*Christopher P. Stocker, Philip D. Lane, Derek J. Siveter, Mark Williams, Tatsuo Oji, Gengo Tanaka, Toshifumi Komatsu and Simon R. Wallis

Session 1B (in parallel with sessions 1A and 1C)
Priory Road complex, Lecture Room B Chair: Luke Parry

09.00 – 09.15 **Exceptionally preserved soft parts in echinoderms from the Fezouata Shale (Lower Ordovician, Morocco)**
Bertrand Lefebvre, Elizabeth G. Clark, Aaron W. Hunter, Martina Nohejlova and Farid Saleh

09.15 – 09.30 **Predatory behaviour and taphonomy of a Jurassic belemnoid coleoid (Diplobelida, Cephalopoda)**
Christian Klug, Dominique Jenny, Dirk Fuchs, Alexander I. Arkhipkin and Rolf B. Hauff

09.30 – 09.45 **The Kingswood Limestone – a Mississippian terrestrial Konservat Lagerstätte**
Andrew C. Scott and Jean Galtier

09.45 – 10.00 **A new Lagerstätte from the Lower Cretaceous La Huérguina Formation in Buenache de la Sierra (Castilla-La Mancha, Spain)**
Jesús Marugán-Lobón, Hugo Martín-Abad, Irene Prieto, Candela Blanco-Moreno, Guillermo Navalón, Fernando Blanco and Mario A. Martinez Monleón

10.00 – 10.15 **Tackling the evolution of the Early Cretaceous palaeowetland of Las Hoyas**
Hugo Martín-Abad, Candela Blanco-Moreno, Jesús Marugán-Lobón, Sandra Barrios-de Pedro, Marian Fregenal-Martínez, Francisco José Poyato-Ariza, Bernard Gomez and Ángela D. Buscalioni

Session 1C (in parallel with sessions 1A and 1B)
Priory Road complex, Lecture Theatre Chair: Sam Giles

09.00 – 09.15 **Different evolutionary dynamics govern body size evolution in dinosaur groups**
Manabu Sakamoto, Chris L. Organ, Joanna Baker, Michael J. Benton, Andrew Meade, Mark Pagel and Chris Venditti

09.15 – 09.30 **A three-dimensionally preserved Middle Jurassic monofenestratan pterosaur from the Isle of Skye, Scotland**
Elizabeth G. Martin-Silverstone and Paul M. Barrett

09.30 – 09.45 **The long and the short of it: a transformational tale of pterosaur tails**
David M. Unwin

09.45 – 10.00 **Long-term climate and environmental changes did not lead to the extinction of dinosaurs: evidence from the latest Cretaceous of Alberta, Canada**
François Therrien, Darla K. Zelenitsky, Don B. Brinkman, Annie Quinney, Kohei Tanaka and David A. Eberth

10.00 – 10.15 **Morphological disparity and the 'double burst' avian expansion**
Thomas L. Stubbs and Michael J. Benton

10.15 – 11.00 Tea/coffee break and posters
Life Sciences Building

Session 2A (in parallel with sessions 2B and 2C)
Priory Road complex, Lecture Room A Chair: Laura Cotton

11.00 – 11.15 **From order to disorder: Pleistocene beetle scales reveal diverse 3D photonic nanostructures**
Luke T. McDonald, Maria E. McNamara, Vinodkumar Saranathan and Peter Vukusic

11.15 – 11.30 **Coralline algae as a recorder of climate change and its impacts in the past and in the future**
Leanne A. Melbourne, Federica Ragazzola and Daniela N. Schmidt

11.30 – 11.45 **A new life for old leaves: can herbarium dried leaves be used in CLAMP?**
David C. Steart and Norman MacLeod

11.45 – 12.00 **Evolution of a lower Famennian (Upper Devonian) fossil assemblage from Kowala quarry (Holy Cross Mountains, central Poland)**
Krzysztof Broda and Anna Łazuka

12.00 – 12.15 **Sunny, rain later: 30 years of the Carnian Pluvial Episode**
Michael J. Simms and Alastair Ruffell

Session 2B (in parallel with sessions 2A and 2C)
Priory Road complex, Lecture Room B Chair: Maria McNamara

11.00 – 11.15 **Giant stem group gastrotrichs from the early Cambrian**
Ailin Chen, *Luke A. Parry, Fan Wei, Jakob Vinther and Peiyun Cong

11.15 – 11.30 **Comparative taphonomy of embryo-like fossils from the Ediacaran Doushantuo and Cambrian Kuanchuanpu formations of South China**
*Emma N. Landon, John A. Cunningham, Xi-Ping Dong and Philip C. J. Donoghue

11.30 – 11.45 **Uncovering the impact of palaeogeography on taphonomy: an investigation of the Mazon Creek Lagerstätte**
*Thomas Clements, Mark A. Purnell and Sarah E. Gabbott

11.45 – 12.00 **Synchrotron X-ray fluorescence analysis of melanosomes reveals soft tissue anatomy of fossil vertebrates**
*Valentina Rossi, Maria E. McNamara and Samuel M. Webb

12.00 – 12.15 **Palaeobiology of the Ediacaran Rangeomorpha: resolving morphological disparity**
*Frances S. Dunn, Charlotte G. Kenchington, Philip C. J. Donoghue, Dmitriy V. Grazhdankin, Philip R. Wilby and Alexander G. Liu

Session 2C (in parallel with sessions 2A and 2B)
Priory Road complex, Lecture Theatre Chair: Thomas Stubbs

11.00 – 11.15 **Morphological convergence obscures functional disparity in sabre-toothed carnivores**
Stephan Lautenschlager, Thomas L. Stubbs and Borja Figueirido

11.15 – 11.30 **Convergent evolution of toothed whale cochlea**
Travis Park, Natalie Cooper, Loïc Costeur, Bastien Mennecart and Camille Grohé

11.30 – 11.45 **3D geometric morphometric analysis of endocranial shape variation in the squirrel-related clade and their fossil relatives: contributions of locomotion and phylogeny to brain shape**
Ornella C. Bertrand and Mary T. Silcox

11.45 – 12.00 **Craniodental functional morphology indicate niche partitioning amongst sympatric marine reptiles**
Davide Foffa, Mark T. Young and Stephen L. Brusatte

12.00 – 12.15 **Cracking the link between brain and skull in Archosauria: evolutionary and developmental perspectives**
Matteo Fabbri, Daniel Smith, Miccaela Vergara-Cereghino, Macarena Faunes, Joao Botelho and Bhart-Anjan S. Bhullar

12.15 – 13.30 Lunch and poster session
Life Sciences Building

12.30 – 13.30 LGBTQ+ meet-up
Life Sciences Building, Flyby 1 (LG): Follow the rainbow trilobites and bring your packed lunch for an informal gathering and chat during the lunch break.

Session 3

Priory Road complex, Lecture Theatre Chair: Mark Puttick

13.30 – 13.45 **The distribution and cladogenesis of Middle Jurassic (Callovian) to Early Cretaceous (Valanginian) marine reptiles in the Northern Hemisphere**
Aubrey J. Roberts, Victoria S. Engelschiøn, Lene L. Delsett and Jørn H. Hurum

13.45 – 14.00 **Strontium isotopes reveal migratory behaviour in Late Cretaceous hadrosaurs of Alberta, Canada**
*David F. Terrill, Jason S. Anderson and Charles M. Henderson

14.00 – 14.15 **The extraordinary diversity of Teleosauroidea (Crocodylomorpha, Thalattosuchia): a comprehensive analysis of their evolutionary relationships**
*Michela Johnson, Mark T. Young and Stephen L. Brusatte

14.15 – 14.30 **Using ancestral duplications to date the origin of fundamental genes**
*Holly Betts, Tom A. Williams, Philip C. J. Donoghue and Davide Pisani

14.30 – 14.45 **Recovering from an extinction event: a serpent approach**
*Catherine G. Klein, Davide Pisani, Daniel J. Field, Rebecca J. Lakin, Matthew A. Wills and Nicholas R. Longrich

Annual General Meeting

14.45 – 15.30 Annual General Meeting
Priory Road lecture theatre

15.30 – 16.00 Tea/coffee break and posters
Life Sciences Building

Annual Address

Priory Road lecture theatre

16.00 – 17.00 **Ice in a greenhouse world – 60 Ma and 2060**
Jane E. Francis

Poster session with refreshments

17.00 – 18.45 Life Sciences Building

Reception and Annual Dinner

Bristol City Museum

19.00 – 20.00 Reception

20.00 – 01.00 Annual Dinner

Sunday 16th December

Conference & prizes

Session 4A (in parallel with session 4B)
Priory Road complex, Lecture Room B Chair: Nick Butterfield

09.15 – 09.30 **Reconstruction of skeletal architecture of conodont *Clydagnathus* using non-destructive methods**
Nicola Vuolo, Carlos Martinez Perez, Mark A. Purnell and Philip C. J. Donoghue

09.30 – 09.45 **Does the diversity and succession of microbial communities during decay influence character loss?**
Robert H. Goodall, Martha R. J. Clokie, Christopher J. R. Turkington and Mark A. Purnell

09.45 – 10.00 **Impact of diagenesis on the chemistry of vertebrate eye melanosomes**
Christopher S. Rogers, Maria E. McNamara and Samuel M. Webb

10.00 – 10.15 **A strange case of two fishes: enigmatic disappearance of bone tissue or an originally unossified osteostracan**
Oive Tinn, Liisa Lang, Tiiu Märss and Kalle Kirsimäe

10.15 – 10.30 **Endocranial anatomy of a 400-million-year-old stem-gnathostome: new insights into jawed vertebrate origins**
Sam Giles, You-an Zhu, Gavin C. Young, Min Zhu and Jing Lu

10.30 – 10.45 **Sticky fish: the unusual skeletal taphonomy of Middle Triassic actinopterygians**
Susan R. Beardmore, Patrick J. Orr, Heinz Furrer and Duncan J.E. Murdock

Session 4B (in parallel with session 4A)
Priory Road complex, Lecture Theatre Chair: Delphine Angst

09.15 – 09.30 **Community variation within the Late Jurassic Morrison Formation**
*Elspeth Wallace, Victoria M. Egerton, Philip L. Manning, William I. Sellers and Robert S. Sansom

09.30 – 09.45 **A third "acanthodian" stem-chondrichthyan endoskeleton in a uniquely well-preserved specimen of *Diplacanthus crassisimus***
*Richard Dearden and Martin D. Brazeau

09.45 – 10.00 **The rise of dinosaurs: tetrapod diversity and climate during the Late Triassic**
*Emma Dunne, Alexander Farnsworth, Sarah E. Greene, Daniel J. Lunt, Roger B. J. Benson and Richard J. Butler

10.00 – 10.15 **Testing hypotheses of heterochrony in the skull evolution of strisoran birds**
*Guillermo Navalón, Sergio M. Nebreda, Jen A. Bright, Jesús Marugán-Lobón and Emily J. Rayfield

10.15 – 10.30 **The nature and preservation of soft tissues in exceptionally preserved Jurassic ichthyosaurs**
*Fiann M. Smithwick, Kieran Goss, Ian Fletcher and Jakob Vinther

10.30 – 10.45 **Towards improving the use of morphological data in inferring phylogeny – data from extant archosaurs**
Roland B. Sookias

10.45 – 11.30 Tea/coffee break and posters
Life Sciences Building

Session 5A (in parallel with sessions 5B and 5C)
Priory Road complex, Lecture Room A Chair: Alex Dunhill

11.30 – 11.45 **Diversity of neuropteran larvae (Insecta) in Early Cretaceous ambers**
Ricardo Pérez-de la Fuente, Dany Azar, Xavier Delclòs, Michael S. Engel and Enrique Peñalver

11.45 – 12.00 **Palaeoecology of *Voulteryon parvulus* (Eucrustacea, Polychelida) from the Middle Jurassic of La Voulte-sur-Rhône fossil Lagerstätte (France)**
Denis Audo, Ninon Robin, Javier Luque, Michal Krobicki, Joachim T. Haug, Carolin Haug, Clément Jauvion and Sylvain Charbonnier

12.00 – 12.15 **Ultra- and nanostructure of conodont dental skeleton and implications for its properties**
Emilia Jarochowska, Corinna Böhm, Katrin Hurle, Michel Bestmann, Pat Trimby, Ingo Mey, Vitaliy Pipich, Bryan Shirley and Stephan E. Wolf

12.15 – 12.30 **How an eye of a phacopid trilobite is constructed or the solution of Stürmer's enigma**
Brigitte Schoenemann and Euan N. K. Clarkson

12.30 – 12.45 **Modelling extinction cascades across a Mesozoic hyperthermal event**
Alexander M. Dunhill, Andrew P. Beckerman, Karolina Zarzyczny, Aislinn Vickers-Arrigo, Jed W. Atkinson and Crispin T. S. Little

Session 5B (in parallel with sessions 5A and 5C)
Priory Road complex, Lecture Room B Chair: Xiaoya Ma

11.30 – 11.45 **The Ediacaran fauna of the Llangynog Inlier, Carmarthenshire**
John C. W. Cope

11.45 – 12.00 **Constructional and functional morphology of Ediacaran rangeomorphs**
Nicholas J. Butterfield

12.00 – 12.15 **Early ontogeny of the shells of pelagiellid molluscs from the Cambrian (Stage 4) Pioche Formation, southeastern Nevada, USA**
John L. Moore, Susannah M. Porter and Mark Webster

12.15 – 12.30 **A Cambrian peanut worm and the peramorphic origin of the sipunculan body plan**
Martin R. Smith and Zhifei Zhang

12.30 – 12.45 **Oxygen, temperature, and the stenothermal cradle of Ediacaran evolution**
Thomas Boag, Richard Stockey, Leanne E. Elder, Pincelli M. Hull and Erik A. Sperling

Session 5C (in parallel with sessions 5A and 5B)
Priory Road complex, Lecture Theatre Chair: Rob Sansom

11.30 – 11.45 **The partial skeleton of the docodont *Borealestes serendipitus*, from the Kilmaluag Formation (Middle Jurassic) of the Isle of Skye, Scotland**
*Elsa Panciroli, Zhe-Xi Luo, Julia A. Schultz, Vincent Fernandez, Matthew Humpage, Stig Walsh and Nicholas C. Fraser

11.45 – 12.00 **Changes in mammalian mandibular ecomorphological disparity across the K–Pg boundary**
*Gemma L. Benevento, Matt Friedman and Roger B. J. Benson

12.00 – 12.15 **Developmental innovation in the evolution of complex mammalian teeth**
*Aidan M. C. Couzens and Martin Rücklin

12.15 – 12.30 ***Elephas recki*: the wastebasket?**
*Hanwen Zhang

12.30 – 12.45 **Quantifying patterns of convergent evolution: a case study on mammalian insectivores**
*Robert J. Brocklehurst, Nick Crumpton, Louise Tomsett and Natalie Cooper

12.45 – 14.00 Lunch and Poster Session
Life Sciences Building

Session 6A (in parallel with session 6B)
Priory Road complex, Lecture Room B Chair: Emily Mitchell

14.00 – 14.15 **Growth and development of fuxianhuiid arthropods from the lower Cambrian (Series 2, Stage 3), Chengjiang biota**
David A. Legg, Hong Chen, Yu Liu and Xian-guang Hou

14.15 – 14.30 **Critically exploring the fossil record of the deep biosphere**
Sean McMahon and Magnus Ivarsson

14.30 – 14.45 **A bioturbation control on the Phanerozoic record of shallow marine sole marks**
Lidya G. Tarhan

14.45 – 15.00 **Rooting the eukaryotic radiation with new models of genome evolution**
Celine Petitjean, Gergely J. Szöllősi, David Bass and Tom A. Williams

15.00 – 15.15 **Integrating fossil data refines plant divergence time estimates**
Joseph E. O'Reilly, Philip C. J. Donoghue and Mark N. Puttick

Session 6B (in parallel with session 6A)
Priory Road complex, Lecture Theatre Chair: Manabu Sakamoto

14.00 – 14.15 **Does morphology evolve under drift or selection? Comparing empirical and simulated data**
Robert S. Sansom, Joseph N. Keating and Russell J. Garwood

14.15 – 14.30 **Recent discoveries about the ecology of the dodo and future developments**
Delphine Angst, Anusuya Chinsamy, Lorna Steel and Julian P. Hume

14.30 – 14.45 **Stratigraphic and environmental control on marine benthic community change through the early Toarcian extinction event (Iberian Range, Spain)**
Silvia Danise, Marie-Emilie Clémence, Gregory D. Price, Juan J. Gómez and Richard J. Twitchett

14.45 – 15.00 **Persistence of the Lilliput effect across evolutionary and ecological scales**
Kenneth De Baets and Wolfgang Kiessling

15.00 – 15.15 **When forams go big: drivers of extreme size in the genus *Nummulites***
Laura J. Cotton and Caitlin R. Keating-Bitonti

15.15 – 16.00 Tea/coffee break (take down posters)
Life Sciences Building

Session 7
Priory Road complex, Lecture Theatre Chair: Rachel Warnock

16.00 – 16.15 **Using intra-specific variation to detect sexual reproduction in Ediacaran organisms**
Emily G. Mitchell and Catherine Clark

16.15 – 16.30 **Why is the Chengjiang biota exceptionally well preserved?**
Xiaoya Ma

16.30 – 16.45 **Australia's polar Cretaceous mammals: longer lifespans may be indicative of hibernation**
Pamela G. Gill, Elis Newham, Thomas H. Rich and Ian J. Corfe

16.45 – 17.00 **The independent origin of plant roots and their gradual evolution in lycophytes**
Alexander J. Hetherington and Liam Dolan

17.00 – 17.15 **The first vertebrate skeletal tissues and the 'biomineralization toolkit'**
Duncan J. E. Murdock

Closing business

Priory Road complex, Lecture Theatre

17.15 – 17.30 Presentations from the organizing committees of PalAss 2019 (Valencia) and Progressive Palaeontology 2019 (Birmingham)

17.30 Presentation of the President's Prize and the Council Poster Prize, followed by closing remarks.

Monday 17th December

Field-trip 1: Triassic–Jurassic section in Watchet, North Somerset

07.00 Coach travel from The Hawthorns on the corner of Woodland Road and Elton Road. Expect to return in the late afternoon/early evening.

Field-trip leaders: Benjamin Moon and Jakob Vinther.

Field-trip 2: Classic microvertebrate sites near Bristol

08.30 Coach travel from The Hawthorns on the corner of Woodland Road and Elton Road. Expect to return in the afternoon/early evening.

Field-trip leaders: Mike Benton, David Whiteside and Pamela Gill.

Abstracts of symposium presentations:

Frontiers and Advances in Dinosaur Palaeobiology

Approaches for understanding the evolution of weaponry in dinosaurs

Victoria M. Arbour
Royal British Columbia Museum, Canada

Weaponry is a pervasive trait among amniotes that appears to evolve in predictable patterns when underpinned by similar socioecological and habitat parameters. Within dinosaurs, the tail clubs of ankylosaurid ankylosaurs are a unique form of rare caudal weaponry that contrasts with the cranial horns, domes and bosses found in many ornithischian and saurischian species. Multiple techniques and approaches can be used to investigate the evolution and functional morphology of weapons such as tail clubs. Biomechanical modelling can test hypotheses of function and combat behaviour; these approaches have shown that ankylosaurid tail clubs were capable of delivering and withstanding forceful impacts and are best interpreted as weapons rather than ornaments. Correlation analyses and tests of convergent evolution provide insights into the constraints surrounding the evolution of tail clubs, and show that tail weaponry is rare within amniotes because it is associated with a restricted suite of features including armour, large body size, and herbivory. Whether or not tail clubs evolved under natural selection (as antipredator defences) or sexual selection (as weapons for male-male combat) remains an unresolved question in the study of ankylosaur palaeobiology.

Dinosaur biomechanics: a tale of hard tissues and soft evidence?

Karl T. Bates
University of Liverpool, UK

Biomechanical reconstructions of extinct animals represent a crucial step towards understanding palaeoecological interactions, selective pressures and macroevolutionary patterns in the fossil record. In recent years functional analyses of extinct organisms have been revolutionized by the widespread adoption of quantitative computational approaches. These approaches have many advantages, but one challenging aspect to their use on extinct animals is that they require precise specification of numerical values for soft tissue parameters that are rarely, and in some instances never, preserved in fossils. Confronting and overcoming this uncertainty surrounding soft tissue parameters has repeatedly been cited as the major challenge facing studies of evolutionary biomechanics. Herein, I use a suite of examples from dinosaur form and function research to illustrate recent successes and ongoing difficulties in quantitative soft tissue reconstructions of extinct vertebrates. In particular, I highlight two keys areas that have recently yielded major steps forwards in terms of constraining the functional capabilities of dinosaurs: greater integration of quantitative soft tissue data from extant vertebrates, and extension and validation of computational biomechanical approaches. However, in many circumstances the current lack of appropriate neontological data to guide soft tissue reconstruction in dinosaurs means high levels of uncertainty remain in quantitative biomechanical predictions.

Embryonic genesis of the dinosaur body

Bhart-Anjan S. Bhullar
Yale University, USA

Virtually every musculoskeletal region of the bird body is drastically modified from the ancestral reptilian condition; the history of avian anatomy can be traced back along the dinosaur, and then the archosaur, line. Because evolutionary transformations are the result of modifications to developmental programmes, we have been examining the morphology of embryos and juveniles, extant and fossil, to determine when in early ontogeny dinosaur-specific and avian-specific features appear. Imaging of extant taxa takes advantage of a modified CLARITY technique for making transparent entire immunostained embryos. In the head, we have found that early proportional changes and repatterning at the phylotypic stage are responsible, respectively, for the unique architecture of the archosaur and the avian face. In several postcranial regions, in contrast, we have discovered late addition of bird-specific features to a more generalized skeletal form. This late addition stands in contrast to the way in which features specific to many other major terrestrial vertebrate clades are added and suggests that there is something unique, at the embryonic level, about the way in which dinosaurs became birds.

The rise and fall of the dinosaurs

Stephen L. Brusatte
University of Edinburgh, UK

Dinosaurs are icons of prehistory, and long after their Mesozoic heyday, persist today as over 10,000 species of birds. The evolutionary history of dinosaurs is coming into increasing focus, as the modern, diversifying generation of palaeontologists discovers new species across the globe and uses new techniques to study dinosaur anatomy, biology and behaviour. In this public talk, I review the evolutionary story of dinosaurs, from their Triassic origins, through their Jurassic rise to dominance, and to the end-Cretaceous extinction of the non-avian species. I highlight recent research that shows how dinosaurs evolved from humble cat-sized ancestors in the aftermath of the end-Permian extinction, gradually rose to dominance over 30+ million years of the Triassic, and became pre-eminent in the Jurassic, after the end-Triassic extinction. I discuss how some species evolved colossal size, keen intelligence and neurosensory behaviours (as revealed by computed tomography scanning), and feathers, wings and flight, before the non-avian species suddenly went extinct after the Chicxulub bolide impact, setting the stage for the Age of Mammals. I provide examples of recent fieldwork, statistical studies and laboratory work that help piece together this story, including the work of my students at the University of Edinburgh and our colleagues.

The trophic habits of Mesozoic birds: data from the Jehol avifauna

Jingmai K. O'Connor
Institute of Vertebrate Paleontology and Paleoanthropology, China

Although direct associations that reveal diet are extremely rare in the fossil record, the rich Lower Cretaceous Jehol Lagerstätte has produced dozens of specimens preserving ingested items, which together reveal important information regarding the early evolution of the avian alimentary canal. *Jeholornis* and *Sapeornis* ate seeds and, like living granivores, utilized a gastric mill, although only the more derived *Sapeornis* possessed a crop for food

storage. Most direct evidence pertains to Ornithuromorpha, indicating a structurally and functionally modern alimentary canal was present in even the earliest members of this clade. Similar evidence is altogether lacking in Enantiornithes suggesting a primitive alimentary canal may have factored into their extinction. The role of the gizzard in the loss of teeth in Aves is more complex than in non-avian theropod lineages. As in neornithines, gastroliths in basal ornithuromorphs may not be entirely indicative of herbivory although this diet does appear to correlate with complete tooth loss in this clade. Positive selection for specialized tooth morphologies persists throughout the evolution of Aves and the diversity of recognized dental patterns including enamel specializations observed in Jehol enantiornithines suggests effective resource partitioning and that teeth had an active participation in enantiornithine feeding strategies.

Why do dinosaurs have different shaped skulls?

Emily J. Rayfield
University of Bristol, UK

Dinosaurs occupied terrestrial and aerial niches and exhibited varied dietary ecologies. Skull form is also highly variable and cranial adornment is common. It may be expected that skull shape is strongly linked to dietary ecology, yet variance in theropod dinosaur skull shape carries a strong phylogenetic signal. There is some functional signal in the data: skull shape is correlated to bony stress during feeding and weakly correlated to skull mechanical advantage (speed or forcefulness of jaw closure). Previous stress data were taken from 2D finite element models of skull function. Here I provide a review and metanalysis of 3D finite element models of dinosaur skull function. Remarkably low feeding-induced stress is experienced in theropod, ornithischian and sauropod skulls, usually less than 10 MPa. As bone fails between 150–200 MPa, these skulls are over-engineered, with high safety factors. If skull stress is low, is resistance to skull stress and strain an important selective factor in dinosaur skull morphological evolution? Experimentally recorded strains in extant taxa and carnivoran skull mechanics provide a benchmark to compare to dinosaur cranial performance. Low stress is commonplace in generalist extant taxa, except in some lineages with divergent dietary ecologies, suggesting a similar trend in dinosaur cranial function.

How fossil biomolecules unveil the hidden stories of dinosaur biology

Jasmina Wiemann
Yale University, USA

Dinosaur hard tissues consist of mineral crystallites with a proteinaceous, cell-bearing, vascularized, innervated scaffold that normally degrades post-mortem. The preservation of soft tissue structures within Mesozoic bones, teeth, scales and eggshells has proved controversial, and such palaeobiological information is little exploited. Decalcification of such hard tissues preserved in oxidative settings releases brownish stained extracellular matrix, cells, blood vessels and nerve projections. *In situ* Raman microspectroscopy, organic compound maps, electron microprobe analysis and scanning electron microscopy show that these fossil soft tissues are a product of diagenetic transformation to advanced glycoxidation and lipoxidation end products, a class of N-heterocyclic polymers generated via oxidative crosslinking of proteinaceous scaffolds. Ecological, physiological and taphonomic signals in N-heterocyclic polymers of fossil soft tissues can be characterized. Hard tissues in reducing environments, in contrast, lack soft tissue preservation. Comparison of fossil

soft tissues with modern and experimentally-matured samples reveals how proteinaceous tissues undergo diagenesis and offers an explanation of biases in their preservation in the rock record. This result demonstrates why oxidative depositional environments should be targeted for evidence of soft tissues in fossil vertebrate skeletons and validates the use in evolutionary studies of the cellular-to-subcellular soft tissue morphologies they yield.

Tracing the evolution of major bird characteristics: recent advances and future prospects

Xing Xu

Institute of Vertebrate Paleontology and Paleoanthropology, China

Reconstructing the evolutionary history of major characteristics of crown-group birds is central to the study of bird origins. The last several decades have witnessed significant advances in our understanding of the evolution of major bird characteristics, notably feathers and flight. These advances have been achieved partly by discovering exceptional fossils of early birds and their close relatives among other theropods, but new methods and techniques have also played an important role, as has integration of newly collected data from disciplines other than palaeontology. It now seems probable that major bird characteristics could have appeared over an interval of up to 170 million years, and evolved at widely varying rates. While the emergence of birds from among dinosaurs now represents one of the best documented of all major evolutionary transitions, a full understanding of the distributions of avian characteristics in space, time and phylogeny has yet to solidify. This step will require more complete fossil sampling, in-depth analyses of the relevant fossils, a better understanding of the development of major bird traits and an even more integrated approach.

Evolution of nesting and reproductive traits in dinosaurs

Darla K. Zelenitsky[1], François Therrien[2] and Kohei Tanaka[3]

[1]*University of Calgary, Canada*

[2]*Royal Tyrrell Museum of Palaeontology, Canada*

[3]*Nagoya University, Japan*

Discoveries of fossil eggs associated with identifiable parental or embryonic skeletal remains over the past 25 years have shed light on reproductive traits of various dinosaur species and provided insight into the evolutionary history of these traits within Dinosauria. Ornithischians and sauropods laid large clutches of eggs in covered nests, similar to the primitive archosaurian condition. Non-avian theropods retained primitive archosaurian reproductive traits with respect to egg elongation, clutch size and the retention of two functional oviducts, but non-avian maniraptorans acquired derived bird-like traits with respect to eggshell ultrastructure, egg symmetry and the production of a single egg per oviduct at a time. An evolutionary transition in nesting style occurred within Theropoda, where eggs were fully buried in covered nests among non-maniraptoran theropods (also in ornithischians), partially buried in open nests among non-avian maniraptorans, and typically fully exposed in open nests in Aves. Partial or full exposure of the eggs appears to coincide with a nesting behavioural change, where adults sat on the eggs. A reduction of the incubation period appears to have occurred within Dinosauria, from extended incubation periods (primitive archosaurian condition) among ornithischians to shorter incubation durations in some non-avian maniraptorans and in birds.

Abstract of Annual Address

The Annual Address will be given on Saturday 15th December at 16.00 and is generously sponsored by John Wiley & Sons.

Ice in a greenhouse world – 60 Ma and 2060

Jane E. Francis
British Antarctic Survey, UK

The polar regions are the areas on Earth most sensitive to climate change, both in the past and today, as we are now seeing so clearly.

Evidence from fossil plants in Antarctic rocks confirms that during the geological past polar climates were much warmer than now, allowing temperate and tropical vegetation to thrive on Antarctica near the South Pole. This has led to the general view that the Cretaceous–Eocene world, 100–50 million years ago, was ice-free.

Was Antarctica really ice-free, even when the continent was over the pole and experienced dark winters? High-resolution studies of Late Cretaceous and Paleocene (75–60 Ma) marine algae (dinoflagellate cysts), correlated with isotope evidence for cold climates during algal blooms, now suggest that seasonal sea ice – and even ice caps – existed on Antarctica while temperate floras lived on the coast.

CO_2 levels were ~400 ppm at that time, much like today. Can the Late Cretaceous provide us with a vision of our future world?

Abstracts of oral presentations

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

Organically-preserved epithelia of a multicellular eukaryote from the late Neoproterozoic of Arctic Norway

Heda Agić[1], Anette E. S. Högström[2], Małgorzata Moczydłowska[3], Sören Jensen[4], Teodoro Palacios[4], Guido Meinhold[5], Jan Ove R. Ebbestad[3], Wendy L. Taylor[6] and Magne Høyberget[7]
[1]*University of California, Santa Barbara, USA*
[2]*Tromsø University Museum, Norway*
[3]*Uppsala University, Sweden*
[4]*University of Extremadura, Spain*
[5]*Keele University, UK*
[6]*University of Cape Town, South Africa*
[7]*Independent*

Multicellularity originated in the Mesoproterozoic Era and arose multiple times since, yet early multicellular fossils are scarce until the terminal Neoproterozoic and often restricted to cases of exceptional preservation. We discovered unusual organically-preserved microfossils from shales of the interglacial Nyborg Formation, Vestertana Group, Digermulen Peninsula in Arctic Norway. The new fossil is a carbonaceous organ-taxon that consists of stacked tubular threads with cup-shaped ends. It was likely a part of a larger organism (a multicellular eukaryote), probably with greater preservation potential than its other elements. The arrangement of tubes and cup-shaped termini invites comparison with cells of an epithelial layer present in a variety of clades and provides additional support for the presence of organisms with differentiated tissues in the late Neoproterozoic. Such tissues may have benefited the organism in: avoiding overgrowth, limiting fouling, reproduction or water filtration. The Nyborg Formation fossil shares characters with extant and fossil groups including red algae and their fossils, demosponge larvae and putative sponge fossils, colonial protists and nematophytes. Regardless of its precise affinity, it was a complex and likely benthic, marine eukaryote exhibiting cellular differentiation, and is a rare occurrence of early multicellularity outside of Lagerstätten.

Recent discoveries about the ecology of the dodo and future developments

Delphine Angst[1], Anusuya Chinsamy[2], Lorna Steel[3] and Julian P. Hume[4]
[1]*University of Bristol, UK*
[2]*University of Cape Town, South Africa*
[3]*National History Museum, London, UK*
[4]*Natural History Museum at Tring, UK*

The dodo, *Raphus cucullatus*, a giant, flightless pigeon endemic to Mauritius in the Indian Ocean, was discovered at the end of the sixteenth century by visiting mariners, and became extinct by the late seventeenth century due to human activities. Although the dodo was contemporaneous with humans for almost a century, little was recorded

about its ecology. In 2017, an unprecedented histological study on 22 bones of the dodo showed for the first time the presence of medullary bone, indicating ovulating females, and by extrapolation using the lines of arrested growth we deduced that the dodo bred around August, in the austral winter. Our study of fibro-lamellar bone further suggests that juveniles grew rapidly to enable them to reach a robust size before the austral summer or cyclone season. Large resorption areas in the bone cortex can be interpreted as evidence of moulting, and suggest that after summer had passed moult began in the adults that had just reproduced; the timing of moult, derived from the utilisation of the lines of arrested growth, is also corroborated by historical written accounts of the dodo. Further research using a multidisciplinary approach will provide information on locomotion, diet, sexual dimorphism and population structure.

Body size changes in bivalve molluscs following the end-Triassic mass extinction event

***Jed W. Atkinson and Paul B. Wignall**
University of Leeds, UK

Fossil assemblages from the aftermath of mass extinction events are often characterized by small body sizes. This may be due to preferential extinction of large species, preferential origination of small species or a reduction in size of surviving species (the Lilliput effect). During the subsequent recovery interval body size increases. As an organism's size can be influenced by environmental factors such as temperature, salinity and oxygen or food availability, subsequent body size increase during recovery intervals may relate to environment amelioration. The recovery from the end-Triassic mass extinction event (*c*. 201 Ma) is recorded within the Lower Jurassic-aged Blue Lias Formation of Great Britain. Here we document body size changes in bivalve molluscs during this recovery interval. We find a body size increase within-species from multiple families and ecologies during the opening two million years of the Jurassic. This size increase is most dramatically demonstrated by the epibyssate bivalve *Plagiostoma giganteum*, which increased in size by 174%. We attempt to relate these body size increases to changing environmental parameters during the recovery from the end-Triassic mass extinction event.

Palaeoecology of *Voulteryon parvulus* (Eucrustacea, Polychelida) from the Middle Jurassic of La Voulte-sur-Rhône fossil Lagerstätte (France)

Denis Audo[1], Ninon Robin[2], Javier Luque[3,4], Michal Krobicki[5], Joachim T. Haug[6], Carolin Haug[6], Clément Jauvion[2] and Sylvain Charbonnier[2]
[1]*Yunnan University, China*
[2]*Muséum national d'Histoire naturelle, France*
[3]*University of Alberta, Canada*
[4]*Yale University, USA*
[5]*AGH University of Science and Technology, Poland*
[6]*Ludwig-Maximilians University of Munich, Germany*

Exceptional and extremely rare preservation of soft parts, eyes, or syn-vivo association provide crucial palaeoecological information on fossil-rich deposits. Here we present exceptionally preserved specimens of the polychelidan lobster *Voulteryon parvulus*, from the Jurassic of La Voulte-sur-Rhône Lagerstätte, France, bearing ocular facets, ovaries,

and a unique association with an epibiont thecideoid brachiopod, giving insights into the palaeoenvironment of this Lagerstätte. In *V. parvulus* the eyes are mostly covered by hexagonal facets, likely representing apposition eyes (well suited for bright light). The holotype, however, also preserves square facets typical of reflecting superposition optics (better suited for dim light). This combination might represent: a) a paedomorphic retention of larval eyes; or b) an artefact of the facet packing. Therefore *V. parvulus* eyes were probably poorly adapted to low light palaeoenvironments, suggesting an allochthonous, shallow water origin. However, the presence of thecideoid brachiopod ectosymbionts on its carapace, usually associated with dim-light paleoenvironments and/or rock crevices, suggests that *V. parvulus* lived in a dim-light setting. Since the La Voulte palaeoenvironment is considered deep water and had a soft substrate, *V. parvulus* migrated or was secondarily transported into the La Voulte Lagerstätte setting. La Voulte biota appears therefore to combine the influence of multiple palaeoenvironments.

Sticky fish: the unusual skeletal taphonomy of Middle Triassic actinopterygians

Susan R. Beardmore[1], Patrick J. Orr[2], Heinz Furrer[3] and Duncan J. E. Murdock[1]

[1]*Oxford University Museum of Natural History, UK*

[2]*University College Dublin, Ireland*

[3]*University of Zurich, Switzerland*

Middle Triassic sediments from Monte San Giorgio were deposited in a small restricted basin below a stratified water column. Here we reconstruct the unusual skeletal taphonomy of the actinopterygian *Saurichthys*. Specimens often exhibit some or all of the following: high overall completeness; high articulation of some skeletal parts yet extensive disarticulation of others; displacement of skeletal units, notably the axial skeleton relative to the lateral scale rows; and twisting of the posterior body. This combination of features can be linked to the process of 'stick and peel'. Following deposition, high articulation and completeness was maintained when specimens adhered to the substrate – the 'sticking' that prevented extensive element movement and removal. The articulated but offset positions of the scale rows and axial skeleton result from the latter ripping away from the substrate – the 'peeling' part of the process. In several specimens, peeled skeletal parts show twisting and rolling, interpreted as the effects of weak current activity. The recognition of such preservational features in vertebrate fossils informs on environmental conditions at the sediment–water interface, as well as the specimens' taphonomic history. This study expands the number of examples of 'stick and peel' identified in fossil vertebrates, which potentially also includes conodonts.

Changes in mammalian mandibular ecomorphological disparity across the K-Pg boundary

***Gemma L. Benevento[1,2], Matt Friedman[3] and Roger B. J. Benson[2]**

[1]*University of Birmingham, UK*

[2]*University of Oxford, UK*

[3]*University of Michigan, USA*

The mammalian adaptive radiation after the Cretaceous–Palaeogene (K-Pg) boundary was a major event in the evolution of terrestrial ecosystems. Clear evidence exists for an increase in maximum body size and body size disparity across the boundary, but patterns for other

traits are less clear, due primarily to a focus on different measures of disparity, individual subclades, or restricted geographic regions. We quantified mammaliform mandibular functional disparity using six mechanically relevant mandibular ratios for 271 species, from the Early Jurassic–Eocene. Total jaw functional disparity was low throughout the Mesozoic, and remained low across the K-Pg. This resulted from a pattern of turnover and replacement, due to a marked decrease in stem-therian disparity, alongside a substantial increase in crown-therian disparity. Paleocene and Eocene therians explored previously unoccupied regions of function space, suggesting that they were able to realize novel ecologies during the Cenozoic. Therian disparity increased bin-to-bin from the Cretaceous until the end-Eocene, and exceeded maximal Mesozoic disparity for the first time during the Eocene. Our results suggest that increases in jaw ecomorphological disparity lagged behind increases in body size disparity. This delayed increase in mandibular morphological disparity likely reflects a period of evolutionary recovery after the K-Pg mass extinction.

3D geometric morphometric analysis of endocranial shape variation in the squirrel-related clade and their fossil relatives: contributions of locomotion and phylogeny to brain shape

Ornella C. Bertrand[1] and Mary T. Silcox[2]
[1]*University of Edinburgh, UK*
[2]*University of Toronto Scarborough, Canada*

Three-dimensional geometric morphometrics was employed to understand the possible association between endocranial shape and variables such as locomotion and phylogeny within the squirrel-related clade. This clade is taxonomically and ecologically diverse, and includes tree squirrels, the mountain beaver and dormice. Virtual endocasts for Ischyromyidae, a primitive group of rodents likely to be related to the squirrel-related clade, were also included. A total of 30 landmarks were taken on 32 extant and fossil specimens. The principal components analysis reveals that endocranial shape is distinct for Sciuridae, Aplodontidae, Gliridae and Ischyromyidae. Endocranial shape variation is associated with changes in the development of the neocortex, cerebellum and olfactory bulbs. In the principal components analysis, flying squirrels show the most distinctive endocranial morphology among squirrels, overlapping the least with other tribes and subfamilies. This result suggests that gliding may have imposed specific constraints on cranial shape and indirectly on endocranial shape. The endocasts of fossil and modern fossorial Aplodontidae have a shape similar to those of Ischyromyidae. This finding could be the result of convergence related to fossorial specializations in later-occurring Aplodontidae, as previously hypothesized. From the data gathered, phylogeny and locomotion both have an impact on endocranial shape in our rodent sample.

Using ancestral duplications to date the origin of fundamental genes

***Holly Betts, Tom A. Williams, Philip C. J. Donoghue and Davide Pisani**
University of Bristol, UK

Gene duplication events can provide us with extra information regarding the divergence times of species by affording an extra calibration opportunity. This works by applying the same calibration to speciation events on either side of a duplication. With this in mind, we aimed to use such events in the phylogenies of ancient genes, along with molecular

clock methods, to date the last universal common ancestor (LUCA) as well as the origin of these genes prior to LUCA. We used eight key genes which are fundamental to cell processes across life, including signal recognition proteins and ATPases, along with 11 robust calibrations based upon fossil and geological information, applied using both cross-calibration and cross-bracing. In each case this produced a timescale for the gene trees beginning >4.4 billion years ago in the Hadean Eon with LUCA diverging soon after >4 Ga. Though the confidence intervals on the nodes in all cases are relatively large, in general they overlap with previously obtained divergence date estimates. This method helps us to delve deep into the evolutionary history of life on our planet, investigating when it originated down to the level of individual genes.

Oxygen, temperature, and the stenothermal cradle of Ediacaran evolution

Thomas Boag[1], Richard Stockey[1], Leanne E. Elder[2], Pincelli M. Hull[2] and Erik A. Sperling[1]
[1]*Stanford University, USA*
[2]*Yale University, USA*

Ediacaran fossils document the early evolution of complex macroscopic life, contemporaneous with geochemical evidence for widespread marine anoxia. This suggests that early animals experienced frequent hypoxia. As such, research has focused on the concentration of molecular oxygen (O_2) required by early animals, while also considering the impacts of climate. One hypothesis is that the Ediacaran biota originated in cold, shallow-water environments due to increased O_2 solubility in such regions. Here we demonstrate, using principles of gas exchange, that temperature does have a critical role in governing the bioavailability of O_2 – but in cooler water the supply of O_2 is actually lower. Further, the fossil record suggests the Ediacara biota first occur as early as 571 Ma in deep-water slope facies, before appearing in shelf environments ~555 Ma. We propose an ecophysiological underpinning for this pattern. Using respirometry physiology experiments, we show that in the shallow mixed layer where seasonal temperatures fluctuate widely, thermal and pO_2 effects are highly synergistic. The result is that temperature change away from species-specific optima impairs tolerance to low pO_2. We hypothesize that deep and particularly stenothermal environments in the Ediacaran ocean were a physiological refuge from the synergistic effects of temperature and low pO_2.

Quantifying patterns of convergent evolution: a case study on mammalian insectivores

***Robert J. Brocklehurst[1], Nick Crumpton[2], Louise Tomsett[3] and Natalie Cooper[3]**
[1]*University of Manchester, UK*
[2]*Royal Society, UK*
[3]*Natural History Museum, London, UK*

Convergent evolution is an important and ubiquitous phenomenon in the history of life. Despite this, quantifying patterns of convergence remains challenging, as current methods require strict *a priori* definitions of convergent taxa, don't cope well with multivariate trait data or can't be used with fossils. Here we explore a new set of methods for identifying and quantifying convergence which avoid all three of these problems. As a case study, we examine patterns of convergent evolution between mammalian insectivores from Afrotheria and Laurasiatheria, comparing tenrecs (Tenrecidae) to moles (Talpidae), shrews

(Soricidae) and hedgehogs (Erinaceidae). We used jaw and skull shape, quantified using geometric morphometrics, as our input phenotypic data. Putatively convergent taxa were identified by comparing phenotypic and phylogenetic distance matrices, with low phenotypic:phylogenetic distances indicating convergence. The degree of convergence between these taxa was then quantified, using a new implementation of the R package 'convevol'. Our results show significant convergence between Tenrecidae and members of Talpidae and Erinaceidae, with convergent evolution closing ~50 % of the phenotypic distance between some taxon pairs. These findings provide insights into patterns of convergence and macroevolution in mammals, and our new methods can be generalized to other groups, including fossils.

Evolution of lower Famennian (Upper Devonian) fossil assemblage from Kowala quarry (Holy Cross Mountains, central Poland)

Krzysztof Broda and Anna Łazuka
University of Silesia, Poland

The lower Famennian (Upper Devonian) fossils from the Kowala quarry (southwestern Holy Cross Mountains, central Poland) have been studied in detail for many years. However, the fossil assemblage present within the strata has never been analysed as an ecosystem. The most common fossils are brachiopods associated with characteristic non-trilobite arthropods, such as Thylacocephala. During our fieldwork a total of 2,438 specimens were collected. At least 32 specimens were collected from each of the beds investigated, regardless of the type or preservation. Each specimen was cleaned and identified. Based on these data, a database was created that allowed us to study the changes in assemblage over time. In the studied strata, a gradual drowning of the Holy Cross Mountains carbonate platform is marked by a slow increase in the amount of nektonic fauna. Additionally, nine peaks of rapid increases in the number of arthropod fossils (especially Thylacocephala) are observed. After these 'events' the number of thylacocephalans decreases. Such relatively short-term changes are likely associated with environmental fluctuations. To test this, geochemical (main and trace elements, biomarkers, total organic carbon, total sulphur analyses), mineralogical (clay mineral analyses) and sedimentological analyses have been performed. The results will be presented.

Constructional and functional morphology of Ediacaran rangeomorphs

Nicholas J. Butterfield
University of Cambridge, UK

Ediacaran rangeomorphs are famously problematic, both in terms of phylogenetic affiliations and how they worked as organisms. Reassessment of their taphonomy and associated fluid dynamics sheds important new light on their construction, feeding and gas exchange. Differential sedimentary infills demonstrate that they were supported by a hydrostatic exoskeleton analogous to that of anthozoan cnidarians. On the assumption that internalized seawater was regularly recharged by ciliary pumps, such compartmentalization further resolves the question of rangeomorph feeding. Although the inertial and advective fluid regimes associated with large size preclude true osmotrophy, the multicellular containment of this process allowed external digestion to be conducted at macroscopic length scales. In a world devoid of motile macroscopic prey there is no expectation that such bag-like bioreactors be accompanied by obvious muscle, mouth

or other feeding structures, though they are likely to have hosted a resident microbiome capable of digesting recalcitrant DOC. While the 'inside' of rangeomorphs introduced a revolutionary new means of external digestion, the current- and turbulence-exposed outside would have fundamentally expanded capacity for both food collection and gas exchange. Phylogenetically, this multicellular bag-like habit can be viewed as a shared derived character uniting all but the most basal total-group eumetazoans.

Giant stem group gastrotrichs from the early Cambrian

Ailin Chen[3], *Luke A. Parry[1], Fan Wei[4], Jakob Vinther[2] and Peiyun Cong[4]

[1]*Yale University, USA*

[2]*University of Bristol, UK*

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The phylum Gastrotricha belongs to the superphylum Spiralia, with their close relatives found among flatworms, brachiopods, molluscs and annelids. Their adult body size does not exceed 3 mm, making most representatives members of the permanent meiofauna. Phylogenomic analyses position gastrotrichs near the base of the spiralian tree of life, along with other microscopic lineages such as gnathiferans and rotifers. On this basis, spiralians have been inferred to evolve from a microscopic ancestor, with large body size representing a later innovation in this diverse group of protostomes. We describe two new species of large-bodied, dorso-ventrally flattened vermiform animals from the early Cambrian Chengjiang biota of southwest China that phylogenetic analyses resolve as stem group gastrotrichs. To the exclusion of all other phyla, these organisms share with gastrotrichs a bipartite gut with a sclerotized pharynx and a triangular lumen, hydropores, a cuticular oral hood, a fine covering of small epidermal spines and putative ventral ciliary bands. These organisms exceed 10 cm in length, making them an order of magnitude larger than any extant gastrotrich. Our results suggest that colonization of the meiofauna has happened repeatedly in spiralians in multiple lineages, including gastrotrichs, annelids and possibly gnathiferans.

Uncovering the impact of palaeogeography on taphonomy: an investigation of the Mazon Creek Lagerstätte

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The preservation of soft-tissues is an incredibly rare occurrence, commonly restricted to specific depositional regimes for brief moments of geological time offering an important 'window' into the geological past. The Mazon Creek Lagerstätte (Illinois, USA) is one such fossil bed, where a diverse assortment of late Carboniferous marine and terrestrial fossils have been described within siderite concretions. Commonly, both recalcitrant (bone, teeth *etc*.) and soft-tissues (integument, organs and pigments *etc*.) are reported to preserve, yet the mode of preservation is poorly understood. In order to elucidate the controls on exceptional preservation in siderite concretions, we utilized museum collections, fieldwork and geochemical analyses (SEM-EDX and XRF) to create the first taphonomic model for soft-tissue preservation in Mazon Creek, identifying that soft-tissues are preserved by clay

templating. We also identify, for the first time, that preservation potential of soft tissues in the Mazon Creek Lagerstätte is not primarily controlled by tissue histology, or salinity as was previously suggested, but by palaeogeography, particularly proximity to the palaeo-coastline. The impact of palaeogeography is an undervalued control on preservation and has important implications for future investigations of exceptionally preserved organisms, especially in geographically vast sites where ambiguous early vertebrates have been described.

The Ediacaran fauna of the Llangynog Inlier, Carmarthenshire

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The Ediacaran fauna of the Llangynog Inlier in South West Wales occurs in rock mapped by the British Geological Survey as being of Early Ordovician (Arenig/Floian) age and is preserved in volcaniclastic sediments. The fauna appears to find its closest comparison in the Fermeuse Formation of Newfoundland, Canada and is likely to be of similar age. The discoid fossil *Aspidella*, the earliest described Precambrian fossil, dominates the Llangynog Ediacaran fauna. These small discs abound on some bedding planes, both as hyporeliefs and epireliefs. Unlike the report by Gehling *et al.* (2000) on the genus in Newfoundland, at Llangynog there is a disjunct size relationship between *Aspidella* and both the larger and much less frequently occurring *Ediacaria* and the flatter *Spriggia* disc preservation, with no size continuum. Preserved axial structures on a few *Aspidella* lend support to the hypothesis that *Aspidella* discs originally supported a frond-like structure. Rarer fossils from Llangynog include the body-fossils *Hiemalora*, *Yelovichnus* and *Palaeopascichnus*; there are also trace fossils, including one form apparently unique to this locality.

When forams go big: drivers of extreme size in the genus *Nummulites*

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Select genera of benthic foraminifera achieve exceptionally large sizes during specific intervals of time throughout geological history. However, the mechanisms driving temporal size variations in larger benthic foraminifera (LBF) remain incompletely understood. The ability of *Nummulites* to achieve extremely large cell size during peak global warming in the Middle Eocene counters size predictions based on first principles of cell physiology. These observations suggest that other abiotic or biotic factors facilitated their attainment of large sizes. As *Nummulites* is well-documented in addition to being one of the best temporarily constrained LBF, we use Tethyan *Nummulites* as a model group to better understand the factors driving their size evolution over the Eocene. We compiled data on both the ecological traits of *Nummulites* and Eocene oceanographic conditions within the Tethyan region, including mean temperature sea-level, oxygen concentration and seawater carbonate saturation. We coupled these biotic and abiotic data to our size dataset of more than 150 species, including both A and B forms. Statistical analysis of this unique dataset will provide new insights into the primary driver(s) that shaped the distribution of *Nummulites*' sizes during the Eocene in addition to shedding light on the evolutionary history of LBF over the Palaeogene.

Developmental innovation in the evolution of complex mammalian teeth

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Increases in morphological complexity are thought to be important in the acquisition of key innovations that permit subsequent adaptive radiation. However, the extent to which increases in morphological complexity are shaped by limits on trait variation imposed by development is uncertain. Mammals have radiated into a remarkable spectrum of ecological niches due in large part to their complex, multicusped chewing teeth, which permit a wide range of foods to be processed. During development, mammalian tooth cusps arise as embryonic gene-signalling centres called enamel knots that regulate the growth and differentiation of the tooth germ. Using a computer model of tooth development, we systematically examined how tinkering with signalling and tissue growth influenced the number and position of tooth cusps. We find that transitions from single to multicusped teeth require large changes in developmental parameters and consistently resulted in antero-posterior iteration of enamel knots. This produced dental phenotypes reminiscent of the transition from eucynodonts to basal mammaliaforms like morganucodontids. More complex teeth (>five cusps) exhibited higher nearest-neighbour disparity than simpler teeth and had enamel knots arranged in a triangular configuration. Our results suggest that fundamental shifts in cusp patterning in basal holotherian mammals enabled the rapid evolution of complex therian mammal dentition.

Stratigraphic and environmental control on marine benthic community change through the early Toarcian extinction event (Iberian Range, Spain)

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Causes of extinction during the early Toarcian (Early Jurassic) extinction event are debated. Anoxia has been long considered a global trigger, until extinction was also observed in fully oxygenated sediments of the western Tethys. To better understand controls on Toarcian marine ecosystems, we integrated quantitative analyses of benthic macro-invertebrates, high-resolution geochemical analyses on the bulk sediment (TOC, $\delta^{13}C$, $\delta^{18}O$) and brachiopod and belemnite shells ($\delta^{13}C$, $\delta^{18}O$), and sequence stratigraphy, from two western Tethys sections (Iberian Range, Spain). In the shallower section, changes in richness and evenness correlate with TOC, suggesting that variations in nutrient input from runoff, and the possible onset of local low-redox conditions, controlled faunal diversity. In the deeper section, however, community change correlates with changes in $\delta^{18}O$, indicating that temperature and salinity variations might have influenced the fauna. The two localities also show different stratigraphic patterns of extinction, with last-occurrences clustering at the maximum flooding surface in the shallower section, and at the transgressive surface in the deeper one. Our results highlight the importance of local sedimentary and stratigraphic processes in controlling patterns in the geochemical and fossil records, and the need to study multiple localities along onshore–offshore gradients before extrapolating to regional and global scales.

Persistence of the Lilliput effect across evolutionary and ecological scales

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Body size has been a research focus for generations of palaeontologists. Most studies focus on long-term evolutionary trends within or across lineages or on short-term variations in the context of evolutionary crises. Here we address how the oft-cited Lilliput effect compares across spatio-temporal scales, based on a compilation of more than 6,000 interval-to-interval changes of body size in marine taxa. To assess body-size changes, we used the log-ratio of the geometric means of body-size estimates from one interval to the next. There is a tendency of effect size and variance to increase with temporal and taxonomic scale suggesting that changes in body size are largely manifested in macroevolutionary rather than phenotypic processes. Some higher taxa such as crinoids and orthoconic nautilids appear to be more prone to body size changes than others. Effect sizes are weakly but significantly correlated with body size, suggesting that larger organisms are more prone to body size change than smaller organisms. Negative changes of body size are significantly more pronounced during changes from background to crises intervals than in any other combination of the background-crisis-survival-recovery intervals. This maintains that the Lilliput effect in the broadest sense is a common phenomenon during evolutionary crises.

A third "acanthodian" stem-chondrichthyan endoskeleton in a uniquely well-preserved specimen of *Diplacanthus crassisimus*

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The anatomy of the braincase and visceral arches in 'acanthodians', a problematic grade of early chondrichthyans (sharks, rays and elephant sharks), has been instrumental in making and breaking theories of relationships and evolution among early vertebrates. Despite this prominence, acanthodian endoskeletal anatomy remains poorly understood and limited largely to two taxa: *Acanthodes* and *Ptomacanthus*. Here we describe a third acanthodian endoskeleton in a uniquely well-preserved specimen of the Middle Devonian (393–383 Ma), diplacanthid *Diplacanthus crassisimus*. The dermal skeleton of *Diplacanthus* is relatively completely known and morphologically dissimilar from *Ptomacanthus* and *Acanthodes*, making its endoskeleton a valuable third source of information. The architecture of the braincase and branchial skeleton in *Diplacanthus* conforms with general expectations for a stem-chondrichthyan, having a ventral fissure, anotico-occipital fissure and five branchial arches. Like *Acanthodes*, and unlike more 'shark-like' stem-chondrichthyans, the parachordal region of the neurocranium in *Diplacanthus* is laterally constricted, and a foramen is present in the metapterygoid of the palatoquadrate for the facial branch of the trigeminal (V) nerve. Unexpectedly, the median dorsal aorta of *Diplacanthus* is invested in the basicranium. The similarity between the braincases of *Diplacanthus* and *Acanthodes* supports the proposal that acanthodids, diplacanthids and ischnacanthids comprise a clade which is the sister group to all other chondrichthyans including climatiids.

Modelling extinction cascades across a Mesozoic hyperthermal event

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In order to fully understand ecosystem collapse across mass extinction events, it is essential to consider extinction dynamics within a trophic community framework. Ecological theory suggests that many victims of past extinction events did not become extinct as a direct effect of abiotic stress, but probably did so in response to cascading secondary effects. Here we use data from the Whitby Mudstone Formation, Cleveland Basin, UK to investigate extinction cascades in response to the early Toarcian extinction event (EToE; *c.* 183 Ma, Lower Jurassic), a second order mass extinction event associated with hyperthermal warming that caused the loss of around 25 % of marine genera. Species and guild-level food webs were reconstructed for pre- and post-extinction ecosystems using optimal foraging models that predict food web structure based on body size, the number of links and additional foraging trait data. Trophic extinction cascades were simulated across the extinction event in order to assess ecosystem robustness to informed and random primary extinction events. Model outputs were then compared to empirical post-extinction food webs to determine the likely abiotic driver of ecosystem collapse. Results show benthic organisms with high metabolic demands were selected against, which fits well with an anoxia/high temperature primary kill mechanism.

Palaeobiology of the Ediacaran Rangeomorpha: resolving morphological disparity

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The late Ediacaran (~571 – 541 Ma) Rangeomorpha are a group of frondose organisms that recent studies suggest are ancient metazoans. However, until increased resolution of their potential relationships to extant animals is achieved, their capacity to inform early animal evolution cannot be fully realized. We present a reassessment of the anatomy and ontogeny of the rangeomorph genera *Charnia*, *Fractofusus* and *Hylaeculullus*, which together sample the major rangeomorph groups (uniterminal, biterminal and multiterminal) to provide a comprehensive overview of the current state of knowledge regarding the biology of the rangeomorphs. We reveal a sympodial organization of the central axis, and a departure from diagnostic rangeomorph branching architecture, in *C. masoni*; a novel pattern of growth – termed 'eccentric branching' – in *H. fordii*; and confirm indeterminate growth in *Fractofusus*. Integration of this new information with recent palaeoecological studies permits us to present a new model for the biology of the rangeomorphs, illustrating far greater anatomical and ontogenetic diversity amongst the Rangeomorpha than previously recognized.

The rise of dinosaurs: tetrapod diversity and climate during the Late Triassic

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The Late Triassic was a key interval in tetrapod evolution, encompassing the radiations of several major lineages, such as mammals, crocodylomorphs and dinosaurs. Current hypotheses propose climate-driven palaeolatitudinal structuring of Late Triassic tetrapod faunas (*e.g.* sauropodomorph dinosaurs are proposed to have been absent from low latitude regions due to 'unstable' climatic conditions). However, these hypotheses remain largely untested. We investigated global patterns of Late Triassic tetrapod diversity using sampling standardization and tree-based biogeographic approaches. To test specific hypotheses linking dinosaur diversity with climate, we utilized, for the first time, the results of a spatially-explicit general circulation climate model. We found that Late Triassic tetrapods do not conform to a modern-type latitudinal biodiversity gradient and that communities were palaeolatitudinally-structured, suggesting that faunas tracked global climate zones. Our results support the previous assumption that palaeolatitude is a good proxy for mean annual surface temperature (MAT). When compared to all tetrapods, dinosaurs preferentially occupied drier and hotter environments, with less seasonal variation in precipitation. However, sauropodomorphs occupied areas with significantly lower MAT and high seasonal temperature ranges. This work provides the first quantitative support for palaeoclimate as a major control on the distribution of Late Triassic tetrapods, including early dinosaurs.

Cracking the link between brain and skull in Archosauria: evolutionary and developmental perspectives

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The brain has a primacy in early cranial development. Extant birds underwent an enlargement of the brain in comparison to other reptiles. This process caused important changes to the bird skull, in particular the skull roof. However, a link between the brain regions and the skull roof elements has never been formally addressed. CT scanning, immunofluorescence and confocal imaging were combined to track mesenchymal condensation and ossification patterns of the skull roof along the development of the brain in a developmental series of archosaurs. Correlation tests between the boundary of brain regions and the suture between frontal and parietal were statistically significant, suggesting a deep evolutionary link. Mesenchymal cells condense early in organogenesis between the forebrain and midbrain and midbrain and hindbrain. However, it is only after establishment of the facial region and its chondrogenesis that the mesenchymal condensations of the skull roof start to express Collagen I. We found no support for Sox9 and Collagen II expression in these mesenchymal condensations. Birds show a delayed patterning of the skull in comparison to reptiles. We suggest this is due to the positive allometry of the bird brain, contrary to the negative trajectory observed in reptiles.

Craniodental functional morphology indicates niche partitioning amongst sympatric marine reptiles

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Jurassic marine ecosystems (*c.* 201–145 Ma) were dominated by three different lineages of reptiles – plesiosaurians, ichthyosaurians and thalattosuchian crocodylomorphs. Using datasets of functionally significant dental and craniomandibular characters, we investigated the mechanisms enabling the coexistence of these three groups in the Jurassic Sub-Boreal Seaway (JSBS) across ~18 million years of environmental perturbations. Our multivariate approach establishes an objective protocol to categorize species into 'Feeding Guilds', making it possible to track the evolution of ecologically meaningful groups through time. Our quantitative results validate previously-assessed feeding ecologies based on qualitative characters, and reveal multiple instances of convergent evolution. The lack of overlap amongst groups in our multivariate ordination spaces suggests that morphofunctional differentiation may have enabled niche partitioning/specialization. Time-binned disparity analyses also indicate that the decline and success of different clades over time may be linked with ecological changes related to sea-level fluctuations. Specifically, sea level deepening would have favoured the diversification of large-bodied, macrophagous pelagic clades, and decline of small-bodied, piscivorous coastal groups. As modern marine tetrapod faunas are also characterized by niche partitioning and spatial variation related to sea depth, we suggest that a conserved set of ecological assembly rules structured marine ecosystems through evolutionary time.

Endocranial anatomy of a 400-million-year-old stem-gnathostome: new insights into jawed vertebrate origins

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The past decade has seen a revolution in our understanding of stem-gnathostome evolution, in particular with placoderms being reinterpreted as a paraphyletic group. More recently, however, major discrepancies in the relative branching positions of different 'placoderm' clades, as well as renewed suggestions of 'placoderm' monophyly, indicate that current hypotheses of relationships may not be robust. Key to solving this problem is a detailed understanding of the endocranial anatomy of key taxa, many of which were described decades ago on the basis of external morphology. Here we redescribe the endocranial anatomy of *Brindabellaspis*, typically resolved as an early-diverging member of the 'placoderm' grade. CT scanning of the braincase reveals an unexpected mosaic of characters. An anteriorly directed hypophysial complex and wide separation between the labyrinth and cranial cavity are reminiscent of jawless fish braincases, while the elongate sinus superior and well-developed crus commune are crown gnathostome features. These new anatomical details have a profound effect on placoderm interrelationships, suggesting that *Brindabellaspis* may branch closer to the gnathostome crown node than previously thought, and that typical placement of antiarchs and arthodires may not be accurate. Together, these results have important implications for our understanding of early jawed vertebrate evolution.

Australia's polar Cretaceous mammals: longer lifespans may be indicative of hibernation

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Excavations in Victoria, Australia have produced rare Early Cretaceous (Aptian) mammals. In the Aptian, the site lay within the Antarctic Circle, so what strategies did these tiny mammals use to survive the polar winter, with months of twilight and relatively low temperatures? Although the jaws have suffered some deformation, the internal preservation is excellent and synchrotron radiation computed tomography (SRCT) reveals histological detail. Two lines of evidence suggest longer lifespans than would be expected from extant mammals of similar size. One is from counts of tooth cementum, a tissue with incremental annuli, from which individual age at death can be assessed. The other is the presence of secondary osteons, produced by bone remodelling, due to micro damage. These are rare in small animals which do not experience high loading, but are found in mammals with longer lifespans where there is time to create significant micro damage. There is a strong correlation between body mass, lifespan and basal metabolic rate (BMR). The small size and extended lifespans of these mammals therefore suggests a low metabolic rate and/or heterothermy, entering torpor or hibernation during the polar winter.

Does the diversity and succession of microbial communities during decay influence character loss?

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The correct interpretation of fossils is fundamentally linked to our understanding of decay, especially in the case of exceptionally-preserved soft bodied remains. Decay influences the preservation potential of characters, and patterns of character loss appear to be conserved between related taxa, even when experimental conditions are altered. This undoubtedly reflects both the results of decomposition by microbes and the nature of soft tissues; however, our understanding of microbial decay in this setting is limited. Previous work has investigated bacterial biofilm formation, the effect of clays on microbial community success, and patterns of microbial succession in terrestrial vertebrates as it relates to forensics. But how rates and sequences of character loss are linked to the diversity and succession of microbial communities during decay is unknown. Here we use next-generation sequencing of bacterial DNA to investigate the relationship between the diversity/abundance of microbial communities (bacteria and archaea) and the rate/sequence of character loss during controlled amphioxus decay. We address important questions regarding the degree to which microbial succession controls decay, and how different clay mineral substrates affect the succession of microbial communities and sequences of character loss.

The independent origin of plant roots and their gradual evolution in lycophytes

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Mapping fossil traits on to the land plant phylogenetic framework indicates that there were at least two independent origins of roots among extant vascular plants – one in lycophytes (clubmosses) and independently in euphyllophytes (monilophytes and seed plants). Three rooting structure bauplans are preserved in the extensive lycophyte fossil record. First, the common ancestor of lycophytes lacked roots and instead developed bilaterally symmetric regions of horizontal axes that developed rhizoids. Subsequently rooting axes evolved but these lacked root hairs and root caps. Finally, roots evolved comprising axes on which root hairs and root caps developed. Recognizing these three rooting bauplans demonstrates that the defining characters of extant lycophyte roots evolved gradually in the lycophyte lineage.

Ultra- and nanostructure of conodont dental skeleton and implications for its properties

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Conodonts were the first vertebrates to develop a biomineralized phosphatic skeleton. Their dental tools resemble teeth functionally, but their internal structure and the mechanism of growth are unique. Over nearly 300 million years of their evolution, conodont feeding apparatuses achieved stupendous morphological diversity, hypothesized to reflect a broad dietary, ecological and developmental variation. In order to investigate whether dietary adaptations are expressed at the ultrastructural level, we undertook a systematic characterization of the ultrastructure of conodont dental tissues. Using electron backscatter diffraction, X-ray diffraction, small-angle neutron scattering and atomic force microscopy, we demonstrate that conodont biomineralized tissues have a hierarchical organization, in which mesoscopic crystals are formed by nanosized crystalline units separated with an intergranular organic sheath. This nanogranular structure is emerging as a common feature of many biominerals, associated with distinct structure-relationship properties.

The extraordinary diversity of Teleosauroidea (Crocodylomorpha, Thalattosuchia): a comprehensive analysis of their evolutionary relationships

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Thalattosuchia was an extraordinary group of marine crocodylomorphs that flourished within the Mesozoic Era, evolving many feeding specializations and environmental adaptations. One of the two major thalattosuchian groups is Teleosauroidea, which has been historically dismissed as simply a group of Jurassic marine 'gavials'. But teleosauroids

attained a near-global distribution, were diverse morphofunctionally as well as in body size, and frequented shallow marine/brackish ecosystems throughout the Jurassic. Despite increased anatomical research over the past ten years, the evolutionary relationships within Teleosauroidea are still poorly understood and little studied. One particular problem in teleosauroid taxonomy is the waste-basket genus '*Steneosaurus*', whose validity is in question. Here we present an in-depth, comprehensive phylogenetic analysis of Teleosauroidea. Our dataset includes 152 crocodylomorph taxa (26 teleosauroids) scored for 495 characters. We recover two major subclades within Teleosauroidea: 1) a Sub-Boreal northern European/Tethyian/Eastern Gondwanan '*Steneosaurus*' + *Machimosaurus* radiation, which were the most successful teleosauroids in terms of species richness, feeding specializations and morphofunctional diversity; and 2) a second Laurasian radiation which includes more terrestrial and bizarre-looking teleosauroids. We highlight and explore the oddities of key taxa, such as marine forms (*e.g. Aeolodon*), heavily armoured forms (*e.g. Platysuchus*), blunt toothed forms (*e.g. Machimosaurus*) and the bizarre, one-of-a-kind, *Mycterosuchus*.

Recovering from an extinction event: a serpent approach

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Mass extinctions have played a key role in shaping biodiversity over macroevolutionary timescales, by repeatedly resetting ecosystems, clearing away vast numbers of taxa and providing opportunities for survivors. Following the demise of numerous vertebrate groups at the Cretaceous–Palaeogene (K-Pg) boundary (66 Ma), studies show that mammals, birds, frogs and teleosts recovered and radiated in the early Palaeogene. However, the effect of the extinction on the macroevolutionary patterns in snakes remains poorly understood. Using a molecular clock approach on sequence data with fossil calibrations, we reveal that crown snakes radiated within the first 5 Ma after the K-Pg extinction event. The radiation was focused within Afrophidia - a clade comprising ~90 % of modern snake taxa – that simultaneously successfully spread to Asia. Our results show a decoupling of diversity and morphological disparity post-extinction, with disparity not recovering until the early Eocene. We also reveal a second extinction and recovery event in the Oligocene, with the extinction of all Palaeogene marine snakes and a concurrent drop in disparity, and the radiation of Caenophidia. These events demonstrate the dramatic influence of abiotic events on the macroevolutionary patterns of vertebrate faunas.

Predatory behaviour and taphonomy of a Jurassic belemnoid coleoid (Diplobelida, Cephalopoda)

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We describe a complete specimen of *Clarkeiteuthis conocauda* (Cephalopoda) from the Toarcian (Jurassic) preserved with a bony fish (*Leptolepis bronni*) in its arms. Based on their arrangement, we suggest that the diplobelid caught and killed the fish while still in well-oxygenated waters and then sank into oxygen-depleted water layers where the cephalopod suffocated. This also explains the exceptional preservation well known from the Posidonia Shale. This raises questions regarding the hunting behaviour of belemnoid Coleoidea. Using the proportions of soft and mineralized body parts of diplobelids and belemnitids, we determined their body mass, buoyancy and the centres of mass and buoyancy. These latter two points were very close to each other in belemnitids, implying a low hydrodynamic stability (without fins), while in diplobelids the distance between those centres was bigger. This suggests that diplobelids often assumed an oblique to vertical orientation of the long body axis while belemnitids could achieve a horizontal posture. Presuming larger fins were attached to the bigger belemnitid rostra, belemnitids were better swimmers that actively chased prey, while diplobelids were ambush predators covering only short distances.

Comparative taphonomy of embryo-like fossils from the Ediacaran Doushantuo and Cambrian Kuanchuanpu formations of South China

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The 609 Ma Weng'an biota from the Doushantuo Formation of South China famously yields microfossils interpreted as animal embryos, but this affinity is widely debated. Unequivocal animal embryos are known from the early Cambrian Kuanchuanpu Formation, which is within the same succession as the Doushantuo Formation and has a similar diagenetic history, with the fossiliferous beds in both formations comprising phosphatized fossils within a marine limestone. This provides a point of comparison between them, since if they are similar organisms with similar diagenetic histories, they should show similar patterns of preservation. We use a combination of synchrotron X-ray tomography and electron probe microanalysis to demonstrate that the embryos of each formation have different preservational pathways: in Doushantuo fossils, the cell interiors mineralized early, and replicated the original biological structure while the membranes degraded and the voids they left either remained as voids or were later infilled, whereas in the Kuanchuanpu embryos, the opposite occurred. The taphonomic history of Kuanchuanpu fossils compares well to the results of taphonomy experiments which demonstrate that cell contents degrade quickly leaving cell membranes available as substrates for mineral replication over long timescales; Doushantuo fossils exhibit a contrasting taphonomic history which may betray different systematic affinity.

talks

Morphological convergence obscures functional disparity in sabre-toothed carnivores

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Sabre-toothed vertebrates are among the most iconic vertebrate fossils. Due to their unusual appearance, taxa such as *Smilodon* have received considerable academic interest. However, sabre-tooths were much more diverse and abundant than individual, well-known species would suggest. Sabre-tooth morphologies have evolved independently at least seven times over the course of 250 million years in Permian mammal-like gorgonopsians, in the marsupial sabre-tooth *Thylacosmilus*, and five different lineages of carnivorous mammals. It is generally assumed that the cranial function of all sabre-toothed vertebrates was largely comparable. However, this assumption has not been tested in detail from a biomechanical perspective, and it is further unknown if the same evolutionary trends led to the convergent emergence of sabre-toothed morphologies in different clades. Using digital visualization, biomechanical analyses and evolutionary modelling, functional performance measures were compared across seven sabre-tooth groups (absolute/effective jaw gape, bite force, mandibular stability). The results demonstrate that these performance measures varied considerably between different groups and between different species. Evolutionary pathways leading to the sabre-toothed morphology were further found to be significantly different between groups. This demonstrates that functional diversity was widespread among sabre-toothed vertebrates but obscured by superficial morphological similarity, and is likely related to differences in ecological niche occupation.

Exceptionally preserved soft parts in echinoderms from the Fezouata Shale (Lower Ordovician, Morocco)

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In the Zagora area (central Anti-Atlas, Morocco), two fossiliferous intervals of the Lower Ordovician Fezouata Shale have yielded abundant and diverse marine assemblages over the last 15 years, comprising a large proportion of soft to lightly mineralized organisms. Some of these exceptionally preserved taxa were previously only known from younger Lagerstätten (*e.g.* cirripeds, eurypterids, xiphosurans). However, a large proportion of the soft-bodied component of the Fezouata biota is dominated by organisms typical of Cambrian, Burgess Shale-type assemblages (*e.g.* anomalocaridids, lobopodians, marrellomorphs). Exceptional preservation was also documented in various members of the shelly component of the Fezouata Biota: *e.g.* in hyolithids (gut), in machaeridians (chaetae, gut, parapodia), or in trilobites (appendages, gut). Echinoderms represent one of the most abundant and diverse components of the Fezouata biota. Here we document strong evidence of exceptionally preserved soft parts in at least four distinct groups of late Tremadocian echinoderms: 1) in eocrinoids: ambulacral canal and associated tube feet in their feeding appendages (brachioles); 2) in solutans: distal part of the gut; 3) in somasteroids: ambulacral canal and tube feet; and 4) in stylophorans: both ambulacral canal and tube feet in their single feeding arm (distal aulacophore) and gut (proximal aulacophore and theca).

Growth and development of fuxianhuiid arthropods from the lower Cambrian (Series 2, Stage 3), Chengjiang biota

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The fuxianhuiids are a small group of arthropods, composed of just seven unequivocal members, all recovered from a five-million-year interval during the lower Cambrian, in what is now Yunnan Province in southwest China. Despite their paucity they are famed for preserving the oldest examples of neural and cardiovascular remains in the fossil record, and occupy a crucial position in most phylogenetic analyses, close to the origin of the arthropod crown group. A study of over 3,000 specimens attributed to various members of this group demonstrates that, despite previous claims, *Fuxianhuia* (the namesake and best-known member of the group) did not accumulate segments gradually throughout its lifetime, but instead observed variations in segment number representing geographical variation. Likewise, claims of parental care could not be verified, with an extensive morphometric analysis indicating that some 'juvenile' specimens attributed to this species actually belong to a different species of fuxianhuiid altogether, namely *Chengjiangocaris longiformis*. Unlike the former, this species did grow via the gradual addition of segments throughout ontogeny. Comparisons to other closely related taxa suggest this mode of development (hemianamorphic development) is the plesiomorphic condition for crown group arthropods.

Why is the Chengjiang biota exceptionally well preserved?

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Elected as a World Natural Heritage site in 2012, the Chengjiang biota is renowned for its exceptional soft-tissue preservation, which provides crucial evidence for early metazoan evolution. However, it is not yet clear why the Chengjiang biota is exceptionally preserved. In recent years, this question has received greater scrutiny with the reporting of exceptionally preserved decay-prone tissues, namely neural, cardiovascular and visual structures. It has often been assumed that these labile tissues do not withstand fossilization and should decay away shortly after the animal's death. However, mounting evidence supports the interpretation of these exceptionally preserved labile structures as true anatomical characters, further highlighting the gap in our understanding of exceptional preservation in Cambrian fossils. In this presentation, I will show how the latest developments in geochemical research shed new light on our understanding of exceptional preservation of the Chengjiang biota. The contrasting redox conditions in the event and background beds indicate that the Chengjiang biota was flourishing in persistently oxic shallow marine environments, while the animals were buried and transported to an adjacent dysoxic deep-water depositional environment, allowing internal tissues to be organically preserved with fidelity. Polymerization appears to be central to the long-term survival of normally decay-prone tissues.

talks

A three-dimensionally preserved Middle Jurassic monofenestratan pterosaur from the Isle of Skye, Scotland

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The Middle Jurassic was a critical time in pterosaur evolution, and several major divergences occurred within the clade during this interval. These included the appearance of monofenestratans, including the 'transitional' wukongopterids and, possibly, the origin of more derived pterodactyloids. However, there are few pterosaur-bearing formations worldwide from this time, so any new discoveries have the potential to substantially improve our understanding of these events. Here we report a three-dimensionally preserved partial pterosaur skeleton found in 2006 in the Bathonian Kilmaluag Formation, near Elgol, Isle of Skye. The specimen is partially prepared and embedded in matrix. Computed tomographic scanning and 3D reconstruction has revealed elements of the wing, axial column and hindlimbs. The presence of a relatively long, slender wing metacarpal supports referral to Monofenestrata, making it one of the earliest monofenestratans known, as well as one of the earliest UK pterosaurs known from an associated skeleton, second only to *Dimorphodon macronyx*. This specimen provides the first solid evidence that monofenestratans were globally distributed before their better-documented diversification in China. As the first pterosaur described from the Isle of Skye, it also provides an important addition to the increasingly diverse Middle Jurassic terrestrial faunas of Scotland.

Tackling the evolution of the Early Cretaceous palaeowetland of Las Hoyas

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Since the early 1990s, the excavations at the upper Barremian Las Hoyas site (Cuenca, Spain) have followed a layer-by-layer procedure with the objective of recording the taphonomic data associated with every fossiliferous layer. This systematic methodology aims towards an interpretation of the ecological dynamics of this palaeowetland at three complementary levels: 1) seasonal facies; 2) complete stratigraphic sections; and 3) horizontal distribution. Firstly, at the seasonal facies level, the occurrence of different proportions in the animal associations in wetter versus drier facies has been detected. Secondly, the analysis of the fern associations, tetrapod remains and tetrapod tracks in sections of the southern area of the locality suggest a tendency towards a shallower water column system. Thirdly, the fossil record of the three different areas in the locality, whose stratigraphic correlations are not yet known, present distinctive characteristics: the western area has almost complete fronds of ferns and the gobiosuchid *Cassissuchus*; the northern area lacks squamates and pterosaurs; and the southern area has the albanerpetontid *Celtedens* but otherwise presents a notably lower proportion of amphibian remains which clearly dominate the tetrapod associations of the other two areas. It is often these small differences that hold the key to understanding the evolution of the ecosystem.

A new Lagersttäte from the Lower Cretaceous La Huérguina Formation in Buenache de la Sierra (Castilla-La Mancha, Spain)

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Two new quarries have been discovered in the La Huérguina Formation in Castilla-La Mancha (Spain), probably from the same unit as the palaeowetland of the Las Hoyas site (Upper Barremian). Both sites are in the region of the village of Buenache de la Sierra, in the province of Cuenca, only 4 km away from the Las Hoyas site. One of the quarries, La Cantera, was open decades ago and was only prospected. The other, el Cerrojón, was newly-opened and excavated systematically. Two short summer campaigns have yielded more than 500 specimens, highlighting the overwhelming fossil richness of these new localities. Both quarries present a high diversity of plants and animals, including ferns, podocarpacean and cheirolepidacean gymnosperms, and the angiosperm *Montsechia*, invertebrates (mainly 'vermiform' impressions, molluscs, and several classes of crustaceans), and a remarkable diversity of holostean and teleostean fish. The remains are exceptionally well preserved, and include soft tissues, impressions and 3D preservation. Remarkably, this palaeocommunity is only partially different, yet coeval and regionally linked, to that of Las Hoyas, suggesting that its study offers an unprecedented opportunity to understand the ecological dynamics and regional macrostructure of the whole palaeowetland system.

From order to disorder: Pleistocene beetle scales reveal diverse 3D photonic nanostructures

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Light-scattering photonic nanostructures are abundant in extant arthropods, underpinning the typically vibrant structural colours displayed by many insects. In animals, structural colours play instrumental roles in inter- and intraspecific visual communication strategies including sexual signalling, aposematism and crypsis. Scale-bearing insects, particularly weevils and longhorn beetles, frequently exhibit spectacular optical effects that are produced by complex 3D photonic nanostructures housed within the scale envelope. These structures are under-represented in the insect fossil record literature; to date, 3D photonic nanostructures have been reported in only a single fossil weevil and therefore the evolutionary history of these tissue architectures, and the forces driving their evolution, are unknown. Here we report the discovery of 3D photonic nanostructures in diverse fossil beetles from the Pleistocene of North America. We used small-angle X-ray scattering in tandem with electron microscopy to characterize the fossil scales' ultrastructure, revealing the preservation of 3D nanostructures that range from highly ordered to amorphous. Further, the more highly ordered nanostructures correspond to a single-diamond crystallographic structure, with predicted reflections ranging from red to near-infrared wavelengths (*i.e.* 650–800 nm). These data will serve as a platform to deliver novel insights into the evolution, development and functionality of scales in coleopteran species.

Critically exploring the fossil record of the deep biosphere

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Micro-invertebrates, fungi, and prokaryotes populate a global 'deep biosphere', hosted by rocks and sediments underground and beneath the seafloor. These geological environments contain more of Earth's living biomass than any other biome except forests, and are the focus of a concerted global research effort in microbial ecology involving mines and boreholes around the world. Subsurface microbes mediate diagenetic reactions, interact with minerals, and fix carbon and sulphur into the crust. Evolutionary, geodynamic and redox trends are likely to have driven large changes in the size and activity of the deep biosphere through geological time with potentially far-reaching consequences in the Earth-Life system. Unfortunately, the fossil record of this vast habitat remains cryptic, sparsely sampled and widely neglected. Candidate microbial fossils in the mineralized pore spaces of diverse lithologies have been reported worldwide, but it is difficult to demonstrate robustly that these are both biogenic and indigenous to a particular depth and time beneath a palaeo-surface. Here I will discuss these challenges in relation both to previously-described material, which I will briefly review, and to new fossil evidence of possible subseafloor microbes preserved in the Mesozoic ophiolites of Liguria, Italy.

Coralline algae as a recorder of climate change and its impacts in the past and in the future

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Coralline algae are habitat formers found in shallow marine environments. Through their 3D structures, these specimens create structurally and functionally complex beds that support a high level of biodiversity. While being impacted by climate change, their skeletons are also ideal recorders of past climate information. We investigate how plastic the organism's environmental response is by assessing plasticity in the internal structure, annual and seasonal growth rate and elemental composition for both today and historical collections from Oban and Falmouth in the UK. We quantify the intra- and inter-species variability and the variability through time to understand the full plastic range of these organisms. Results show that variation in cellular and mineral properties within a species is large, but there are clear differences in the structure between warm and cold temperate species leading to the warm temperate species forming weaker skeletons. Structural integrity is therefore affected by changes in growth parameters in response to the environment. Climate change is further impacting on the skeleton through the changes in growth and elemental composition. Applying these methods to the fossil record provides a powerful tool to assess adaptation to climate change and its ecosystem impacts.

Using intra-specific variation to detect sexual reproduction in Ediacaran organisms

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Ediacaran macrofossils are among the oldest (~566 Ma) known examples of macroscopic eukaryotic organisms. Ediacaran bedding planes from Newfoundland, Canada preserve thousands of specimens of *Fractofusus*, a 'fractally-branching' rangeomorph of unresolved phylogenetic affinity. The preservation of this sessile organism in large *in situ* bedding planes allows original spatial distributions to be analysed. Previous analyses determined that *Fractofusus* has a complex life history of multigenerational stolon-like asexual reproduction, punctuated by dispersal via waterborne propagules. However, whether these propagules were sexually-produced gametes or asexually-produced fragments or buds has not previously been resolved. *Fractofusus* populations from three surfaces in Newfoundland, Canada were recorded using a laser-line probe to produce high-resolution (50 µm) 3D community maps. Colonies were identified using spatial analyses, with a colony defined as the dispersal-generated aggregation around large/founding specimens. There were significant differences in intra-specific variation (length to width ratios and number of primary branches) between colonies, with no significant differences between founding specimens and the next generation. This result is consistent with the hypothesis that founding members were sexually produced via waterborne gametes while the subsequent generations were asexually produced. Thus, this study provides evidence of the oldest instance of sexual reproduction of macroscopic organisms in the fossil record.

Early ontogeny of the shells of pelagiellid molluscs from the Cambrian (Stage 4) Pioche Formation, southeastern Nevada, USA

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While mollusc protoconchs can preserve a record of early ontogeny, few convincing examples are known from the Cambrian, so it has remained controversial whether early molluscs had feeding (planktotrophic) or non-feeding (lecithotrophic) larvae. We report specimens of two species of pelagiellid molluscs from the Cambrian Stage 4 Combined Metals Member of the Pioche Formation from the Pioche–Caliente region of southeastern Nevada, USA. Several fossils have a delicate phosphatic layer preserving the outer surface of the shell, including details of ornamentation and growth lines. Costate shells of *Costipelagiella nevadense* show a distinct, *c*. 85 µm-tall, hemi-ellipsoidal cap at the apex of the shell, which we interpret as the embryonic shell. The succeeding portion of the shell is smooth; the first costae appear *c*. 45 µm past the edge of the embryonic shell. A second pelagiellid species, whose post-metamorphic shell bears low spiral grooves, likewise has a hemi-ellipsoidal embryonic shell *c*. 90 µm in height. In both species, the absence of a clear protoconch II stage suggests they did not have planktotrophic larvae. Their protoconchs are unusually small for lecithotrophic molluscs, however, showing they were able to metamorphose at a smaller size than Recent molluscs do.

The first vertebrate skeletal tissues and the 'biomineralization toolkit'

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Conodonts are the earliest vertebrates with a mineralized skeleton. Otherwise entirely soft-bodied, conodonts possessed a set of phosphatic tooth-like elements. First known from the Guzhangian, paraconodonts (with a dentin-like skeleton) gave rise to euconodonts in the Jiangshanian, after the evolution of 'crown' tissue, an enamel-like euconodont apomorphy. Between the latest Neoproterozoic and the end of the Cambrian, biomineralization also evolved independently in virtually every other group of animals with hard parts, contributing to a dramatic ecological turnover through this period. Observations from developmental and molecular biology suggest that all animals inherited a common 'toolkit' of genes, independently co-opted to similar tasks, including building skeletons. This initially imprecise 'toolkit' was subsequently honed by the acquisition of more and more complex gene regulatory networks. This predicts a pattern of initial mineralization of a pre-existing organic skeleton with loose control followed by increased control via the accumulation of lineage-specific secretory mechanisms, and skeletal fabrics. Here I use the fossil record of the conodont skeleton to compare the histological disparity close to the origin of each component tissue, with observations of equivalent assemblages from later in conodont evolutionary history, thus providing evidence to test the predictions of the 'biomineralization toolkit' hypothesis.

Testing hypotheses of heterochrony in the skull evolution of strisoran birds

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Strisores is a clade of neoavian birds with a rich fossil record and a modern diversity that encompasses hummingbirds, swifts and caprimulgiforms, a series of nocturnal, mostly insectivorous, lineages. Swifts and caprimulgiforms exhibit cranial morphologies with several traits reminiscent of juvenile birds such as enlarged orbits, wide flat skulls and weak ossification. These similarities raise the question of whether strisoran cranial anatomy was acquired via one or several heterochronic events (evolutionary changes in the timing and/or pattern of ontogenetic events). To explore this, we quantified cranial shape ontogenesis by means of 3D geometric morphometrics and obtained measurements in all the families of strisorans and five outgroups, comprising 104 specimens in total (including embryos and some fossils). Our results indicate both paedomorphic and neomorphic processes directed cranial shape evolution in strisorans. For instance, while nightjars retain a juvenilized cranial morphology throughout ontogeny, frogmouths and oilbirds experience a great deal of novel shape change. We also found that the divergent cranial morphology of hummingbirds likely originated through a process of general acceleration of cranial ontogenetic change. Our study stresses the pervasiveness of heterochronic shifts underlying large phenotypic evolution in vertebrates and bears implications for correctly interpreting stem members of the strisoran lineage.

Integrating fossil data refines plant divergence time estimates

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Traditionally, divergence time estimation methods have relied on node-based fossil calibration to produce age estimates measured in absolute time. This approach does not make full use of all available fossil data and requires the difficult practice of representing prior expectation of clade age as a parametric distribution. The fossilized birth death (FBD) process provides an alternative approach, in which more fossil data than before can be applied alongside extant molecular data to estimate divergence times without the construction of calibration distributions. We apply the FBD framework to the estimation of divergence times in Embryophyta by extending a dataset previously used for node calibration with the inclusion of large quantities of fossil occurrence data. We demonstrate that this approach has a significant impact on the posterior age estimates of many key plant clades, redefining the timescale of plant evolution. We also demonstrate that when the amount of fossil data available is so large that it becomes impractical for analysis, only certain sub-samples of these data will produce meaningful age estimates with the FBD process.

Clarifying the Kukruse–Haljala stage boundary in northwest Estonia

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The Peetri outcrop in northwest Estonia has been an object of research interest for almost a century. Descriptions of regional geology in northwest Estonia are based on previous detailed palaeontological and lithological studies and have remained largely unchanged for the past 30 years. The Peetri succession exposes the boundary between the Kukruse and Haljala regional stages. Despite extensive work on the Peetri outcrop, previous palaeontological studies did not address the entire section and paid insufficient attention to the stage boundary. In order to better understand the regional geology and biostratigraphy, the whole section was sampled for conodonts. In addition, ostracod and chitinozoan samples were taken across the stage boundary. Although a lack of the lower substage of the Haljala was suggested in previous papers due to a well-known sedimentary hiatus in the lower part of the Haljala regional stage, our results confirm the presence of both substages of the Haljala regional stage in the Peetri outcrop. Conodonts demonstrated more reliable results in the Haljala regional stage. Only uncertain classification of key conodont taxa was possible in the upper part of the Kukruse regional stage, where in northwest Estonia ostracod and chitinozoan data are more reliable.

talks

The partial skeleton of the docodont *Borealestes serendipitus*, from the Kilmaluag Formation (Middle Jurassic) of the Isle of Skye, Scotland

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The partial skeleton of the docodont mammal, *Borealestes serendipitus* (Docodonta, Mammaliaformes), was recovered from Skye in 1972, and is now held at National Museums Scotland. It includes the cranium, upper and lower tooth rows and a partial postcranial skeleton. It is the most complete Jurassic mammal fossil described from the UK to date, and one of the most complete known outside China. Synchrotron scans of the skeleton were obtained at the European Synchrotron Radiation Facility (Grenoble), and coupled with micro-CT scans to digitally reconstruct the specimen for analysis and 3D digital visualization. These data have been used to provide an updated diagnosis of *B. serendipitus*. Morphologically, *Borealestes* is more gracile than *Haldanodon*, with features resembling *Agilodocodon*. The petrosals have extensive pneumatic and vascular structures resembling those in *Haldanodon*, but new vascular structures have been identified: the trans-cochlear sinuses anterior and posterior. Multivariate analyses of the calcaneum, alongside a dataset of calcanea from extant small mammal taxa (<5 kg), provide inferences for locomotor mode in this taxon. *B. serendipitus* was scored for new dental, cranial and postcranial characters for an updated phylogenetic analysis. Initial results of this analysis place *Borealestes* in broader phylogenetic context within Docodonta.

Convergent evolution of toothed whale cochlea

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Odontocetes (toothed whales) are the most successful marine mammal lineage. The catalyst for their evolutionary success is their ability to use echolocation – a form of biological sonar that allows them to sense their environment using high-frequency sound, which is produced in the forehead and detected by the cochlea. In recent years, several studies have identified different echolocation types, largely correlated with habitat, with an emerging consensus that the morphology of the cochlea is an excellent proxy to distinguish both of these in extant and extinct taxa. Given this strong influence on cochlear shape, we tested whether convergent evolution of the cochlea has occurred within Odontoceti. To do this we used SURFACE, a method that fits Ornstein-Uhlenbeck (OU) models with stepwise AIC (Akaike Information Criterion) to identify convergent regimes on a phylogeny. We fitted

SURFACE models to a phylogeny of odontocetes and identified three convergent regimes: True's and Cuvier's beaked whales; sperm whales and all other beaked whales; and kogiids and Dall's porpoise. We then used distance-based convergence metrics to test whether these convergences were statistically significant. Finally, we discuss which factors may have driven these convergent shifts.

Rooting the eukaryotic radiation with new models of genome evolution

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The deep relationships among the main lineages of eukaryotes, and in particular the root of the eukaryotic tree, remain debated. Two main rooting hypotheses are actively discussed. The first, the Unikont/Bikont hypothesis, places the root between the Unikonts, including Metazoa, Fungi, Amoebozoa and some related protist lineages, and the bikonts, *i.e.* all the other lineages, including Archaeplastida and a large diversity of unicellular eukaryotes. The second hypothesis, Neozoan/Excavate, proposes the root to be between the excavates, a very diverse group of protists, and all the other eukaryotes. Each of these hypotheses has major implications for the nature of the last eukaryotic common ancestor, as its complexity level, gene content or the evolution of the main features of each lineage. In order to solve this fundamental evolutionary question, we are exploring the use of concatenation, multispecies coalescent and recently-developed approaches to gene tree-species tree reconciliation that allow species trees to be rooted without an outgroup. Our analyses make use of a broadly-sampled dataset of 98 complete genomes and largely-complete transcriptomes of Eukaryotes, including new lineages. We present ongoing work on the topology and root of the eukaryotic tree and the metabolic capabilities of the last eukaryotic common ancestor.

Diversity of neuropteran larvae (Insecta) in Early Cretaceous ambers

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Neuroptera (lacewings and relatives) are a relict insect group that had a greater diversity and disparity during the Mesozoic. The latter is true as well for their predatory, typically active larvae based on recently described diversity including bizarre, highly specialized forms from ~99 Ma Burmese amber and other Cretaceous ambers. Some green lacewing (Chrysopidae) larvae are debris-carriers, selecting and carrying exogenous elements for camouflage and physical protection. Two new debris-carrying green lacewing morphotypes are known from ~130 Ma Lebanese amber: a first instar described from multiple neonates preserved together with the eggshells from which they hatched, some bearing egg bursters, and a late instar associated to debris-packet remains, likely soil fragments. Unlike modern

representatives, both morphotypes have extremely elongate tubercles dorsally for retaining debris. Furthermore, three new straight-jawed larval morphotypes are known from ~105 Ma Spanish amber: one is a beaded lacewing (Berothidae) remarkably resembling modern relatives, whereas another has unclear affiliations and displays some unique features. Compared to other insect groups, neuropteran larvae are relatively abundant in amber and exhibit plenty of external characters due to their campodeiform bodies. Therefore, Neuroptera are an ideal group to tackle how morphological, ecological and behavioural traits evolved in larval holometabolous insects.

The distribution and cladogenesis of Middle Jurassic (Callovian) to Early Cretaceous (Valanginian) marine reptiles in the Northern Hemisphere

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Previously, the scarcity of high-latitude marine reptile fossils has made estimating geographic ranges for individual taxa problematic, particularly for the interval around the break-up of Pangea. The recent collection of Mesozoic marine reptile specimens from high-latitude regions enables a more comprehensive appraisal of their palaeobiogeography. Here we present preliminary quantitative assessments of the biogeographic distribution of major marine reptile clades during the mid-Jurassic–Early Cretaceous, by employing ancestral states analysis. Our results show that moderate-high plesiosaurian and ichthyosaurian taxonomic exchange took place between most geographic regions of interest during this interval. Furthermore, the ancestral states analysis indicates that derived clades of plesiosauroids likely stemmed from a Sub-Boreal ancestor. In contrast, the ophthalmosaurid distributions are more complex, due to their wider distribution. The DEC+J model (diversification, extinction, cladogenesis and founder-event) fits the data significantly better than the other models tested and displays a large founder-event component. Cladogenetic events coincide with global sea-level highstands (transgressive events), and thus the opening of seaways between major oceans may have been the driver for the founder effect in these clades. However, additional data particularly from other clades of marine organisms are required to further compare and test this hypothesis.

Impact of diagenesis on the chemistry of vertebrate eye melanosomes

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Melanin, a pigment common in vertebrate melanosomes, often binds metal ions such as Fe, Cu and Zn. The concentration of metals bound to melanin is known to vary between different tissues and taxa. Fossilized vertebrate melanosomes are known to be enriched in Cu; it is unclear, however, whether this is a biological or taphonomic signal. To explore the effects of diagenesis on melanin trace element chemistry, melanin extracts from the eye of the European sea bass (*Dicentrachus labrax*) were experimentally matured in distilled water or solutions of Cu or Zn at 200 °C for one hour. The trace element chemistry of matured and untreated melanin extracts was investigated using synchrotron rapid scanning-X-ray fluorescence (SRS-XRF) and X-ray absorption near edge structure (XANES) spectroscopy.

Our data reveal that the Zn:Cu ratio is much lower in fossil eye melanosomes with respect to those in extant taxa and that the relative concentration of Cu associated with melanosomes increases during maturation. These results demonstrate that diagenesis has an impact on the chemistry of melanosomes; this must be considered when interpreting the trace element chemistry of fossil melanosomes.

Synchrotron-X-ray fluorescence analysis of melanosomes reveals soft tissue anatomy of fossil vertebrates

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Melanin is a pigment stored in melanosomes, micron-sized organelles, in vertebrate and cephalopod tissues. Most research on melanosomes has focused on their occurrence in integumentary tissues and eyes, but our recent research has shown that melanosomes are also ubiquitous in vertebrate internal organs. Determining the source of melanosomes is therefore critical for accurate reconstruction of melanin-based integumentary colouration in fossils. Our pilot study of four vertebrate fossils suggested that melanosomes from different body regions possess distinct geometries and trace element inventories. Here we present an expanded fossil dataset spanning representatives of higher vertebrate classes from eight fossil localities ranging in age from 300 to 10 Ma. We mapped fossils and host sediments using synchrotron X-ray fluorescence analysis. Multivariate analysis shows that the trace element composition of melanosomes differs among localities, confirming a broad diagenetic control on melanosome chemistry. Analysis of data from individual specimens reveals that the chemistry of melanosomes is statistically different from that of the sediment. Critically, a strong tissue-specific signal is preserved. The trace element chemistry of fossil melanosomes is thus a novel tool for interpreting the anatomy of fossil vertebrates.

Different evolutionary dynamics govern body size evolution in dinosaur groups

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With over 150 million years of evolutionary history and spanning six orders of magnitude in body size, dinosaurs are an ideal group on which to test hypotheses of phenotypic evolution. However, owing to their diverse biological nature, it has proven difficult to model patterns and processes of phenotypic evolution in dinosaurs using traditional methods and simple evolutionary models. Here we apply a sophisticated but flexible non-homogenous model of trait evolution on a proxy for body size ($\log_{10}$ femur length) in relation to time, speciation events and the Jurassic–Cretaceous boundary, using the Variable-Rates phylogenetic regression. We found a strong overarching effect of speciation on body size evolution across the different clades of dinosaurs (Sauropodomorpha, Ornithischia, and subclades of Theropoda) but with differential effects through time and across different groups. Additionally, at least one theropod group shows a marked reduction in body size across the Jurassic–Cretaceous boundary, potentially hinting at a Lilliput-like effect. Our results

demonstrate that there is more to body size evolution in dinosaurs than time-dependent processes – evolutionary history, ecological opportunities and mass extinction events all have subtle but distinct effects that can only be teased apart with careful modelling.

Does morphology evolve under drift or selection? Comparing empirical and simulated data

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Recent debates surrounding the efficacy of different phylogenetic methods for morphology now hinge upon a much broader question: how do discrete morphological characters evolve? For molecular sequence data we can apply models based on empirical observations and theoretical predictions. For discrete morphological characters, however, it is unclear if there are any common mechanisms of character evolution, or whether available models are applicable to real situations. Here we compare 35 empirical total-evidence datasets with datasets generated by simulations using either genetic drift or natural selection (MBL2017 and TREvoSim respectively). We use metrics for tree shape, data dimensions, and a wide range of homoplasy measures relative to true simulated trees, derived most parsimonious morphological trees and independent molecular trees. Plotting the datasets in multidimensional principal coordinate space finds clear separation between the simulations under drift and selection; PC1 (>80 %) largely accounts for metrics of homoplasy whilst PC2 (<5 %) represents tree shape. Empirical datasets are more closely aligned with simulations under natural selection, rather than drift. This suggests that selection rather than drift may be the dominant force of morphological evolution. This is potentially problematic given that our simulation studies found all methods of morphological phylogenetic inference to perform relatively poorly under such circumstances.

How an eye of a phacopid trilobite is constructed, or the solution of Stürmer's enigma

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Wilhelm Stürmer (1917–1986) was head of the radiology department at Siemens corporation. Being fascinated by fossils, and a specialist in X-ray methods, he bought a VW-bus, equipped it with an X-ray machine, and from 1960 to 1986 travelled from quarry to quarry in the Hunsrück area of Germany, exploring Lower Devonian black shales originally intended to become roof tiles. In the compound eyes of phacopid trilobites he found very atypical long fibres, which extended from the periphery to a common centre. He interpreted them as light-guiding structures – a very revolutionary idea about visual systems at that time. The reaction of his colleagues was intense, and negative. The eyes of phacopid trilobites appear to be very special, because the lenses can be comparably wide, and are not densely packed, but separate from one another. We reinvestigated Stürmer's material and found that several units composing a compound eye may reside under one big lens each, sharing its wide aperture. Stürmer's fibres turned out probably to be the bundled efferent nerves of each complex. Thus, Stürmer was correct that these 'fibres' really exist and are a functional element of the highly specialized compound eye of phacopid trilobites.

The Kingswood Limestone – a Mississippian terrestrial Konservat-Lagerstätte

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The fossil plants from the Late Mississippian (late Visean) of Kingswood in Fife, Scotland are preserved in limestones associated with volcanic ashes and may be considered as a terrestrial Konservat-Lagerstätte. These ashes were erupted by a basaltic phreatic eruption and the plants grew on the inner flanks of the post-eruption crater. The plants living near the crater-lake were preserved as calcareous permineralizations and included gymnosperms and the herbaceous lycopsid *Oxroadia*. The vegetation higher on the crater flank was subjected to frequent wildfires and the resultant charcoalified plants washed down into the lake. The plants thus preserved include a wide variety of gymnosperms including several pteridosperms that are represented by a wide range of leaves, pollen organs, ovules and stems. The flora is of a similar age to the nearby Pettycur Limestone. However, there are no elements in common and it is believed that this later flora was associated with either lowland peat-forming environments or disturbed volcanic environments, and the sediments containing the plants were ripped up and incorporated into basaltic lava flows. We will present new data on the Kingswood flora based on both scanning electron microscopy (SEM) and synchrotron radiation X-ray tomographic microscopy (SRXTM).

Trace fossil insights into Early Devonian terrestrial ecosystems – a case study from Gaspé, Quebec

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The Early Devonian was an interval of great change in terrestrial ecosystems, marking the culmination of the first phase of colonization of land by animals. The trace fossils left by these organisms provide a high-resolution insight into the palaeoecology of early non-marine ecosystems, recording interactions between animals and the depositional environment even where body fossils are scarce. Whilst trace fossils from many Siluro–Devonian terrestrial settings worldwide have been documented in detail, the strata of the Gaspé peninsula of eastern Canada have largely been overlooked from an ichnological standpoint, despite hosting a number of Early Devonian Lagerstätten containing plants (*e.g.* Campbellton Formation) and fish (*e.g.* Miguasha). This presentation describes invertebrate trace fossil associations from the Emsian Battery Point Formation and the implications that these have for our understanding of early terrestrial habitats. These signatures are compared to those from other sites from the Old Red Sandstone of Europe and North America as well as coeval sites from Australia to provide greater understanding of the global record of the terrestrialization event.

talks

Sunny, rain later: 30 years of the Carnian Pluvial Episode

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The Carnian Pluvial Episode is among the most significant, yet little known, environmental and biotic perturbations of the Mesozoic. First announced at the PalAss Annual Meeting 30 years ago, its discovery owes much to field observations in the Bristol region and to a chance conversation linking two seemingly disparate events. We found diverse evidence for increased rainfall in the Late Triassic correlating with significant changes (both extinctions and radiations) among marine and terrestrial biotas, but we were unable to ascertain its full geographic extent or do more than hint at a possible cause. Virtually ignored for more than a decade, interest has increased dramatically since 2006. New sedimentological evidence, from terrestrial to deep marine, shows that the climatic change was essentially global. Oxygen isotopes indicate warming and increased precipitation. A negative $\delta^{13}C$ excursion at the onset of the Carnian Pluvial Episode correlates with eruption of the Wrangellia Large Igneous Province, probably the ultimate cause of the Episode. Refinement of biotic data, from dinoflagellates to dinosaurs, has demonstrated the profound and far-reaching nature of ecosystem changes at this time. It has even been suggested that the Carnian Pluvial Episode may be a useful analogue for the effects of current climate change on today's biota.

A Cambrian peanut worm and the peramorphic origin of the sipunculan body plan

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Sipunculans (peanut worms) are a taxonomically rarefied but geographically widespread group of marine trochozoans. Their distinctive body plan comprises a cylindrical trunk, a hook-bearing, retractable introvert and a subterminal crown of feeding or respiratory tentacles. Long considered a separate animal phylum, sipunculans are now considered to be highly derived annelids – though their precise evolutionary origins remain obscure. Based on new exceptionally-preserved fossils from the Chengjiang Lagerstätte, we identify the Cambrian 'phoronid' *Iotuba chengjiangensis* as a stem-group sipunculan. The short introvert of *Iotuba* bears a circumferential ring of sclerotized spines and a tentacle-fringed mouth that migrates through ontogeny from a ventral to a terminal position. The fossils exhibit features of sipunculan larvae, and suggest that the sipunculan body plan evolved by the peramorphic addition of a new metamorphic stage to an ancestrally annelid-like lifecycle.

The nature and preservation of soft tissues in exceptionally preserved Jurassic ichthyosaurs

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Ichthyosaur fossils have long been known to often preserve soft tissues. Several Lagerstätten in the UK and Germany have produced ichthyosaurs showing extensive soft

tissue preservation, including dark organics and fibre-like structures previously identified as dermal collagen fibres. Here we examine the soft tissues of three different genera of ichthyosaurs from three different Lagerstätten in the UK and one from Germany. We find that these soft tissues include remains of the epidermis including *in situ* melanocytes, and dermis with a dispersed layer of melanophore-derived melanosomes and a phosphatized fibrous network as well as underlying internal organ organics. The fibrous layers are preserved as phosphatized sheets consisting of peaks and troughs rather than individual three-dimensional fibres, suggesting that only impressions have survived. In some specimens, multiple fibrous sheets overlay one another, while in others only a single layer running parallel to the body axis is present. Retinal tissues in the eye are also preserved with different melanosome morphologies occurring in three distinct layers. Distribution of melanocytes and dermal melanosomes reveal a countershaded pattern in at least three specimens. The prevalence of high-fidelity soft-tissue features in multiple specimens from different locations suggests that such exceptional preservation may be common in ichthyosaurs.

Towards improving the use of morphological data in inferring phylogeny – data from extant archosaurs

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Phylogenies for fossils must rely on morphology. Phylogenies based on DNA are increasingly accurate, but often disagree with those based on morphology, calling into question the accuracy of fossil-based phylogenies. Here, data from extant archosaurs are investigated in order to shed light on how to improve phylogenetic inference from morphology. The homoplasy of morphological characters on a DNA-based phylogeny for extant Crocodylia and Aves is investigated. Cranial characters are significantly ($p=0.05$) less homoplastic for crocodilians but not for birds. Crocodilian characters passing two tests – 1) complete scoring accuracy, and 2) clear and biologically plausible state delimitation – were significantly ($p=0.01$) less homoplastic than others. A phylogeny inferred using only characters passing these tests placed *Gavialis* (gharial) in the same position as the DNA phylogeny but was less resolved than the original phylogeny; when inaccurately scored characters were rescored, resolution was improved and the placement of *Gavialis* remained the same. Use of an extant (*Varanus*) outgroup also yielded a topology more similar to DNA. Trees inferred using data from cranial surface scans for crocodilians and birds reflected ecomorphology and paedo/peramorphosis not phylogeny, and removal of the rostrum did not improve accuracy, but placement of species and separation of disparate clades was correct.

A new life for old leaves: can herbarium dried leaves be used in CLAMP?

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Dried leaves kept in herbarium collections constitute a significant but under-utilized resource in plant ecophysiological shape studies. This is due in part to concerns that fresh, green leaf morphology differs from specimens pressed and dried for herbarium storage, and that these differences may affect palaeoclimate inferences. Several studies

have demonstrated leaf shrinkage occurring during the voucher drying process. As a result, many researchers have concluded that herbarium-dried leaves cannot be used in ecophysiological studies such as CLAMP, which links 31 leaf shape categories to 11 climate variables. We test this assertion. Forty-four leaf species (305 leaves) from 21 families with diverse leaf morphologies were dried and pressed using standard procedures from fresh to dried voucher specimens and scored for CLAMP characters when fresh and at six weeks. Whilst leaf size changes did occur, CLAMP character-state data were resistant to artifactual variation so long as a sample of leaves ($n \geq 5$) was used. We observed only small changes to climate variable inferences (*e.g.*, MAT varied by ≤ 0.11 °C). These results suggest that dried leaves can be used as climatic inference and prediction tools in CLAMP studies with confidence, though further experimental research into this issue is desirable.

Silurian and Devonian trilobites of Japan: 'eye witnesses' to the early geological evolution of the Japanese islands

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Trilobites are widely represented in the Silurian and Devonian strata of Japan, with Palaeozoic taxa described from the South Kitakami, Hida Gaien and Kurosegawa terranes. Here we present a palaeobiogeographical review of nine trilobite groups represented in the Japanese rock succession that have received recent taxonomic revision: Illaenidae, Scutelluidae, Phacopidae, Proetida, Aulacopleurida, Encrinuridae, Cheiruridae, Calymenidae and Lichidae. Silurian illaenids and scutelluids show generic and species links with the Australian segment of the Gondwana palaeocontinent; encrinurids indicate generic-level links between the three Japanese terranes, as well as with Australia and the South China palaeocontinent; whilst Devonian phacopids, and possibly proetids, suggest generic-level links with the North China palaeocontinent. Devonian lichids suggest generic-level links with Australia. Cheirurids and calymenids show uncertain palaeobiogeographical relationships at present but are undergoing further appraisal. The markedly different patterns between different groups may in part reflect the fragmentary biostratigraphical record of Japanese trilobites, but also appears to reflect their lithofacies ranges and palaeoecology. These constraints caution against the use of the Japanese trilobite assemblages for palaeobiogeographical assessment without a fuller understanding of their palaeoenvironmental context.

Morphological disparity and the 'double burst' avian expansion

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Bird evolutionary history is characterized by two important phases of expansion. The first radiation occurred in the Late Jurassic and Early Cretaceous, when birds evolved flight, greatly diversified and underwent a series of anatomical transformations. The second major expansion happened in the early Palaeogene, when modern bird clades diversified after the end-Cretaceous mass extinction. Birds are an exemplary group for comparing diversification driven by a key innovation (flight) and by ecological opportunity (post mass extinction). In this study we focus on morphological disparity, specifically limb disparity, an important part of bird ecomorphology. We use multivariate analysis of limb morphometric data to identify major features of morphological variation, generate morphospaces and calculate disparity statistics. Results show that the first bird diversification was associated with morphospace saturation, and the second with massive morphospace expansion. There was no substantial shift in morphospace occupation when comparing Mesozoic birds to Palaeogene birds. Instead, Palaeogene birds considerably expanded the bounds of morphospace, evolving previously unseen morphologies. These extreme forms show adaptations to terrestrial lifestyles or highly aerial niches. Results are consistent when incorporating phylogenetic history to account for the non-independence of taxa. Our study highlights that different catalysts for evolutionary radiations can lead to contrasting macroevolutionary trends.

A bioturbation control on the Phanerozoic record of shallow marine sole marks

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The presence of erosive sole structures, such as tool and flute marks, in the sedimentary record can be used to interpret flow dynamics of ancient storm-dominated settings, as well as seafloor sediment properties. The formation and preservation of these structures require a hydroplastic and cohesive substrate; therefore, their temporal distribution can be employed to track secular changes in seafloor rheology. I present a global compilation of Phanerozoic shallow marine successions bearing erosive sole structures. The frequency of sole mark preservation in shallow marine environments has dramatically declined through the Phanerozoic, indicating that the rheological nature of the seafloor experienced major secular transformations over the past 541 million years. I attribute this change in seafloor sedimentary properties to increases in the extent of bioturbation through the Phanerozoic, as the activity of sediment-mixing infauna dramatically increases the fluid content of the shallow sediment pile, decreasing the hydroplasticity necessary for sole mark formation and preservation. The gradual decline in the frequency of abiogenic sole marks in shallow marine successions through the Phanerozoic indicates that the development of bioturbation was a similarly protracted process. Additionally, bioturbation-mediated changes in seafloor rheology have important ramifications for secular developments in seafloor ecology, fossilization and biogeochemical cycling.

talks

Strontium isotopes reveal migratory behaviour in Late Cretaceous hadrosaurs of Alberta, Canada

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With the discovery of dinosaurs in polar regions, discussions around the abilities of dinosaurs to migrate to lower latitudes has been the subject of much debate. Traditionally, migration studies have relied on identifying the geographic distribution of dinosaur species and genera; however, that approach can prove challenging as species identification is not always easy or straightforward. This approach also does not account for the possibility of a species being widely distributed while employing limited migratory behaviours. Some studies have approached the problem from a geochemical perspective, analysing oxygen and carbon isotopes preserved in the enamel of dinosaur teeth. One approach that has had great success in migration studies of archaeological and palaeontological remains from the Holocene and Pleistocene is the analysis of strontium isotopes, which are controlled primarily by the weathering of bedrock by fluvial processes, and are therefore more strongly tied to specific geographic regions than are oxygen and carbon. Here we have analysed strontium isotopes preserved in hadrosaur enamel and other taxa to determine the migratory range of an individual hadrosaur from the badlands of Alberta, Canada. Our results support a hypothesis of migratory behaviour in hadrosaurs but suggest the range is limited to Southern Alberta.

Long-term climate and environmental changes did not lead to the extinction of dinosaurs: evidence from the latest Cretaceous of Alberta, Canada

François Therrien[1], Darla K. Zelenitsky[2], Don B. Brinkman[1], Annie Quinney[2], Kohei Tanaka[3] and David A. Eberth[1]
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Deposits of the Edmonton Group of Alberta, Canada preserve a record of the climate, palaeoenvironments and terrestrial faunas that prevailed during the 7 million years preceding the Cretaceous–Palaeogene (K-Pg) mass extinction. The stratigraphic distribution of dinosaurs, fish, crocodiles and turtles and of palaeoclimate and palaeodrainage indicators derived from palaeosols reveals a complex history of faunal and climate change at the end of the Cretaceous. Following a prolonged warm and humid time interval, rapid cooling and a decrease in rainfall occurred at ~71 Ma followed by a slow warming trend and increase in rainfall over the following 2.5 million years. Fluctuations from wetlands to well-drained habitats occurred independently of climatic fluctuations during that time interval. Well-drained habitats, high temperatures and low rainfall prevailed during the last 700,000 years of the Cretaceous, but a sudden drop in temperature and shift to wetlands occurred just before the K-Pg boundary. Interestingly, aquatic microvertebrate diversity fluctuated greatly in response to climate change, some taxa even disappearing during cooler intervals, whereas dinosaur diversity remained stable. These results indicate that dinosaur faunas were capable of withstanding major climatic fluctuations, and that long-term climatic and environmental changes were not responsible for the extinction of dinosaurs at the end of the Cretaceous.

A strange case of two fishes: enigmatic disappearance of bone tissue or an originally unossified osteostracan

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The Kalana Lagerstätte (Aeronian, Silurian, about 440 Ma) in Estonia has revealed a diverse and exceptionally preserved non-calcified algal flora. Many of these algal fossils show spectacular preservation, exhibiting the finest anatomical details. Although several fossils of soft-bodied animals have been discovered from Kalana, the majority of faunal fossils show a 'classical' type of preservation with a calcium carbonate skeleton only, mostly without preserved soft parts. The locality has also revealed two vertebrate fossils: one osteostracan head shield and a complete telodont. The preservation of these two fossils is contrasting. The osteostracan is preserved as a fine carbonaceous film, without any detectable internal structure. The telodont, on the other hand, shows a well-preserved calcium phosphate dermal skeleton, with beautifully preserved sculpture and distinguishable multilayered architecture. As bone is generally regarded as one of the best preservable organic tissues, there is a theoretical possibility that the specimen lacked apatitic bony structures originally. In this case, however, it would be the first unossified osteostracan known by far.

The long and the short of it: a transformational tale of pterosaur tails

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New finds and re-evaluation of historic specimens show that tail length and structure is far more variable in pterosaurs than previously thought. Basal forms, 'rhamphorhynchoids', are typified by highly elongate complex tails with up to 40 caudals supported by bundles of zygapophyseal and haemapophyseal processes, but shorter, simpler tails lacking supportive bundles are found in some basal taxa (*e.g. Preondactylus*), and both long and short tails are found within Anurognathidae. Basal monofenestratans have long complex tails, while most pterodactyloids have relatively short, simple tails, although longer more complex structures have been found in *Pterodaustro* and several ornithocheirids, while azhdarchoids seemingly lack caudals. A postnatal growth series of *Darwinopterus* demonstrates a short simple tail in neonates, an intermediate tail in juveniles and a long, complex tail in mature individuals. This, and a partly comparable sequence in *Rhamphorhynchus*, suggests that anatomical variation in pterosaur tails was primarily generated through heterochrony – in this case, changes in growth rates of the caudals compared to the rest of the skeleton. Likely modulated by Hox13 genes, heterochrony can explain the entire range of observed variation including the short, apparently neotenic tails of some anurognathids and most pterodactyloids, and the complete loss of the tail in azhdarchoids.

talks

Reconstruction of skeletal architecture of conodont *Clydagnathus* using non-destructive methods

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Despite their almost ubiquitous diffusion in marine Palaeozoic sediments and their paramount biostratigraphical importance, knowledge of conodont apparatus architecture has always been frustrated by the rarity of articulated 'natural assemblages': in fact conodonts are generally found as disarticulated skeletal elements, leaving few hints about the position of the elements in the apparatus. Furthermore, in most cases it is difficult to separate single elements from the assemblage without destroying them. To overcome these difficulties we obtained high resolution CT scans of some articulated natural assemblages of the conodont *Clydagnathus* using synchrotron-based tomography (SRXTM), a non-destructive method. We used the software Avizo to create separate models for each of the elements and combine them into a model apparatus without damaging or disjointing the assemblages. The conodont genus *Clydagnathus* presents an architecture typical of ozarkidinids, showing a 15 element apparatus with two couples of bilaterally opposed P elements, a couple of opposed M elements and nine S elements; one S0 element in median position and two series of opposed S1, S2, S3 and S4 elements. Comparison between 3D apparatus models and pictures of the original bedding planes allowed us to reconstruct the original position and collapsing patterns of the apparatus.

Community variation within the Late Jurassic Morrison Formation

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The Late Jurassic Morrison Formation is ideal for palaeoecological studies; it covers over 1-1.5 million km^2 and is one of the best sampled Mesozoic terrestrial deposits globally. Traditional palaeoecological studies have ascertained the diversities, relative abundances, biomass and ecological guilds of the Morrison Formation biota; however, community analysis has not been widely applied and is often limited to dinosaurian taxa. Here we identify the existence of palaeocommunities within the Morrison Formation and analyse variation between these communities using a dataset of 1,157 plant and animal genera, sourced primarily from the Paleobiology Database. This has been achieved by applying a number of indices and techniques, such as the Sørensen-Dice index, Simpson index and Forbes coefficient, to presence–absence data. These methods provide a robust, quantitative way of analysing palaeocommunity variation for the first time in the Morrison Formation, which can be used to test previous community ecology hypotheses. This analysis provides a novel insight into Morrison Formation palaeocommunities which will further elucidate the palaeoecology of this charismatic Mesozoic deposit.

Elephas recki: the wastebasket?

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The *Elephas recki* complex of Plio-Pleistocene Africa has traditionally been held as an anagenetic transitional series from an *Elephas*-type ancestor to the immediate precursor of Eurasian *Palaeoloxodon*, comprising five successive chronosubspecies (*E. recki brumpti*→*E. r. shungurensis*→*E. r. atavus*→*E. r. ileretensis*→*E. r. recki*). However, this model is now under contention as ancient DNA reveals the phylogenetic closeness of *Palaeoloxodon* to *Loxodonta* (the genus which includes the living African elephant species), rather than to *Elephas* (the genus which includes the modern Asian elephant). Extensive re-examination of cranial materials from Ethiopia and Kenya reveals that, whereas the nominotypical form of this supposed lineage is morphologically consistent with *Palaeoloxodon* (thus *Palaeoloxodon recki*), other earlier remains attributed to *recki* exhibit far greater cranial disparity than can be explained by anagenesis. The Late Pliocene skull from southern Ethiopia attributed to *brumpti* is most morphologically similar to the contemporary *E. planifrons* of the Siwaliks and *Phanagoroloxodon* from southeastern European Russia; whereas the Early Pleistocene *atavus* shares substantial similarities with the contemporary Siwalik *E. hysudricus*. Reconciling these morphological observations with a novel cladistic analysis (>130 characters) reveals crucial new insights about the systematics, biogeography and morphological evolution of early crown elephantids.

Abstracts of poster presentations

*Posters eligible for the Council Poster Prize are marked with an asterisk.
Underlined author denotes the designated presenter.

Dietary diversity among Paleocene mammals from the San Juan Basin, New Mexico

***Neil F. Adams[1], Stephen L. Brusatte[2], Thomas E. Williamson[3] and Mark A. Purnell[1]**
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The Paleocene is an important interval for mammalian palaeontologists, because it marks the start of the Cenozoic 'Age of Mammals' when adaptive radiation occurred among many eutherian mammal groups. It is often presumed that these mammals were colonizing ecospace left vacant after the end-Cretaceous mass extinction, but drivers and mechanisms of mammalian adaptive radiation have remained largely speculative. Studies of taxonomic diversity alone are unlikely to be able to unpick such complex macroevolutionary processes, but this unpicking may be possible using measures of ecological diversity. Resource use and partitioning, as reflected in diet, are integral to ecosystem function, and reconstructing dietary diversity is a useful proxy for ecological diversity within an ecosystem. Here we apply dental microwear texture analysis and morphological analyses of tooth shape to Paleocene mammals from the San Juan Basin in New Mexico, USA. The fossil record of Paleocene mammals from this basin is one of the richest in the world and makes it a prime place to study the mammalian adaptive radiation. We focus on taxa that are particularly important parts of this radiation, including early primates, and provide estimates of dietary diversity among this Paleocene mammalian palaeocommunity for the first time.

Rate and amplitudes of climate change – are there tipping points in pelagic ecosystems?

***Monsuru Adebowale[1], Daniela N. Schmidt[1] and Ellen Thomas[2]**
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Climate change is a global phenomenon that affects terrestrial and marine ecosystems. Climate change results in warming, acidification and deoxygenation, all of which are projected to impact marine organisms. Often impacts are assessed using laboratory experiments, but by their nature these are too brief to assess potential for acclimation and adaptation. In this study, we use the Paleocene–Eocene Thermal Maximum (PETM) as a geological analogue to study the response of benthic foraminifers to a climate perturbation similar to today. The carbon injection into the ocean during the PETM led to a warming of 5 °C in the deep ocean, extensive acidification indicated by changes in the carbonate compensation depth and local deoxygenation. Size, number of chambers, size of the first chamber and calcification are studied at locations covering the World Ocean. The environmental stress led to a dwarfing of foraminifers. Calcification of *N. truempyi* was reduced during the event compared to before and after the carbon cycle perturbation and in disagreement with a similar study with a different location and species. We will discuss the question of species-specific responses versus local adaptation.

Modified acid-maceration method for extracting palynomorphs from Neoproterozoic glaciogenic diamictites

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Glaciations can have a calamitous effect on the biosphere, yet assessing their direct impact is often challenging. They are represented in the fossil record by poorly sorted sediments (diamictites). Heterogeneous, coarse composition makes diamictites unsuitable for preserving evidence of ancient biosphere (Precambrian organic-walled microfossils), but some diamictites may contain fine-grained matrix. During the palynological maceration procedure, larger grains mechanically destroy microfossils that may have gotten preserved in the finer sediment. We present a modified acid-maceration method for recovering microfossils from diamictites. The new method was applied to recover an acritarch assemblage from fine-grained matrix of two late Neoproterozoic glaciogenic diamictites: Mortensnes Formation (Digermulen Peninsula, Arctic Norway), and the Trinity Diamictite (Bonavista Peninsula, Newfoundland). The novel approach yielded more abundant and larger-sized microfossils from the Mortensnes diamictite compared to standard maceration, including long-chained and toroidal cellular-aggregates. A twofold increase was observed in the max. number of taxa/level extracted using the new method. Additionally, large-sized taxa (>100 µm) were recovered comprising 33 % of the assemblage, that were under-represented in standard macerate (7 %). Standard processing didn't return microfossils from the Trinity diamictite, while the novel method recovered leiosphaerids. This modified method may help unearth palaeontological material from understudied facies and intervals in Earth's history.

Tetrapod spatial biodiversity patterns across the end-Permian mass extinction and recovery interval

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The modern-day latitudinal diversity gradient (LDG) is a general trend of increasing biodiversity from the poles to the equator. However, our understanding of the underlying processes is limited, and it remains unclear whether this pattern was present throughout the Phanerozoic. One approach to answering these questions is to examine spatial biodiversity patterns in the geologic past, across different global climate regimes and continental configurations. The Late Permian–Middle Triassic (~250 Ma) represents an ideal time interval, characterized by large-scale volcanic episodes, extreme greenhouse temperatures and mass extinctions and recoveries, while continental configuration was also markedly different from today (*e.g.* supercontinent Pangea). We examined tetrapod spatial biodiversity patterns across this time window by applying established quantitative techniques to a database of global tetrapod occurrences, to investigate the role of climate change and continental distribution in driving LDGs. During the Late Permian and Early Triassic, peak tetrapod diversity moved from tropical to temperate latitudes, resulting

in a bimodal richness distribution. However, a pattern akin to modern LDGs arose in the Middle Triassic, with highest tetrapod diversity in equatorial regions. These results are consistent with the hypothesis that extreme equatorial temperatures drove tetrapod extinction and migration in the wake of the end-Permian mass extinction.

Taphonomic experiments reveal environmental bias during decay of insects

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Fossil insects are an important component of palaeoecological and palaeoenvironmental studies, but their taphonomy is incompletely understood. In particular, the impact of the chemistry of the depositional environment on insect taphonomy is unknown. Cuticles from five extant insect taxa were treated at 25 °C under various pH conditions for up to 180 days. Compositional changes in the cuticles were analysed by gas chromatography–mass spectrometry. The results show that in untreated and treated cuticles, the relative abundance of fatty acids, alkanes, alkenes and sugars varied across taxa and experimental conditions. For *Harmonia axyridis*, untreated cuticle had a higher relative abundance of fatty acids than treated cuticle, in which alkanes and alkenes were the most abundant compounds detected after 60 days of treatment. Despite initial variation in chemistry observed between cuticles treated in neutral or basic versus acidic conditions, namely the occurrence of sterols in the former, the chemistry of the cuticles converged as the experiments progressed. Sugars and fatty acids were the most abundant compounds under all treatments when the experiments terminated after 180 days. There is thus no clear evidence that environmental pH exerts a long-term control on the rate or pattern of chemical decay of insect cuticle. The differences in chemistry of the cuticle after 60 days, however, suggest that environmental pH may drive differences in the early stages of decay, potentially impacting on the relative preservation potential of fossil insects in different depositional settings.

The latest Ediacaran Khesen Formation: a new Doushantuo-style fossil Lagerstätte

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A newly discovered Doushantuo-style microfossil Lagerstätte occurs in phosphorites of the upper Khesen Formation, Khuvsgul Group, northern Mongolia. A latest Ediacaran age for the Lagerstätte is established by lithostratigraphic and $\delta^{13}C$ correlation with the Zavkhan Terrane of southwestern Mongolia. Eight preserved genera include only the second occurrence of the putative multicellular fossil animal embryo *Megasphaera* (represented mostly by a new species *M. minuscula*) outside the iconic Doushantuo Formation, the Doushantuo-Pertatataka-type acanthomorphic acritarchs *Appendisphaera*, *Cavaspina* and *Variomargosphaeridium* (including a new species *V. aculeiparvum*), and the possible alga

Archaeophycus yunnanensis. The Khesen Lagerstätte represents the youngest assemblage of Doushantuo-Pertatataka-type microfossils yet reported. It fills a gap in the record of phosphatized embryo-like forms between those of the ~600 Ma Doushantuo Formation and Cambrian examples. The Lagerstätte emphasizes the potential of Mongolian strata to provide new palaeontological data on the Ediacaran–Cambrian transition, and to resolve the phylogenetic debate surrounding *Megasphaera* embryo-like taxa.

Assessment of the evolution of cranial complexity in Placodermi (Gnathostomata) using Anatomical Networks Analysis

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Placoderms are an extinct class of primitive fishes spanning the lower Silurian to the latest Devonian. They are the most basal gnathostomes and form a paraphyletic species-rich, anatomically diversified assemblage. Since placoderms are the most primitive jawed vertebrates, the structure of their cephalic shields informs us on the reconfiguration that the vertebrate skull underwent with the development of jaws. One of the most intriguing properties of anatomical structures is morphological complexity; however, evaluating how it changed throughout time and lineages is challenging. Here we use a novel approach of Anatomical Networks Analysis (AnNA) to evaluate connectivity patterns of the placoderm skull roof. By modelling skulls as networks we can calculate topological variables (*i.e.* network parameters) that correlate with morphological properties such as structural complexity. AnNA has previously been used to tackle Williston's Law regarding tetrapods but it has never been applied to early vertebrates. Thus, we used AnNA to assess the structural complexity of the skulls of placoderms. Our analyses revealed several evolutionary trends operating on their network parameters; correlations between these trends show a net increase in structural complexity linked to a reduction in the number of bones in the skull roof throughout the phylogeny of placoderms.

From decapod to isopod and *vice versa*: a new perspective on *Tricarina gadvanensis* (Lower Cretaceous of Iran) and errors in orientation of malacostracan crustaceans

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The body orientation of extinct animals is sometimes reconstructed incorrectly, and fossil remains do not need to be *Hallucigenia* to be challenging to orient. *Tricarina gadvanensis* Feldmann *et al.*, 2007, is a Lower Cretaceous, incomplete arthropod fossil found from a borehole in Iran. Originally, the fossil was interpreted as the carapace (cephalothoracic shield) of a decapod crustacean and was attributed to a new species, genus and family of achelate lobsters; later it was transferred to polychelidans lobsters by Karasawa *et al.* (2013). Our new observation shows that the proposed interpretation suffers many

problems: the segments are visibly inverted and what was interpreted as antennae are too far apart from each other. Doubting the orientation of the specimen, we made detailed comparisons with isopod crustaceans. This allows us to claim herein that the specimen represents a posterior exoskeletal portion of a serolid isopod (Isopoda: Serolidae). There are more such cases: for instance, Feldmann and Charbonnier (2011) reinterpreted a putative slipper lobster as an isopod after recognizing its correct body orientation. *Tricarina gadvanensis* illustrates perfectly the real difficulty of an apparently simple task: correctly interpreting the orientation of fossil remains.

'Norwegian blue' – characterization of melanosomes generating non-iridescent structural colour and their detection in the fossil record

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Structural colours in the plumage of birds are produced by the scattering of light on nanostructural assemblages on the surface of the feather and are classified as iridescent and non-iridescent (NISC). The colour-producing nanostructure in NISC is a hollow keratin matrix of the feather barbs with an underlying melanosome layer that absorbs the unscattered light. However, how do the melanosomes involved in NISC compare to melanosomes involved in the production of iridescence and melanin-based colours? Here we have analysed melanosomes from a phylogenetically wide assemblage of NISC feathers to describe their morphology and compare to previously-studied colour categories that can be detected by melanosome shape. We find NISC melanosomes to be markedly wider, oblong and consistently distinctive from all melanosome categories. Only melanosomes involved in the production of grey colouration overlap occasionally with NISC, indicating an ontogenetic, and perhaps also evolutionary, relationship. While keratin doesn't fossilize, melanosomes do; to corroborate the likelihood of detecting NISC in the fossil record we analyse an Eocene roller, *Eocoracias* (Aves: Coraciiformes). We discuss also the likely relationship between NISC and grey and suggest that their similarity is due to the relationship between melanosomes and shape in self-assembly during feather ontogeny.

Convergence and functional evolution of feeding strategies in Crocodylomorpha

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The convergent evolution of longirostry (long, slender snouts) has occurred in several crocodylomorph lineages throughout their evolutionary history. Thalattosuchians and eusuchians are two such examples, and it has been proposed that the Early Jurassic basal teleosaurid thalattosuchian *Pelagosaurus typus* had similar feeding habits to the modern gharial, *Gavialis*. Here we compare evidence for different jaw muscle arrangements and skull stress-strain accommodation by digitally reconstructing musculoskeletal anatomy and simulating the mechanical response to feeding loads via finite element models. Although *Pelagosaurus* and *Gavialis* share similar patterns of stress distribution, we conclude

that *Pelagosaurus* was a highly specialized piscivore that fed on softer and smaller prey, indicated by lower mechanical resistance. Additionally, positive selection on feeding-related mandibular traits in Crocodylomorpha was investigated with an evolutionary rates analysis in BayesTraits including 60 species. Innovation of feeding strategies was achieved by rate acceleration of functional characters of the mandible, a key mechanism for diversification of clades like thalattosuchians and eusuchians. Different rates of functional evolution suggest divergent diversification dynamics between teleosaurids and metriorhynchids in the Jurassic. This study highlights the relevance of feeding specialization in the diversification of crocodylomorphs and the need to explore classic cases of convergence from a functional point of view.

Abiotic factors are not a main driver of shark evolution throughout the Cenozoic

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The evolutionary drivers of shark biodiversity remain largely under-explored. Here we test the role of temperature and sea-level in the evolution of lamniform and carcharhiniform sharks based on a Campanian–Recent morphometric dataset of teeth (n = 1,956). The diversity of lamniform and carcharhiniform tooth morphologies was highest during the Late Cretaceous and a noticeable decline in lamniform dental disparity occurred during the Miocene. Apart from these specific deviations, lamniform dental disparity was largely static, whereas carcharhiniform disparity was more episodic. Overall, disparity was similar between these clades, with no obvious inverse relationship between one another. On average, these shark groups diverge morphologically; carcharhiniforms have cutting-type dentitions, whereas lamniforms have clutching-type dentitions associated with a gradual loss of lateral-cusplets. The onset of this divergence occurred in the immediate aftermath of the end-Cretaceous mass extinction and was maintained throughout the Cenozoic. A generalized least squares model found support for a weak correlation between sea-level and disparity in lamniforms, but not with temperature. Applied to carcharhiniforms, we failed to reject a null-model of random change through time. Considered jointly, these relationships suggest a peripheral role of climate in driving the post-Mesozoic evolution of shark tooth morphology, and hint at more biology-grounded mechanisms.

New exceptionally preserved *Ichthyornis* specimens: shedding new light on a classic taxon

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The Late Cretaceous toothed bird *Ichthyornis dispar* is recognized as one of the closest relatives of crown birds among Mesozoic stem birds. As such, the skeletal morphology of *Ichthyornis* may be more representative of the ancestral condition of crown birds than

that of any other known Mesozoic avialan, and its study has crucial implications for understanding the origins and early evolution of crown birds. Here we present high-resolution scans of new, exquisitely preserved three-dimensional specimens of *Ichthyornis* from the Late Cretaceous of Kansas, USA, corresponding to a partial skeleton from a single individual, more complete and in better condition than the classic material. This new skeleton, preserving most of the pectoral girdle, including a three-dimensional complete sternum, the wing and the hindlimbs, shows certain morphological differences to the classic material, including the absence of some autapomorphies for this taxon and differences in some previously recognized diagnostic features for *Ichthyornis*. Thus, the new material may represent a previously unknown species, or it could indicate that the morphological disparity within *Ichthyornis* may be larger than previously appreciated. Ongoing work on these and other new *Ichthyornis* specimens will shed new light on morphological evolution across the crownward region of the stem bird phylogenetic tree.

A 'traumatic' summation of palaeopathological rates in Ornithopoda (Dinosauria, Ornithischia)

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Palaeopathological lesions have been recorded extensively in ornithopod dinosaurs and their study has contributed significantly in recent years to a more profound understanding of the lifestyle and behaviour of these animals. A total of *c*. 200 specimens has been recorded to date, with the basal-most osteopathy recognized in a 'hypsilophodontid' tibia from Australia. Analysis of the published lesions has revealed interesting trends: lesions recorded include trauma (36.7 %), infections (14 %), tumours (15.5 %), osteochondrosis (3.4 %), pseudoarthroses (3.4 %), spondyloarthropathy (1.4 %), developmental disorders (3.8 %) and other less prevalent diseases. These values are based solely on published specimens, however, and a complete survey of ornithopod palaeopathology is still missing. Here we present a first comparison of pathological rates among basal and derived taxa, categorized by classes of pathologies and body regions. Lesions predominantly occurred in the tail (particularly the distal portion) and the dorsal vertebrae. A notable finding is the occurrence of a similar pathological condition in the dorsals of *Huehuecanauthlus*, *Amurosaurus* and *Gryposaurus*, which may indicate similar behaviours. Previously undescribed material from Canada has revealed the presence of healed severe fractures, a possible chondroma and birth defects in mature individuals, thereby providing evidence suggestive of resilient immune systems.

Dental microwear textural analysis: reconstructing diets of non-mammalian fossil taxa from the Solnhofen archipelago

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Dental microwear textural analysis (DMTA) is a robust technique for testing dietary hypotheses in extant and fossil taxa. Microwear is produced as interactions with food items create characteristic tooth surface textures that vary with diet. Most DMTA research focuses on mammals, but new evidence suggests modern reptile microwear (crocodilians

and monitor lizards) also contain dietary signals. Modern reptiles can thus serve as DMTA analogues for non-mammalian fossil taxa, thereby assisting in the reconstruction of past food webs. A classic example is the Upper Jurassic Solnhofen biota of Germany. Current dietary hypotheses for Solnhofen tetrapods are largely based on qualitative assertions, making them an ideal subject to determine whether DMTA can detect dietary differences in non-mammalian taxa. We compared microwear from non-occlusal tooth surfaces of several Solnhofen taxa, including pterosaurs, crocodylomorphs, sphenodontids and the first bird, *Archaeopteryx*, with modern crocodilians and monitor lizards (including insectivorous, piscivorous and carnivorous species). DMTA demonstrates partial niche partitioning between the extinct taxa. Microwear exhibited by *Archaeopteryx* and sphenodontids indicates invertebrate-dominated diets, while pterosaur and crocodylomorph microwear indicates piscivory. DMTA provides novel, robust insights into the ecological roles of the Solnhofen biota, and the technique has great potential for reconstructing other non-mammalian dominated past food webs.

Fossil colour patterns in marine shelly taxa reveal evolution of vision and predator-prey landscapes during the Palaeozoic

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Fossil colour patterns may hold clues to how visual predation shaped evolution. Such patterns are occasionally preserved in shelly marine organisms, with examples extending back to the middle Cambrian. Here we analyse the fossil record of these patterns through the Palaeozoic. Simple high-contrast patterns, such as regular zigzags, stripes and spots, are the dominant colour patterns throughout the era. Similar patterns occur throughout the time period, although spotted patterns are known only from the Devonian onward. We confirm the previously observed increase in colour patterns during the Devonian and Carboniferous, showing that this cannot be ascribed to biases in preservation, or rock availability. There is a distinct transition of taxonomic composition. In particular, pre-Devonian occurrences consist mainly of trilobites and cephalopods, while benthic taxa such as gastropods, bivalves and brachiopods comprise a much greater proportion of colour-patterned taxa in the post-Devonian. We argue that the appearance of colour patterns was not due to the need for waste removal or a quirk of shell growth, but due to the evolution of visual predation. The Early Palaeozoic was dominated by arthropod visual systems, while the Devonian rise in colour patterns may be due to the radiation of durophagous gnathostome fishes.

Somosaguas fossil site project: 20 years filling the gap between palaeontology and society

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During its 20 year history, the Somosaguas fossil site (Pozuelo de Alarcón, Spain) has always had the mission of bringing palaeontology to new generations of scientists, but also

to society. To quantify progress, we performed an asset evaluation and compared it with two previous evaluations performed in 2000 and 2012. We made the asset evaluation on the basis of 21 criteria; 15 previously proposed and six new criteria, which are divided into scientific and sociocultural categories. The new criteria proposed for the scientific category are the number of scientific publications and meetings contributions. This would evaluate not only the scientific interest of the fossil site, as previous criteria rate, but also the academic performance. On the sociocultural category, we proposed four more criteria that measure the didactical interest, outreach interest, impact on conventional media and online media. A better asset evaluation was obtained for Somosaguas taking into account the 15 criteria previously rated: 25/30 points in the current evaluation versus 22/30 in the 2012 evaluation and 10/30 in the 2000 evaluation. We also obtained a very good score with the new criteria (33/40 points). Therefore, we conclude a positive evaluation for the progress of the Somosaguas fossil site.

The fuxianhuiid arthropod *Liangwangshania biloba* from the Lower Cambrian Xiaoshiba biota (Yunnan, China)

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The fuxianhuiid arthropod *Liangwangshania biloba* Chen, 2005, is described from the lower part of the lower Cambrian (Series 2, Stage 3) Hongjingshao Member (Canglangpu Formation), situated near Xiazhuang village in Yunnan (Southwest China). Specialized post-antennal appendages are recognized for the first time in this species, with micro-CT scans of the type material also demonstrating their presence. This is the first report of this species from this Formation, having previously only been recognized from outcrops of the underlying Yu'anshan Member (Qiongzhusi Formation). This is the first fuxianhuiid species to straddle this boundary, although two of the three previously recognized genera of fuxianhuiid from the Hongjingshao Member have representatives in the Yu'anshan Member. The presence of this species in the Xiaoshiba biota increases similarities between this and the Chengjiang biota, thus supporting prior arguments that these Lagerstätten represent part of a continuous succession rather than discrete entities.

Total-evidence framework reveals complex morphological evolution in nightbirds (Strisores)

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Strisores is a clade of largely insectivorous neoavian birds that includes specialized fliers such as swifts and hummingbirds, as well as a large diversity of nocturnal species such as nightjars. Despite the use of large-scale molecular datasets, the precise phylogenetic relationships between major strisorian groups remain controversial. Given the lack of consensus between results based on molecular data, we examined the possibility that incorporating morphological data from fossils might improve the resolution of this phylogenetic problem. We adopted a total-evidence approach, assembling a dataset that incorporated 117 morphological characters scored for 24 strisorian taxa (of which

14 were fossil taxa) as well as DNA sequences from the extant taxa. This dataset was analysed using Bayesian phylogenetic methods in MrBayes, resulting in a novel phylogenetic topology of Strisores that is nonetheless largely congruent with the findings of a comprehensive recent molecular phylogenetic analysis of modern birds. However, we found that integration of molecular and morphological data did not result in increased confidence in specific phylogenetic topologies. We suggest that strisorians experienced high levels of morphological homoplasy and that several strisorian lineages gained distinctive specializations early in their evolutionary history, rendering identification of their ancestral morphologies difficult.

Sinoburius lunaris (Arthropoda) from the early Cambrian Chengjiang biota revisited

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Sinoburius lunaris is an uncommon and unique trilobitomorpha arthropod from the Chengjiang biota (Cambrian Series 2, Stage 3). The first description of this species was based on only two specimens. Due to the limitation in the number of specimens and that in the visualization techniques, morphologies of the appendages have remained unclear for several decades. Consequently, the phylogenetic positioning of *Sinoburius* is still under debate. Here, we employed advanced visualization techniques such as fluorescent microscopy and micro-CT to restudy *S. lunaris* and to provide more accurate morphological features for phylogenetic coding. We further propose that the visualization techniques used in this study should be employed in a wider range to include all Chengjiang arthropods and other Cambrian arthropods with similar preservation. This will help us to test and correct some of the existing phylogenetic outcomes.

A total evidence-based approach to scorpion phylogenetics

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Scorpion phylogenetics is notoriously convoluted – previous studies using parsimony and likelihood-based techniques have failed to reach consensus, particularly regarding the placement of certain contentious scorpion groups that share morphological aspects of both the two main extant scorpion lineages – Buthida and Iurida. Furthermore, there has been a distinct lack of scorpion fossil data incorporated into these analyses, constraining efforts to interpret scorpion macroevolution correctly. For the first time, we produce a total evidence-based phylogenetic tree for scorpions, combining morphological, transcriptome and fossil age data, producing a fully dated tree. This clarifies debate surrounding contentious extant taxa and gives us further insight into the emergence and divergence of these arachnids. Future work will focus on creating a fuller scorpion morphology matrix, comparing other dating methods, and testing the validity of our total evidence-based dating method.

Posture in the fossil record: can bone microstructure be used to more accurately reconstruct past behaviour?

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Anoplotherium latipes, an early Oligocene tylopod artiodactyl, has been reconstructed as a facultatively bipedal browser from its skeletal anatomy. Trabecular bone microstructure can respond to mechanical loads within an organism's lifetime, and hence leave a signature of locomotor ability or posture within the internal structure of the bone. To test this facultative browsing hypothesis, micro-CT scans were used to quantify and compare the differences in proximal femur microstructure of *Anoplotherium* and seven extant taxa, with varied postural behaviours. Cortical bone thickness distributions show thicker areas towards the posterior femoral head in the facultatively bipedal gerenuk (*Litocranius walleri*: Bovidae, Artiodactyla), which also showed significantly more anisotropic bone trabeculae than other species. However, the trabecular bone of *Anoplotherium* was significantly less anisotropic than any of the extant taxa. The interpretation of *Anoplotherium* as a facultative biped appears not to be supported by the trabecular architecture of the proximal femur. Poor contrast of the *Anoplotherium* micro-CT data was problematic and further work with a larger sample size, and higher-contrast micro-CT data, may reveal further postural information.

Digital palaeoneurology of 'chirodipterid' lungfishes from the Devonian

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Lungfish are a group of 'lobe-finned' fish that first appeared over 400 million years ago. One genus known from the Late Devonian of Europe for almost 70 years is *Chirodipterus*. Since that time, six more species of *Chirodipterus* have been described, including forms from China and Australia (as well as other 'chirodipterids' such as *Pillarahynchus*, *Sorbitorhynchus etc.*), suggesting a global distribution. However, it has been noted that *Chirodipterus* forms a paraphyletic group, with the various species not recovered as closely related in recent phylogenetic analyses. It is vital to clarify the relationships of this group and others for their influence on theories of palaeobiogeography and early evolution of vertebrates. Advances in scanning technology have recently elucidated aspects of neurobiological evolution of early lungfishes, with one of the most recent contributions the digital endocast of *Chirodipterus australis* from the Gogo Formation of Australia. Endocranial characters have previously been demonstrated to be useful for determining interrelationships within lungfishes. We herein present synchrotron scan data of another 'chirodipterid' from Gogo, *Pillararhynchus*, and compare with the recently scanned *Chirodipterus wildungensis*, the holotype specimen that originally sparked the study of palaeoneurology in lungfishes. These results will aid in clarifying the taxonomy of this problematic genus.

Was the Devonian *Titanichthys* a filter feeder?

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Filter-feeding organisms utilize a filtering mesh (*e.g.* elongate, evenly-spaced gill rakers) to capture small, often planktonic prey suspended in water. By focusing on the base of the trophic pyramid, filter-feeders have repeatedly attained body masses exceeding those of their macrophagous counterparts – as in the Mesozoic pachycormids, whale sharks and modern baleen whales. The Late Devonian placoderm *Titanichthys* has tentatively been considered to have been a mega-suspension feeder, primarily due to its gigantic size and narrow, edentulous jaw. This has yet to be confirmed, owing to the absence of evidence of a filtering structure. Here the potential for microphagy and other feeding behaviours in *Titanichthys* is assessed via a comparative study of jaw mechanics in *Titanichthys* and other placoderms that utilized differing strategies. Finite element models of the lower jaws of *Titanichthys*, the (inferred) macropredatory *Dunkleosteus terrelli* and durophagous *Tafilalichthys* were produced, revealing considerably less resistance to stress and strain in the jaw of *Titanichthys*. Validatory comparisons investigating a selection of large-bodied extant taxa, with feeding strategies ranging from filter-feeding to durophagy, revealed similar disparities in jaw stress resistance. These results conform to the hypothesis that *Titanichthys* was a filter-feeder, with its jaw being unsuited for alternative, macrophagous, predatory strategies.

Inferring mode of life for extinct avians and theropod dinosaurs using measurements of curvature for the ungual phalanx

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Past workers have observed a relationship between curvature of the keratinous sheath of the claw of pedal digit III and mode of life for avians and squamates. This relationship has been used to infer certain lifestyles for fossil taxa such as *Archaeopteryx* and *Microraptor*. However, claw sheaths are composed of soft tissue prone to decomposition and deformation for fossil specimens; the inner ungual phalanx is more commonly preserved and less prone to deformation. This study seeks to improve analysis of fossil claws by determining a similar relationship between measurements of curvature taken for the ungual phalanx of pedal digit III and mode of life for a large and taxonomically diverse sample of modern birds and squamates. Ungual bone data have been acquired by X-ray imaging using a handheld dental imaging device, the NOMAD® Pro radiography unit. Measurements of curvature have been taken in custom-made software DinoLino.exe to find ventral and dorsal curvatures of ungual phalanges and keratinous sheaths. Statistical analyses including LDA (Linear Discriminate Analysis) have been performed using these measurements in R statistical software. The resultant statistical models have been used to infer terrestrial, predatory, perching and/or climbing behaviours for fossil avians, avialans, and maniraptoran dinosaurs.

Using phylogenomics to resolve early events in bacterial evolution

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A rooted tree of Bacteria is essential to reconstruct the evolutionary history of Bacteria, including ancestral gene content, metabolism and physiology. Many current ideas pertaining to the nature of bacterial evolution are informed by hypotheses of prokaryotic phylogeny. However, rooting the tree of Bacteria has proven difficult. Recent discoveries of a huge diversity of new uncultured phyla provide new data but are often difficult to resolve within the bacterial tree, with the relationships between the major bacterial lineages still showing little resolution. We attempt to construct a rooted tree of Bacteria using several methods, including traditional outgroup rooting, the relaxed molecular clock, minimal ancestor deviation (MAD) and probabilistic gene tree-species tree reconciliation methods. The latter are hierarchical models in which horizontal gene transfers (HGTs), gene duplications and gene losses are integrated into an overall model of genome evolution using amalgamated likelihood estimation (ALE), where patterns of gene family evolution contain information about the root of the tree. Using these different rooting methods, we may produce a rooted tree and reconstruct ancestral gene content and metabolism for the internal nodes, including the last bacterial common ancestor (LBCA), and can infer information about the early evolution of life.

The diversity of soft-bodied fossils from the background mudstone of the Chengjiang deposit

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The celebrated Chengjiang biota is well known for its exceptionally preserved soft-bodied fossils that occur in the so-called event mudstone of the Yu'anshan Member, Chiungchussu Formation (Cambrian Stage 3, Series 2), Southwest China. Recent field excavations and laboratory studies reveal, however, that the background mudstone of the Yu'anshan Member also bears well-preserved soft-bodied fossils, such as the neural system of radiodonts and the circulatory system of fuxianhuiids, thus opening a long-ignored window to allow us to study the morphology of animals in the early Cambrian. Here we present the first compilation of the taxonomic diversity and specimen abundance of the fossils with soft tissues from the background mudstone of the Chengjiang deposit based on our last 20 years of collection. The result reveals that the pelagic-swimming taxa, such as *Isoxys* and radiodonts and, surprisingly, benthic sponges (with well-articulated body) are the dominant groups, while the free-swimming taxa in the water column and the active benthic taxa are very rare. We propose that the reasons underlying this preservation bias might be controlled by physical/geochemical filters that favour pelagic-swimming taxa (*e.g.* seawater stratification) and differences in the ecological community structure in nearshore and pelagic regions (*e.g.* more predation by swimming taxa in the pelagic region).

Sedimentology and palaeontology of the Ediacaran–Cambrian transition in Estonia and western Russia

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Exceptionally preserved and undeformed mudstones from Estonia and western Russia capture the transitional interval between the Precambrian and Phanerozoic Eons. These mudstones contain rich assemblages of exceptionally preserved small carbonaceous fossils (SCFs), which could hold key insights into the processes involved in the Cambrian Explosion. However, reliable interpretation of these fossils is hampered by a lack of constraint on the depositional environment. Detailed petrographic analysis and submillimetre-scale logging of thin sections from representative core sections of the Kotlin Formation (Ediacaran) and the Lontova Formation (Fortunian/Cambrian Stage 2) was undertaken and microfacies and facies associations were identified. Fossil material was extracted, identified and interpreted alongside petrographic analysis of the thin sections. The microfacies identified in the Cambrian and Ediacaran sections indicate a sedimentation regime dominated by mud-rich microturbidite flows. The palaeontology is dominated by filamentous cyanobacteria and algae, as well as some unique forms previously unseen in the literature. The depositional setting is interpreted here as a shallow marine, inner to mid-shelf environment; a maximum depth of 200 m is suggested due to dominant cyanobacterial and algal growth on the substrate. Results indicate a rapid transition from a microbially-dominated substrate to a ventilated substrate across the Ediacaran–Cambrian boundary.

Evaluating the palaeobiology of the pentaradial Ediacaran organism *Arkarua* using computational fluid dynamics

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The late Ediacaran period (575–541 Ma) was characterized by the first appearance of large and morphologically complex multicellular organisms. Fossils from this period include forms that have been assigned to modern animal groups, but in most cases their palaeobiology and phylogenetic position remain controversial. One such fossil is the small disc-like organism *Arkarua*, characterized by five grooves radiating from a central depression on the upper surface, interpreted as the earliest known echinoderm. To gain an improved understanding of this enigmatic Ediacaran organism, three-dimensional digital models of *Arkarua* and two Cambrian echinoderms, *Cambraster* and *Stromatocystites*, were constructed and used in computer simulations of fluid flow (computational fluid dynamics). Simulations were carried out using different models for *Arkarua* to account for the variation observed in fossil specimens. The results reveal patterns of fluid flow around the putative feeding structures in *Arkarua* and the ambulacra in *Cambraster* and *Stromatocystites*, with implications for the ecology of these extinct taxa.

Functional morphology of the pectoral girdle of ichthyosaurs

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The locomotion of Ichthyosaurs has been classically interpreted as being similar to that of dolphins and mackerel sharks, with beating of the caudal fin and posterior torso providing propulsion and the forelimbs being used solely for stability. However, no prior study has thoroughly investigated the function of the pectoral girdle and the forelimb, especially with regard to musculature. Considering the importance of muscles to the function of this region, any study performed without such consideration would be incomplete. We investigate the function of the pectoral girdle of the early Jurassic parvipelvian ichthyosaurs *Hauffiopteryx typicus* and *Stenopterygius triscissus*, from the now inaccessible Strawberry Bank Lagerstätte of Somerset. Using CT scanning technology, the osteological elements retained within the matrix were scanned, segmented and realigned to produce a life-like digital model of the ichthyosaur's pectoral girdle. Following this, extant phylogenetic bracketing was used to infer the position of the muscle attachment sites on the pectoral girdle and muscular topology; this allowed for full digital reconstruction of the major muscles of the pectoral girdle and forelimb. Reconstruction of these muscles allowed comparison against bracketing taxa and apparent convergents (*e.g.* cetaceans), producing a thorough model of the function of this region in ichthyosaurs.

Palaeoenvironmental context of a large *Arthropleura* fossil from the middle Carboniferous Stainmore Formation, northeast England

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A newly-discovered partial arthropod body fossil, 80 cm in length and at least 35 cm in width, is here attributed to *Arthropleura*. The fossil was discovered within a fluvial channel sandstone of the Lower Pennsylvanian Stainmore Formation of Northumberland, northeast England. The purpose of this poster is to offer a preliminary description of the fossil and its palaeoenvironmental context. *Arthropleura* fossils of similar dimensions and completeness are extremely rare in the global rock record, meaning that the Northumberland specimen may shed new light on an archetypal Carboniferous organism, most commonly known from its trace fossil record.

Resolving Ediacaran discoidal fossils

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Abundant circular impressions found on the surfaces of siltstones of the late Ediacaran (~560 Ma) Fermeuse Formation in Newfoundland, Canada, are amongst the most common Ediacaran macrofossils. Those historically assigned to the genus *Aspidella* have been considered to represent discrete organisms, component parts of frondose organisms, or inorganic or microbial structures. To distinguish between these hypotheses we characterize the morphology and spatial distribution of *Aspidella* specimens, and compare these to bona fide frond holdfasts, tubular body fossil holdfasts, and inorganic structures also found on

late Ediacaran bedding planes. Our findings are further informed by thin section analysis to assess taphonomy and morphological variation across *Aspidella*-bearing bedding planes. Fossils uncovered on recent fieldwork reveal true frondose holdfasts and taxa preserved by volcanic ash in the Fermeuse Formation at Ferryland, suggesting that larger *Aspidella* may indeed be frond holdfast structures. However, some of the larger discs cannot be interpreted as any holdfast structure currently found in Ediacaran assemblages. Spatial statistics comparing the distributions of millimetre-scale *Aspidella* on particularly high density bedding planes with known juvenile frond distributions reveal significant differences between these groups. Together, our findings suggest that *Aspidella* specimens in the Fermeuse Formation reflect a variety of original organisms.

Using computational fluid dynamics to study the evolution of symmetry in echinoderms

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Symmetry is one of the key features of animal body plans. Bilateria, a major group of animals, are, for the most part, characterized by bilateral symmetry. Echinoderms are the only group of bilaterians that show pentaradial (five-fold) symmetry as adults, having diverged radically from the bilateral symmetry seen in other bilaterians. Cambrian fossil echinoderms display a wider range of symmetries than extant forms, including radial (either triradial or pentaradial), bilateral and asymmetrical forms. However, it is uncertain which type of symmetry is plesiomorphic for the phylum and why echinoderms diverged so radically from their bilaterally symmetrical ancestor. To address this, we analysed five Cambrian echinoderms, representing a range of different symmetries (asymmetrical, triradial and pentaradial). We constructed three-dimensional digital models of each taxon and used these in computational fluid dynamics simulations of water flow to assess the hydrodynamic performance of forms with different types of symmetry. Results suggest that feeding efficiency was similar for asymmetrical, triradial and pentaradial taxa, indicating that pentaradial symmetry did not evolve solely as an adaptation to a sessile suspension feeding mode of life.

Does the skeletal composition of marine calcifiers vary with latitude?

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Aragonite and calcite seas have long been primarily viewed as a consequence of the seawater Mg/Ca ratio. However, experiments have demonstrated a strong temperature influence on $CaCO_3$ precipitation, with increasing temperatures favouring the formation of aragonite. Aragonite-calcite sea conditions should thus vary not only in time, but also in space, across latitudes and depth. A temperature effect has been shown for the skeletal mineralogy of some marine calcifiers in experiments and field studies. This leads to the hypothesis that aragonitic calcifiers may have been more successful, on average, in the warm waters of the tropics than in higher latitudes. We use the fossil record of marine calcifiers from the Paleobiology Database as well as recent ecological data from the Ocean

Biogeographic Information System to assess latitudinal differences in the prevalence of aragonitic and calcitic taxa. Across the Ordovician–Pleistocene, no consistent latitudinal or depth-related pattern emerges, and modern bivalves show the highest abundance of aragonitic taxa in high latitudes. We conclude that the temperature effect on calcification, while apparent in some taxa, has not controlled the global distribution of marine calcifiers.

Late-blooming bristle worms: biological traits analysis shows that polychaetes did not radiate until the Mesozoic

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Recent polychaetes exhibit a wide range of lifestyles and feeding habits which is reflected in their great morphological variation. Although rare, soft-bodied polychaete fossils allow a glimpse of the morphological diversity present as early as the Cambrian. However, the ecological roles of these early polychaetes are unclear. We analysed morphological traits of Palaeozoic polychaete taxa and recent polychaete families using morphology-based biological traits analysis. We recovered three clusters in morphospace which showed significant associations with predatory, tubiculous filter-feeding and deposit-feeding lifestyles respectively. Palaeozoic taxa are constrained to the deposit-feeding cluster, showing that predatory and tube-building lifestyles developed after the Palaeozoic, likely in concert with the Mesozoic Marine Revolution. As predation pressure rose, predators adapted to be more efficient hunters while prey evolved more elaborate protection mechanisms, chiefly the construction of stable burrows and permanent tubes. Key morphological innovations such as the radiolar crowns of suspension feeders or the improved eyes of predatory taxa allowed polychaetes to expand into fundamentally new niches over 300 Ma after their first occurrence. The early burst model of adaptive radiation expects high rates of morphological disparity early in a clade's lifetime, but polychaetes instead diversified halfway through their evolutionary history.

Taphonomy of cephalopod ink – the importance of sulfurization and burial history to melanin preservation

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Melanin is the most common pigment in vertebrates, with two main forms: black eumelanin and rufous pheomelanin. Melanin frequently preserves in exceptional fossils and provides means to identify certain tissues and even integumentary colour. In order to confidently determine colour through chemical composition, a better understanding of melanin taphonomy is needed. Here we analyse pure eumelanin from fossil cephalopod ink sacs. We have subjected extant melanin samples to artificial maturation in the presence of sulfur and sulfide in order to assess the potential for secondary sulfurization to lead to conflation with phaeomelanin, which contains sulfur. We show with time-of-flight secondary ion mass spectrometry (ToF-SIMS), Fourier-transform infrared spectroscopy and pyrolysis-gas chromatography-mass spectrometry the progressive dehydration of melanin due to maturation. Sulfurization leads to the formation of thiophenes, but not

thiazines or thiazoles as in phaeomelanin. Multivariate statistical analysis of such a comprehensive dataset allows the resolution of different aspects. We show how to analyse burial history relative to original melanin chemistry with ToF-SIMS data and principal component analysis. Our study, therefore, provides an important step towards a protocol for determining original melanin chemistry and the taphonomic pathways to have in mind when analysing fossil specimens.

Characterizing the evolution of morphological disparity in Osteostraci (Vertebrata, stem-Gnathostomata) by means of categorical and geometric morphometric approaches

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Quantification of morphological variation (disparity) is crucial to test general hypotheses in organismal evolution. Disparity tends to be evaluated through two non-mutually exclusive approaches: 1) quantitatively, through geometric morphometrics, and 2) in terms of discrete categorical characters. Uncertainty over the comparability of these approaches diminishes the potential to obtain nomothetic insights into the evolution of morphological disparity, and the few benchmarking studies conducted so far show contrasting results. Here we apply both approaches to characterizing morphology in the stem-gnathostome clade Osteostraci, in order to assess congruence between these alternative methods as well as to explore the evolutionary patterns of the group. Our results suggest that both approaches yield similar results in morphospace occupation and clustering, but also some differences indicating that these metrics may capture different aspects of morphology. Temporal patterns of disparity recorded by each approach differ considerably, capturing disparity maxima at very different times of the evolutionary history of the group. Therefore, this work provides evidence supporting that categorical and continuous data do not always capture morphological disparity in equivalent ways and that discrepancies reflect differences in the potential of each data type for characterizing more or less inclusive aspects of overall phenotype.

Cosmopolitodus praecursor (Chondrichthyes, Eocene) apex predator in past seagrass

George Forsey

Independent

The extinct shark *Cosmopolitodus praecursor* (Eocene) was a widespread, apex predator in shallow marine environments during the Eocene. Records from teeth are associated with faunal elements that are interpreted as arising from seagrass habitats which *C. praecursor* utilized as prey-rich environments. It is commonly found with early cetaceans (such as basilosaurids), sirenians and other selachians. Less commonly, cheloniids, bony fish and cephalopods were present. These all may have been prey items for *C. praecursor* during its ontogeny. *C. praecursor* was the putative ancestor of *Cosmopolitodus hastalis* (Early

Oligocene–Pliocene) recently noted as an apex predator in past seagrass. This narrative investigates how far *C. praecursor* was similarly engaged with the seagrass ecosystem. Evidence presented here indicates a close association with past seagrass; a trait subsequently inherited by *C. hastalis*. In the absence of further evidence, the reasons for *C. praecursor* visiting seagrass was for predation. Past seagrass has been interpreted using a range of indicators. The extinction of *C. praecursor* by the end of the Eocene may be related to climate amelioration, subsequent reduction in seagrass and prey availability.

Seagrass distribution and global biodiversity hotspot during the Badenian (Middle Miocene) of Central Paratethys as indicated by ostracods and other faunal elements

George Forsey
Independent

Central Paratethys was a series of tectonically-formed basins which were flooded by the sea through restricted seaways to the Atlantic (via the Mediterranean) and from the Indian Ocean (via Eastern Paratethys) during the Oligocene and Miocene. As a result of difficulties of correlation, a regional stratigraphy has been employed in which the Badenian equates to part of the Middle Miocene. Most ostracod-containing faunas from the Badenian of Central Paratethys can be interpreted as past seagrass. These interpretations were reinforced by other seagrass indicators such as sirenians, molluscs and foraminifera. Together these indicated widespread seagrass meadows across much of the shallow marine environments of Central Paratethys during the Badenian. The diverse faunas associated with seagrass suggest that Central Paratethys may have been a global marine biodiversity hotspot during the Badenian. Because of the large number of studies on the Badenian of Central Paratethys, this represents an unrivalled window into seagrass distribution during the Miocene.

A study into the shallow water biodiversity of the London-Brabant Island during the Cretaceous

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The Cretaceous Period was characterized by rising sea levels, which created many new shallow sea environments. For the London-Brabant Massif, at this point the London-Brabant Island, new marine environments appeared in what today would be areas of Southern England. This investigation looked at two sites, Clophill Quarry, Bedfordshire, and Patteson Court Quarry, Surrey, with the aim of identifying tooth fossil remains. Teeth were collected over several trips at both localities, yielding significant fossil material. The sand was sieved on site and the teeth later identified under a microscope. Almost all teeth collected were of extinct, freshwater shark species which emerged in the Cretaceous during a period of adaptive radiation. Some 1,372 teeth were identified from the sites, with *Planohybodus ensis*, *Palaeoscyllium formosum* and *Egertonodus basanus* found in roughly equal abundance at each site, indicating a similarity in the two ecosystems. However, *Lochidion* species accounted for 53.86 % of the total species collected and were found almost exclusively at the Surrey site. Factors that could account for this abundance include: that *Lochidion* may have been better able to adapt to emerging niches due to its larger range of prey; or that their remains, by chance, could have been better preserved.

A juvenile skull of the hornless rhinocerotid *Acerorhinus neleus* (Rhinocerotidae, Mammalia) from the late Miocene locality of Pikermi (Attica, Greece)

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Among the rarest elements of the renowned late Miocene fauna of Pikermi (Attica, Greece) is the hornless rhinocerotid *Acerorhinus neleus* (Aceratheriinae, Rhinocerotidae, Mammalia). A juvenile cranium and mandible, housed at the Museum of Paleontology and Geology at the University of Athens, are documented for the first time. The cranium, missing the nasals, is characterized by the flattened hornless frontals, the relatively elevated orbita and the retracted nasal incision. The mandible shows a similar dental stage of wear. The broken symphyseal region exhibits two well-formed alveoli for functional deciduous second lower incisors. The marked differences observed in the relative distribution and abundance of both horned and hornless rhinocerotid taxa among the Turolian localities of Greece seem to have been primarily influenced by environmentally controlled provincial differences. In Pikermi, *Dihoplus pikermiensis* is the dominant tandem-horned rhinoceros, "*Diceros*" *neumayri* is less frequent, and hornless *Acerorhinus* is present. In Samos, "*Diceros*" *neumayri* emerges as the dominant horned species, *Dihoplus pikermiensis* is infrequent, whereas *Chilotherium* is the sole hornless taxon present. The relatively slender and brachydont *Dihoplus pikermiensis* and *Acerorhinus* appear to have preferred more closed and temperate niches, whereas the more robust and specialized "*Diceros*" *neumayri* and *Chilotherium* favoured more open and dry habitats.

The British Zechstein forest: evidence of a wetter Late Permian environment

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The Late Permian Zechstein Sea was a semi-isolated inland sea that occupied the Southern Permian Basin at equatorial latitudes. The sea endured for 5 to 7 million years during which time it underwent five cycles of evaporation. Previous Zechstein reconstructions show cyclic regressions accompanied by evaporative down draw leading to hypersaline marine conditions, resulting in short term dramatic reductions in biotic abundance and diversity in both marine and terrestrial environments. However, it is hypothesized that transgression phases experienced sufficient precipitation to facilitate ecosystem recovery. Investigation of borehole material from northeast Yorkshire, UK has yielded unexpected palynomorph abundance from the Carnallitic Marl Formation in the fourth cycle, comparable to assemblages reported by Clarke (1965) from the Marl Slate. The assemblage is dominated by taeniate and striate bisaccate pollen accompanied by monosaccates and trisaccates. Typical Late Permian taxa including Lueckisporites, Protohaploxypinus, Taeniaesporites, Nuskoisporites, Perisaccus, Klausipollenites, Vittatina and Illenites have been identified, and lend support to a transient gymnosperm-dominated late Zechstein Euramerican vegetation, dominated by phylogenetically advanced conifers. The presence of this assemblage questions previous assumptions that Late Permian equatorial climates were continuously arid. These findings suggest the climate was at times damp enough to support ecosystem recovery, despite the impending Permian–Triassic extinction event.

Dishing the dirt on dental wear and diet – tooth microwear texture in moles is independent of dietary sand and silt

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Dental microwear is a widely used proxy for dietary reconstruction in fossil mammals. It is based on quantitative analysis of the microscopic textures on teeth caused by food items and by the compressive/shearing forces that act during feeding. Recent papers have questioned the relationship between food/diet and microwear, proposing that extraneous 'dietary grit' (particles of hard silicate minerals) ingested with food are the primary agent of wear. Experimental work on large herbivorous mammals has found that microwear reflects diet, even where 'grit' load is enhanced, but this remains untested in other mammals. Here we provide the first analysis of the relationship between 'grit' and microwear generation in small predatory mammals (relevant to dietary reconstruction in early mammals). Moles are ideal subjects for study because their diet contains significant 'dietary grit'. Irrespective of soil type diet is dominated by worms, but 'grit' content varies significantly between soils. If 'dietary grit' is a significant factor, microwear texture should track sand and silt content of soils, but we find no relationship. This provides further evidence that microwear texture reflects the material properties of food, not just 'grit', and is a reliable proxy for dietary reconstruction.

The Bristol Rhaetian stool chart

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The Rhaetian bone beds from around Bristol are famous for their fossil teeth and bones of fishes and marine reptiles. The bone beds also contain abundant coprolites produced by those fishes and marine reptiles. We identify three coprolite morphologies from hundreds of individual specimens, and the producers have been identified as sharks, actinopterygian fish, reptiles and decapods. This diverse ecological assemblage can be further analysed by observing inclusions within the coprolites, including scales and small bones, though some shell fragments are observed. CT scans of the distinctive spiral coprolites assigned to large bony fish and sharks reveal in detail included scales of smaller fish, including *Gyrolepis*, known to be abundant at this time. The discovery of crustacean coprolites, identified through CT scans revealing their characteristic internal morphology and comparison with modern examples, broadens evidence of the overall fauna and likely food web, and shows an early stage of the Mesozoic marine revolution in documentation of modern groups of crustaceans and fishes and their feeding relationships.

Geochemical composition of conodonts as the record of their growth dynamics

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Conodonts are extinct jawless, eel-like vertebrates common in marine facies from the Cambrian to the Triassic. Despite their wide use in biostratigraphy, little is known about their actual biology. Conodonts were the first vertebrates to produce mineralized

skeletal tissue. Their teeth analogues, called elements, are composed of an apatite-organic composite biomineral and grew through outer periodical accretion of new growth lamellae. Our high-resolution BSE imaging technique provides a new way to analyse conodont growth dynamics by making alternations of dark and light bands forming these growth lamellae visible. The observed growth stages are linked to distinct geochemical changes, mainly of the element strontium, which are measured with EDX. These changes might reflect a transition in the conodont's mode of feeding and/or living. The early life stage of the conodont is characterized by a specific morphology, the lack of wear patterns and high Sr values, which leads to the interpretation as the first, larval stage. Based on the observation of following patterns of wear and repair, as well as low Sr values, a drastic change in the conodont's mode of living towards a more mature type of feeding, possibly as a predator or scavenger, is proposed.

The locomotory ecomorphology of sauropterygian marine reptiles

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Sauropterygians were one of the groups of reptiles that became secondarily aquatic during the Mesozoic. From the durophagous shallow water placodonts to the open-ocean giant macropredatory pliosaurs, they explored a remarkable diversity of ecological niches. Sauropterygians became exceptionally adapted to locomotion in water, and the Jurassic–Cretaceous plesiosaurs evolved quadrupedal underwater flight, a style with no parallel amongst modern aquatic tetrapods. The evolution of swimming modes and locomotor adaptations in Triassic sauropterygians (placodonts, pachypleurosaurs and nothosaurs) remains largely unexplored, but evidence suggests that lateral undulation or forelimb to surface contact propulsion was used. Understanding the link between morphology and major ecological innovations, such as locomotory mode, is an important part of macroevolution. Here we evaluate morphological disparity associated with locomotion in sauropterygians using multivariate analysis of morphometric data. Measurements include body size, and post-cranial features with inferred functional value in locomotion, such as limb proportions, crural and brachial indexes and autopodial aspect ratio. Our data on 25 sauropterygian genera, representing all major morphotypes, clades and time intervals, show that analysis of simple morphometric measurements can discriminate between major locomotory ecomorphotypes, and we highlight key skeletal transformations in the evolution of sauropterygians.

Evidence of a new *Otodus megalodon* nursery area in the middle Miocene of Spain

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Nursery areas, understood as a defined geographical region where juveniles undergo growth and development, are essential for the survival and success of many marine organisms. Nursing, frequently described or inferred in both extant and extinct sharks, has been interpreted as a complex ecological strategy underlying the success of many taxa,

as suggested for *Otodus megalodon* during the late Miocene. Here we describe a second nursery area for the same species during the Langhian (middle Miocene) of the western Mediterranean area, strengthening the idea that this top-predatory shark showed a complex reproductive ecology. Our samples were collected in shallow reef deposits from Tarragona, Spain associated with a rich and diverse faunistic community. In order to estimate the population structure of *O. megalodon* in the region, body length estimations for each individual were obtained from tooth-body length linear regression equations established in *Carcharodon carcharias*. Our results show a bimodal distribution, comprising a first peak of neonates and juveniles and a second peak of adults (probably representing gravid females). Comparison of our data with previously described population structures of living shark nursery areas, the faunal assemblage and the sedimentological context of the studied region, supports our hypothesis.

The invasive foraminifer *Trochammina hadai* as a signal of the Anthropocene in San Francisco Bay

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The invasive Japanese benthic foraminifer *Trochammina hadai* was first collected in San Francisco Bay from sediment samples in 1983. Since 1986 it has been identified in 91 % of sampled sites in the Bay, reflecting the fact that due to their small size, microorganisms are easily transported by local currents. Analysis of archived core material collected in 1990–1993 has quantified *T. hadai*'s biostratigraphic impact on the sedimentary deposits of South Bay where the species first appeared and San Pablo Bay to which it spread. In this study, *T. hadai* has been identified in 80 % of samples, and in some sections *T. hadai* constitutes up to 100 % of the foraminiferal assemblage. This restructuring of the local biosphere, across less than a decade, resulting from an anthropogenic introduction, is the largest perturbation to the foraminiferal record in San Francisco Bay in the last 125,000 years. Consequently, it provides an opportunity to define a biostratigraphic interval that helps identify a unit of the Anthropocene age in the sedimentary deposits of the Bay, one that has the potential to be correlated between widely distributed, anthropogenically-influenced sedimentary successions. The preservation of this striking biostratigraphic signal suggests that San Francisco Bay might be explored for a potential stratotype for the Anthropocene.

Quantifying the effects of changing deposition rates on the stratigraphic distribution of fossils

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The fossil record is inevitably biased by the sedimentary processes that formed it, and it can only be understood within the context of these processes. This makes the incorporation of knowledge of sedimentary conditions into statistical analysis of the fossil record necessary to obtain exact results. Here I present a statistical method that allows quantification of the effects of changing deposition rates on the stratigraphic distribution of fossils on the scale of single sections. This method can be used to correct data for effects of changing deposition rates and to assess how the interpretation of palaeontological hypotheses changes under different deposition models. It can also be used to optimize

sampling procedures, is backwards compatible with previous statistical methods that use the stratigraphic distribution of fossils, and allows us to model the effects of changing deposition rates on the fossil record. This demonstrates the biasing effect of sequence stratigraphy on the fossil record and emphasizes the importance of a sampling procedure that documents not only the distribution of fossils, but also the depositional environment.

Reversing time averaging and reconstructing extinction rates with approaches from image processing

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Last fossil occurrences and fossil abundance are used to make inferences about ecology in the deep past, be it the success of a taxon in a particular environment or the temporal development of extinction rates throughout a mass extinction. However, the Signor-Lipps effect and time-averaging make this type of data only circumstantial evidence of the ecological process that generated it in the first place. Here I present a model that is based on the idea that empirical data as they are generated by fieldwork is a blurred version of the original ecological signal, which can accordingly be obtained by reversing the blurring effect. Generating and reversing these effects is a common task in image processing, which offers a number of algorithms for these tasks that can be deployed for the proposed model. The presented reconstruction method can also be expanded to incorporate the effects of changing deposition rates.

A digital reconstruction of the nasal cavity of *Riograndia guaibensis* (Eucynodontia, Ictidosauria) and nasal cavity evolution in nonmammaliaform cynodonts

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With the aid of modern technologies such as micro-CT scanning and 3D model reconstruction, the internal anatomy of fossilized remains can be easily and non-invasively studied. Here we describe the internal anatomical structures and associated bones of the nasal cavity of *Riograndia guaibensis*, a non-mammaliaform cynodont for the Late Triassic of Brazil. The specimen (UFRG-PV-596-T) is represented by an almost complete skull, articulated right and isolated left hemimandibles that were micro-CT scanned at the University of Bristol in 2016. The 3D reconstruction of the nasal cavity highlights the impression of ridges and canals on the internal surface of the bones that constitute the nasal passage. The presence, dimensions and morphology of these ridges have implications for the possible respiratory patterns, metabolic rate and ecology of this taxon. It is generally accepted that the acquisition of ossified maxilloturbinals is related to the appearance of endothermy in mammaliaforms. However, the presence of cartilaginous maxilloturbinals in *Riograndia*, as indicated by the preserved bony ridges, is very probable. The comparative study of these characteristics in various taxa before and after the appearance of mammals helps to shed light on this much debated moment and is crucial in mammalian evolution.

Molecular palaeobiology reveals the deep evolution of Ecdysozoa

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Ecdysozoa (moulting animals) is a taxon uniting eight phyla of protostomes, including the most diverse and most abundant of all animals – the arthropods and nematodes respectively. Whilst the monophyly of this clade is robust, the internal topology remains unresolved, and its origins obscure. Of particular concern is the monophyly of the supposed vermiform subclade Cycloneuralia, and the timing of divergences in the geological past. This lack of clarity cascades onto adjacent branches of the Tree of Life and presents a considerable constraint on interpreting the origins of the Phanerozoic animal-dominated biosphere, and the nature/existence of a Cambrian evolutionary 'explosion'. To address these issues, we assembled a phylogenomic supermatrix from published genomes/transcriptomes, supplemented by newly sequenced taxa, and employed Bayesian methods to estimate phylogenetic divergence times. Tree inference shows that Cycloneuralia is paraphyletic, with a monophyletic Scalidophora as the sister group to Nematoida + Panarthropoda; and relaxed clock divergence time estimations consistently recover a Precambrian divergence of Ecdysozoa. Our results indicate that 'cycloneuralian' characters (*i.e.* circumpharyngeal nerve rings and introverts/probosces) are likely ecdysozoan plesiomorphies, and that there may have been a considerable 'fuse' between ecdysozoan origin and megadiversity.

posters

Exceptionally preserved Late Ordovician 'starfish beds' from the Tafilalt area, Morocco: implications for the Great Ordovician Biodiversification Event

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The Upper Ordovician series of the Tafilalt area (eastern Anti-Atlas, Morocco) has yielded several echinoderm Lagerstätten, providing a relatively continuous record of successive, nearshore, cool water, echinoderm-dominated assemblages from the early Sandbian to the Hirnantian. During this time interval, the diversity of the majority of the Tafilalt echinoderm assemblages shows relatively little change, with the persistence of the same dominating groups such as crinoids, coronates, diploporitans, edrioasteroids, eocrinoids, glyptocystitid rhombiferans, solutans and stylophorans. However, these assemblages represent one of the earliest episodes where ophiuroids and asteroids also become a significant, and in some cases dominant, part of some of the assemblages. This includes some of the earliest preserved examples of dense aggregations of brittle stars, the echinoderm meadows often observed today in deep water/cool water habits. Unlike assemblages of comparable age such as Lady Burn Starfish Beds, Scotland, these examples are likely to be *in situ*. Closer examination of the generic and specific content of the three main asterozoan assemblages reveals that distinct assemblages first dominated by protasterid ophiuroids appeared in the early Ordovician, while other assemblages contain entirely new taxa of both ophiuroids and asteroids and represent the rapid diversification of these groups during the Great Ordovician Biodiversification Event.

Walking in the shadows of giants: the small theropods of the Early Cretaceous Kem Kem beds of Morocco, North Africa

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The Kem Kem beds of mid-Cretaceous age, southeast Morocco, are renowned for yielding, in abundance, very large vertebrates, leading to the nickname 'River of Giants'. Previous work has focused on the palaeoecology, palaeoenvironment and taxonomy of the larger vertebrates found mainly by local fossil collectors. Much work has centred on the very large theropod dinosaurs, especially the sail-backed *Spinosaurus*. The smaller vertebrates, represented mostly by teeth, have been largely overlooked, resulting in an unbalanced view of the ecosystem. This study focuses on samples of teeth of 10 mm or less in overall size, sieved from mine spoil by the fossil diggers. The teeth were identified using standard comparative anatomical and morphometric methods and using the macrofauna for comparison. A part of the analysis utilized dental serrations and shape morphometrics to assess theropod diversity. Juveniles of each known taxa were recorded, but examples not fitting any previously described morphology are also present in the sample. The preliminary results suggest that the dinosaurs were most likely nesting and raising their young in close proximity to the river, and that the dominance of large carnivores is likely an artefact of sampling by commercial collectors.

Global mammalian response to a mid-Miocene peak in atmospheric carbon dioxide

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North American Miocene mammalian faunas represented non-analogous communities over-rich in large browsing (*i.e.* brachydont) species. These communities were interpreted as a response to the rise and subsequent fall in levels of atmospheric CO_2 in the mid-Miocene, which would have resulted in higher levels of primary productivity. The rise and fall of CO_2 broadly followed the palaeotemperature curve, but these analogous communities cannot be explained by temperature change. The current geochemistry consensus is mid-Miocene levels of around 600 ppm, over twice the Recent pre-industrial levels. Using data from the NOW database, including localities that appear to represent a single faunal sample, we show a similar mid-Miocene (~ 17–14 Ma) browser peak occurring independently in five different Old World regions, supporting the original hypothesis from the North American data. Furthermore, Australian mid-Miocene localities, containing herbivorous mammals with different taxonomic affinities to the Northern Hemisphere faunas (marsupials versus placentals), and that evolved in unique habitats independently of faunal or tectonic events affecting other continents, show a comparable response. We conclude that the patterns of mammalian herbivore diversity worldwide support the hypothesis of a faunal response to changing levels of primary productivity driven by changing levels of atmospheric CO_2 during the mid-Miocene.

Brood care in troubled waters: first evidence of fossil Eucarida brood care and its palaeobiological and taphonomical interpretations

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Konservat-Lagerstätten are exceptional fossiliferous sites since they deliver truly exquisite and never-seen-elsewhere palaeobiological information allowing a better understanding of fossilization processes. The Konservat-Lagerstätte of La Voulte-sur-Rhône (Ardèche, France) is a Middle Jurassic deposit yielding a diversity of finely-preserved crustacean fossils thriving in this deep (>200 m) hydrothermal environment. Here we report the exceptional find of two female polychelidan lobsters with their internal organs preserved, including mature ovaries in one and the other was brooding *c.* 500 preserved eggs under its pleon. X-ray microtomography allowed those details to be revealed from carbonate nodules. This is the first fossil evidence of brood care in the Eucarida group and consequently confirms that this type of brood care was indeed already present in Pleocyemata Burkenroad, 1963, of which it is the defining character. Since fossil evidence of brood care remains extremely rare, this find underlines the importance of using non-destructive imaging methods, such as X-ray tomography, to extract the maximum information from otherwise overlooked collection items without risking damaging the preserved structures. Our taphonomical model developed on other crustaceans from La Voulte-sur-Rhône implies that the morphological preservation of such delicate structures was possible through early mineral precipitation associated, paradoxically, with rapid biodegradation.

Tail-length estimations for "*Metailurus parvulus*" (Felidae, Mammalia) from Kerassia (northern Euboea, Greece)

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In this study, the tail length of "*Metailurus parvulus*" is estimated, using a variety of methods. The studied material consists of a sacrum and four associated caudal vertebrae excavated from the late Miocene locality Kerassia-1 in 2001. These specimens are the first remains of the tail of "*M. parvulus*". The fossils were compared to different extant Felidae species. The first method used was the sacral index (Ankel 1965), which is based on the narrowing of the neural canal in the sacrum. The results of this method indicate that the tail of "*M. parvulus*" was probably relatively short. The other method used concerns the number of the caudal vertebrae that preserve the neural canal. This method suggests a short tail for "*M. parvulus*" (*nM. parvulus* = 3), possibly even shorter than that of the extant short-tailed *Lynx lynx* (*nL. lynx* = 3-5). The results suggest that the tail length of "*M. parvulus*" was most likely relatively short. This conclusion may provide further insight into the ecology of the species.

Cladistic matrix: a tool for taxonomical identifications and evolutionary research

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This study proposes that matrices can be used in taxonomical identification by using the phylogenetically significant differences preserved in them. The 'morphological difference' between the unidentified sample and the typical form of a known species can be calculated through a simple set of formulas. The species that results to the minimum difference is proposed to be the accurate one. During the application of the aforementioned method, a non-zero difference between the sample and the fitting species is frequently dealt. This non-zero difference indicates that phylogenetic characters occasionally retain a considerable degree of variability. Therefore, this method contributes to the comparison of different groups of individuals, such as different populations, sexes or age stages, leading to the detection of their distinct adaptational trends. This study provides a new point of view on cladistic matrices. Identification can be easily fulfilled using the maximum number of available characters, and evolutionary trends of intraspecific groups can be revealed. Both aspects are fundamental in palaeontology, in taxonomical and evolutionary studies respectively. The utility and simplicity are the benefits of the proposed method, which will be a very convenient tool in future studies.

Unexpected mode of tooth development in an Early Devonian sarcopterygian from the Canadian Arctic

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Understanding the origins and evolution of teeth requires knowledge of the diversity of dental development in early members of the osteichthyans and chondrichthyans. Here we present new micro-CT data on sarcopterygian jaw material from the Early Devonian of Prince of Wales Island, Arctic Canada. The material is probably attributable to *Powichthys thorsteinssoni* Jessen, 1980. Morphologically complete teeth, sometimes arranged in rows, are buried within the jawbones. These teeth are labial to the marginal shedding tooth row, do not form ordered tooth families, and are covered by bone and cosmine. These initial teeth differ from the cone-like marginal shedding teeth in their laterally compressed and recurved shape and the absence of signs of resorption. Development of the dentition can be reconstructed: early generations of teeth are overgrown by bone and shedding teeth develop on the lingual side. This mode of initial appositional dental organization and later fixation on a shedding row is similar to the condition described for the putative stem osteichthyan *Andreolepis* from the late Silurian of Gotland. Our data suggest a more widespread distribution of this supposed primitive mode of tooth development among early osteichthyans and urges further study into the diversity of dental development.

The Toarcian extinction event bivalve fauna of central England

Robin Knight

Independent

The Toarcian extinction event is preserved as the highly condensed 'Transition Beds' in central England. However, the fossil fauna is well-preserved, with bivalves being on the whole unfragmented, showing minimal wear and on occasion still being articulated. The fossil bivalve fauna preserved in the 'Transition Beds' has distinct components when compared to those observed in other UK and European sections preserving the Toarcian extinction event. The main variation occurs in species across the Parallelodontidae, Astartidae and Ceratomyidae. This represents a shallow versus deeper water variation in taxa, with the 'Transition Beds' providing a rare insight into nearer shore high-energy environment faunas during the Toarcian extinction event. These environments may have acted as 'refugia' for some taxa with arcid and astartid species apparently being present in the Lower Inferior Oolite.

Microfossils and hominids: analysing the Pleistocene environment of the Nihewan Basin, northern China

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Important archaeological sites regarding the spread of early humans are situated in the fluvio-lacustrine Pleistocene stratigraphy of the Nihewan Basin. The Nihewan Basin is one of the most intensively studied areas of human occupation in higher latitude areas, due to the concentration and availability of archaeological sites between 2.0–0.8 Ma. However, correlation of sites without an established geochronology within the basin proves difficult, as the nature of the sediments impedes accurate correlation. Nonetheless, preliminary results have shown that it is possible to correlate sites without prioritizing the use of magnetostratigraphy. Two sites Majuangou (MJG), correlated within the basin using magnetostratigraphy, and newly exposed Shigou C (SGC) were selected. Results show that SGC has a coarser grain size and high concentration of *Ilyocypris* ostracods suggesting a river environment, whilst MJG's grain size is finer and has a more varied ostracod assemblage indicative of a shallow water environment. The ostracod *Cytherissa lacustris* occurs at both sites allowing the correlation of these sites. These preliminary results suggest it is possible to correlate palaeoenvironments in the Nihewan Basin without use of prioritizing magnetostratigraphy. Furthermore, these results will aid the interpretation of the palaeoenvironment in which early hominids occupied higher northern latitudes.

A new look at the evolution of the *Palaeoloxodon* skull

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Species of the extinct Pleistocene elephant *Palaeoloxodon* from across Afro-Eurasia have long been discriminated based on the so-called "Stuttgart" and "*namadicus*" cranial

morphs, demarcated respectively by a weakly/moderately or strongly developed parieto-occipital crest (POC), which characterizes the genus. The Calabrian *Palaeoloxodon recki* from Africa already possesses most characteristic synapomorphies of the genus, but with only a slightly developed POC. The contrasting maturation of a strong POC observed in subsequent Middle Pleistocene species, *P. antiquus* (Europe), *P. namadicus* (Asia) and *P. "mnaidriensis"* (Sicily) shows a consistent pattern: no infolding yet at the M1 stage; complete folding at the M2 stage; further projection at the M3 stage. Intrapopulational variability of the POC known from single-locality samples does not support the presence of two distinct *Palaeoloxodon* species in Pleistocene Europe, neither is there definitive evidence for sexual dimorphism in POC development. Instead, POC morphology and variation are the results of complex interactions of phylogenetic, ontogenetic and allometric factors. Differences in cranial morphology (including POC variation) support the specific separation of *P. namadicus* and *P. antiquus*. The Japanese *P. naumanni* possesses a combination of primitive and derived, autapomorphic characters, supporting its interpretation as an early offshoot of the Eurasian *Palaeoloxodon* lineage.

A revision of the Family Banffidae (vetulicolians) from the Chengjiang biota

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Despite lacking lateral pouches in the type genus *Banffia*, the family Banffidae is now widely conceived as a subgroup of vetulicolians, an iconic problematic Cambrian fossil group that is difficult to assign into the main clades of Bilateria. *Heteromorphus*, the other genus of this family, is only known from the Chengjiang biota and is represented by one species, *H. confusus*. The absence of *Banffia* in Chengjiang has long been accepted in the literature since '*Banffia confusa*' was revised as *Heteromorphus confusus* in 2002. Here we present unequivocal evidence showing there are two morphotypes of banffids in the Chengjiang biota, both of which bear a posterior section with well-developed annulations, a key character distinguishing Banffiidae from other vetulicolian families. With the first morphotype identified as *Heteromorphus*, the second morphotype shows striking similarities with *Banffia constricta* from the Burgess Shale, such as the body outline, the morphology of the anterior section, and the conjunction of the anterior and posterior sections, thus can be confidently assigned into the genus *Banffia*. Most intriguingly, lateral pouches are present in some well-preserved specimens in Chengjiang *Banffia*. A revision of the family Banffidae is accordingly conducted and the systematics of vetulicolians is reappraised.

Chitinozoan biostratigraphy of the elusive *P. linearis* graptolite Biozone in Girvan, Scotland

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Graptolites of the *Pleurograptus linearis* Biozone have long been used to identify the boundary between the British Caradoc and Ashgill Series (C-A) of the Ordovician. This is largely based on observations of these graptolites in the Whitehouse Subgroup of the classic Girvan area, where they straddle the C-A boundary. However, in the type Cautleyan-

Rawtheyan area of northern England, graptolites of the same biozone have been observed to range into the Rawtheyan by Rickards (2002), and would thus be significantly younger. This revised age for the *linearis* zone has not been widely accepted, which has created considerable confusion with regard to the regional and global correlation around the C-A boundary. Here we suggest that the problem may revolve around the sporadic occurrence of index fossil *P. linearis*, and that accessory graptolite species are used to identify the biozone. Instead, our approach is to use chitinozoan microfossils to correlate the same strata in an independent manner. The Girvan samples yielded several Baltoscandic index species, such as *Lagenochitina baltica*, *Lagenochitina prussica* and *Tanuchitina bergstroemi*, while *Belonechitina americana* and *Hercochitina cristata* have a typical Laurentian signature. These assemblages can also be correlated into key sections of the historical Anglo-Welsh C-A type area.

Head segmentation in a three-dimensionally preserved Cambrian embryo

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The head is a remarkable evolutionary innovation critical to the enduring success of some of the most prolific animal phyla on the planet. The concentration of sensory organs, nervous tissue and the mouth into the frontal regions of early animals triggered a step-change in evolution, with implications for sensing, locomotion and food processing. Appendages specialized into sophisticated sensory equipment, whilst anteriorly-concentrated nerve ganglia, or brains, became control hubs for nervous activity. Nevertheless, the origins of cephalization are uncertain, and the segmental homologies of specialized appendages relating to development remain disputed. This study describes the head segmentation of a Cambrian (Stage 3) embryo, preserved in the 'Orsten' fashion in the Chengjiang Formation of China. The fossil possesses ventrolateral lobopod-like trunk appendages and a ventral oral cavity, which is situated between paired ventrolateral eyes and antenniform appendages. The antenniform appendages extend from an intriguing non-segmental chamber predominating the pre-oral head region. Taken together, the fossil has features akin to both panarthropods and annelids. A complete three-dimensional model shows internal evidence of segment boundaries. This unique specimen thus provides a framework for segment homology, as well as offering a remarkable first insight into the early developmental processes of Cambrian bilaterians.

The skull anatomy and niche partitioning of oviraptorosaurs

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Oviraptorosaurs are beaked theropods with a general skull shape that diverged from that of most other theropods. Over the last decade, the known diversity of oviraptorosaurs has greatly increased thanks to new fossil discoveries, particularly in Ganzhou, southern China. Despite this, little is known about how skull shape and function vary among oviraptorosaurs. Here we investigate the anatomy and functional disparity of oviraptorosaur skulls. First, we used two-dimensional geometric morphometrics

and principal component analysis (PCA) to quantify the variation pattern of the form of oviraptorosaur crania, mandibles and beaks (premaxillae and dentaries). Second, we developed a list of mandibular characters likely to have functional relevance in oviraptorosaurs. The measurements were subjected to principal coordinate analysis (PCOA) to obtain a functional morphospace. The Ganzhou oviraptorosaurs are widely spread in the functional morphospace, indicating that dietary-related niche partitioning might have facilitated their coexistence. Functional PCO1 shows significant and strong correlations with mandible and beak shape whereas PCO2 shows significant correlation with beak shape only. It is likely that Ganzhou oviraptorids partitioned their feeding niches by developing different mandible and beak shapes, which allowed them to radiate and form the diverse Ganzhou oviraptorid fauna.

Disparity across time and macroevolutionary transformation of the maniraptoran manus

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The transformation of the manus from a prensil structure to a wing component across the paravian grade (*i.e.* including modern birds) is an intriguing morphological event of tetrapod macroevolution. Thus far, the evolutionary pattern of its shape variation and disparity, however, has not been studied comparatively and quantitatively at a broad evolutionary scale. Arguably, this pattern could be related to allometry, but this hypothesis has not been tested either. Here, with a dense sample of 129 maniraptors, including 53 fossils and 76 extant birds, we propose a new methodological approach to study this pattern and hypothesis. To such end, we propose the use of Procrustes methods on one-dimensional coordinates, obtained from transforming traditional lengths of the manus. Analyses neatly show a transitional pattern of morphological change between basal, paravian and avian derived forms, whereby modern birds show a strikingly low disparity. While there is a significant allometric tendency of hand growth in basal maniraptorans and Enantiornithes, manus size and shape are decoupled in the crown-group modern birds, suggesting an interplay between functional and developmental constraints in maniraptoran manus evolution.

Worms on film: bioturbation and the decline of matgrounds

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The Precambrian seafloor was characterized by matgrounds – communities of microbes held together by biological glue – which created 'sticky' sedimentary conditions and contributed to prevalent sedimentary anoxia. By the middle Cambrian, however, matgrounds were in decline, replaced by communities of diverse burrowing animals (infauna), which mixed

and oxygenated the sediment through bioturbation. The causes of and mechanisms behind this transition are controversial, not least in respect to how infauna first penetrated the microbially bound sediments, and how early infauna survived in the anoxic sedimentary conditions associated with the matgrounds. The Cambro–Ordovician successions of Bell Island, Newfoundland, Canada preserve a diverse assemblage of trace fossils in association with microbial sedimentary structures, as documented by Harazim *et al*. (2013), and provide a unique window into this transitional period. The interaction between these matgrounds and infauna was examined during fieldwork, with the aim of identifying functional groups (burrowing behaviours) that had the greatest impact on matgrounds. Initial observations indicate that near-surface, deposit-feeding infauna interacted more frequently with the microbial mats, and contributed actively to matground breakup and decline. This suggests that near-surface burrowers may have played a major role in facilitating the rise of infauna during the early Cambrian.

Geoconservation research to inform management policy at the Mistaken Point UNESCO World Heritage Site

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The late Ediacaran rocks of the Mistaken Point Ecological Reserve, Newfoundland, record the oldest-known assemblage of large, complex fossils. Recognizing this, the Reserve was inscribed on the World Heritage list in July 2016. UNESCO status has driven tourist demand, increasing the risk of damage to the site. Viewing the fossils on the famous 'D' and 'E' surfaces requires visitors to walk on the bedding planes, raising concerns that footwear abrasion may be occurring. To mitigate this risk, visitors must wear protective quilted 'bama-booties'. Experiments testing the efficacy of this approach indicate that while implemented with the best of intentions, alternative footwear would yield improved conservation outcomes. In addition, the use of *in situ* cameras and annual LiDAR surveys reveals that if the outstanding universal value of the locality is to be preserved, gravel slopes next to the surfaces will need to be stabilized. Without well-managed sites and specimens, concepts such as holotypes and stratotypes would be meaningless. Thus, researchers have an ethical duty towards the localities they study, as the progress of scientific understanding and geoconservation are inextricably intertwined. Geoconservation studies are a necessary part of geological research, and should therefore be an integral part of research at significant sites.

Genome duplication and the evolution of arthropod phenotypic complexity

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Whole genome duplications are events that double the total amount of genes. These events have been studied within the vertebrate lineage and are attributed to the vast differences in disparity between taxa that have undergone at least one more event than their ancestor. A possible whole genome duplication within Chelicerata suggests that disparity may not react as such. To confirm this duplication and understand how exactly disparity is affected, molecular and morphological datasets were utilized. The datasets were processed in R to generate two gene duplication-through-time plots as well as several disparity-through-time

plots, a phylomorphospace and a character state change through time tree. These revealed two possible whole genome duplications, one located on the branch after the pycnogonids diverge, and the branch after the xiphosurans diverge. The disparity-through-time plots demonstrated that disparity was unaffected by any mass extinction and chelicerates achieved peak maximal disparity in the middle Cretaceous. Chelicerate inter-order disparity is greater than intra-order disparity, where pycnogonids occupy the largest area of phylomorphospace. Pycnogonida is the only chelicerate clade to not benefit from a whole genome duplication. Therefore, this demonstrates that whole genome duplications are not a requirement for disparity.

The trilobite fauna of an uppermost Katian (Upper Ordovician) echinoderm Lagerstätte from South West Wales

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Recent sampling of the hitherto largely neglected uppermost Katian (Rawtheyan) Slade and Redhill Mudstone Formation in the Llanddowror area of Carmarthenshire, South West Wales has yielded a trilobite fauna totalling some 25 genera. The formation contains several thin sandstones yielding abundant, articulated crinoids. In addition to crinoids, one of these echinoderm Lagerstätten includes articulated cystoids, mitrates and ophiuroids. It also contains a rich trilobite fauna, brachiopods and bryozoans along with rare conulariids and orthocones. All of the fossils are randomly orientated in the uppermost part of a 5 cm thick fine sandstone bed, briefly revealed in a temporary road cutting. Whilst all of the trilobites are known from other localities within the area, the fauna is distinguished by the numerical dominance of specimens of illaenids (*Parillaenus* and *Stenopareia*), several of which are enrolled or in other degrees of articulation. There are also complete or nearly complete specimens of *Sphaerocoryphe*, *Tretaspis* and an odontopleurid, as well as isolated sclerites of species of *Calyptaulax*, *Platylichas*, *Allolichas*, *Remopleurides*, *Toxochasmops* and indeterminate calymenids and harpetids. Like most of the echinoderms, at least some of the trilobites are considered to have been transported and killed during an obrution event.

Unravelling the palaeontology of the Maltese limestones

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The islands of Malta have long been of interest to palaeontologists. The fossil-rich limestones host a plethora of organisms; from microfossils to vertebrates. Despite being a well-documented fossil location, very little is known about the macrofossil differences between the five main limestone units on the islands. This study set out to find common, distinctive macrofossils that are unique to each unit, to aid in the identification and geological mapping of lithologies on the island of Gozo. Here we show the diversity of fossils found within each of the lithologies. Echinoderms and bivalves were by far the most common groups identified in all lithologies, but the individual species and genera varied greatly. To date 40 genera and 62 invertebrate species have been identified. Our analyses also indicate that when the Middle and Upper *Globigerina* Limestone units were being

deposited, living conditions were poor. In both of these units a significant drop in species richness, diversity and evenness can be observed. Our results demonstrate that invertebrate macrofossils can easily be used to aid in the identification of weathered lithological units in the field. We anticipate our findings will be the starting point for more detailed biostratigraphical analyses of these units.

3D reconstruction of dicynodont skulls from the late Permian of Zambia

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The dicynodont *Diictodon feliceps* is recognized as one of the most wide-spread and successful small herbivorous synapsids of the late Permian and is known from abundant specimens, most notably from the Karoo Basin of southern Africa. This study describes two previously unpublished specimens of *D. feliceps* within ironstone nodules from the late Permian Upper Madumabisa Mudstone of the Luangwa Basin, Zambia – a basin geologically related to the Karoo but geographically 2,000 km distant. As these ironstone nodules were resistant to mechanical or chemical preparation, micro-CT scanning and 3D reconstruction were used to digitally segment individual cranial bones when possible to visualize key elements. Cranial, mandibular, vertebral and limb elements were identified, and seen to be comparable to *D. feliceps* material from other localities. Endocranial casts of the braincase, osseous labyrinths, and cranial nerves and vasculature were also created and compared with other taxa. The brain conserves a generalized reptile-like morphology similar to other non-mammalian synapsids and *D. feliceps* specimens from outside Zambia; this is reflected in encephalization quotients calculated for both specimens (0.12; 0.20). Despite taphonomic deformation, key neural structures can be clearly distinguished from the endocasts such as enlarged paraflocculi, the olfactory bulbs, the pons and medulla oblongata.

Who ate the sea urchin? Bite traces in the test of an *Echinocorys scutatus* from the uppermost Cretaceous of Stevns Klint, Denmark

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A specimen of the irregular echinoid *Echinocorys scutatus* found in the uppermost Maastricthian chalk at the UNESCO World Heritage Site of Stevns Klint, Denmark contains four circular puncture traces in the upper part of the test, distributed around the test. The traces are interpreted as predation traces from a large vertebrate animal that has attacked the sea urchin from above with the tip of its jaws. The traces are circular, 5–10 mm in diameter, and the distances between the traces are on average 40 mm, suggesting a predator with teeth that are circular in cross section and widely spaced in the jaw. Possible trace-makers from the Danish chalk are three mosasaur genera, *Mosasaurus*, *Plioplatecarpus* and *Carinodens* and thoracosaurine crocodilians. Thoracosaurine crocodilians have long slender teeth and are regarded as piscivorous. The durophagous mosasaur *Carinodens*, which would be the most intuitive choice of trace-maker on the sea urchin, has closely spaced teeth, that are oval, short and blunt and does not fit the morphology of the circular, widely-spaced bite traces. That leaves the most likely candidate for the predation traces to be either *Mosasaurus* or *Plioplatecarus*, which are the most common mosasaur fossils in the Danish chalk.

Inferring the temperature at which the last universal common ancestor lived

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Cellular life is incredibly diverse, and although split into different domains, all life shares a common ancestor. Reconstructing the last universal common ancestor (LUCA) is key to understanding how early life evolved. Here, we reconstruct LUCA by comparing extant organisms and applying statistical models of genome evolution to determine which genes and proteins were present at the root of the tree of life. We show how amino acid content can be used as an indicator for the optimal growth temperature of prokaryotes, even when only a small subset of the proteome is known. Amino acid compositions of extant organisms were examined for a group of specific amino acids, which were used to predict their growth temperature. These predictions were compared against reported values from the scientific literature and a strong correlation was found. We then reconstructed a proteome for LUCA, using a new phylogenetic model which improves upon the standard model. We conclude LUCA was adapted to cooler temperatures, whereas the last archaeal and bacterial common ancestors were hyperthermophiles.

Early high disparity and rates in the evolution of ichthyosaurs

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Ichthyosaurs were a diverse clade of Mesozoic marine tetrapods; however, the evolution of the group has been understudied. Previous work shows an evolutionary bottleneck across the Triassic–Jurassic boundary, based only on a subset of genera. Here we present a macroevolutionary analysis of ichthyosaurs using a recently published species-level dataset. We use an established disparity workflow to explore evolutionary rates of discrete skeletal and continuous characters related to body size. Reduction of disparity across the Triassic–Jurassic boundary is less than previously thought, followed by a long-term decrease. Post-Triassic ichthyosaurs notably occupy different morphospace to Triassic ichthyosaurs, supporting a substantial turnover; however, resolution and preservation is insufficient to be certain on the timing and length of this. Magnitude of early high disparity is dependent on resolution but is accompanied by high initial rates of evolution in discrete characters and in body and skull size predominantly in the Early–Middle Triassic; these trends are agnostic of the time-scaling used. Our results evidence rapid shifts in morphology associated with changes in ecology early in ichthyosaur evolution, followed by relative stasis as taxa specialize within their niches. They also build the framework for future investigations of the marine incursions of major tetrapod clades.

2D extruded finite element analysis: a validation study using extinct and extant vertebrates

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Finite element analysis (FEA) is a powerful engineering technique used in vertebrate biomechanics to reconstruct stress and strain in digital structures like the skull and jaw.

Such models are commonly built using CT scan data, which is expensive and not always readily available. Here we introduce an alternative method called 2D extruded FEA, which uses 3D computer-generated models built from simple 2D outlines of hemi-mandibles. We present five separate case studies on the validation of this method: three extant taxa (ostrich (*Struthio camelus*), alligator (*Alligator mississippiensis*), macaque (*Macaca mulatta*)) and two extinct mammaliaforms, *Morganucodon watsoni* and *Kuehneotherium praecursoris*. We compared FE results obtained from 3D models generated from CT datasets with those obtained from analysing 2D models and two sets of 2D extruded FE models. Models of extant taxa were further compared to experimentally-derived strain. In terms of stress magnitude, FE models of extinct and extant taxa with relatively flat jaws (*i.e.* alligator, macaque and mammaliaforms) performed well in comparison to those obtained from 3D models, particularly with models of increasing geometric complexity. Our results provide support for the use of 2D extruded FE models in comparative studies.

High-resolution palaeoenvironmental reconstruction of the mid-Barremian Munk Marl Bed, Danish North Sea based on calcareous nannofossils

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The mid-Barremian (Early Cretaceous) was characterized by an episode of widespread deposition of laminated black shales in the Boreal Realm (Hauptblätterton in northwest Germany, Munk Marl in the North Sea), interpreted as a regional oceanic anoxic event (OAE). In order to better constrain the palaeoenvironmental setting of this event, well-preserved calcareous nannofossil assemblages of two North Sea cores have been studied across the Munk Marl. Due to their abundance in pelagic sediments and sensitivity to environmental change in sea-surface waters, these phytoplanktonic algae constitute an excellent proxy for changes in temperature, fertility and distance to the land. Our results show an increase in the relative abundance of *Watznaueria barnesiae* together with a decrease in abundance of fertility index taxa across the Munk Marl. We also observe a threefold compartmentation of the Munk Marl. The lower and upper part of the Munk Marl are characterized by low abundances of *Micrantholithus* spp. and *Rhagodiscus asper* (coastal and warm water proxies) whereas the central part shows a high abundance in Nannoconids (oligotrophic indicators). Our results thus suggest that the mid-Barremian event was associated with warmer temperatures and lowered productivity in sea-surface waters, triggered by a warm and arid climate and reduced terrigenous run-off.

Dickinsoniomorpha, BMP signalling and the origins of the major eumetazoan body axes

***Arsham Nejad Kourki, Jakob Vinther and Philip C. J. Donoghue**

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Axial organization is a crucial character in early metazoan evolution. This comprises the antero-posterior and dorso-ventral axes in Bilateria, and the oral-aboral and directive axes in Cnidaria. Porifera and Placozoa lack well-defined axes while the phylogenetic placement of Ctenophora is currently debated. Overall, the homology relations between the axes and the ancestral character states of deep nodes within Metazoa are unclear.

The fossil record might provide clues: Dickinsoniomorpha have recently shown to be metazoans based on morphological and geochemical evidence, while possessing a modular architecture and a distinct body plan. Given their likely status as early eumetazoans, we evaluate the dickinsoniomorph body plan and its potential for understanding the evolution of the eumetazoan body axes. Based on comparison between the dickinsoniomorph and the eumetazoan body plans, as well as the expression patterns of Hox gene expression and the role of the BMP/Chordin signalling pathway in the early development of Cnidaria and Bilateria, we suggest homology between the antero-posterior axis and the directive axis, and also propose that BMPs were first used as growth factors and only later as axial specifiers. Finally, we discuss the plausibility of this scenario relative to others.

Biases and pathways to authigenic mineralization of soft tissues by phosphatization – a case study from the Sirius Passet Lagerstätte

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Mineralized soft tissues give an extraordinary opportunity to study certain anatomy of extinct animals. At the lower Cambrian Sirius Passet Lagerstätte, North Greenland, fossils frequently preserve internal tissues such as nerves, guts and muscles. Guts and muscles are preserved three-dimensionally as a black mineral. This mineralization appears homogeneous, but the composition depends on the original type of tissue; muscles are preserved as silica and guts as calcium phosphate. We have scrutinized a database of ~2,830 specimens for authigenic mineralization and used SEM-EDS and silicon isotope analysis to assess the original elemental composition of the black mineral and the temperature of its formation. In total, 718 cases of phosphatization occur in the database. We show that the black mineral derives from a primary phosphatization where the muscles have subsequently been replaced by silica under high-temperature conditions. The phosphatization exhibits strong taxonomic and ontogenetic biases as the potential for phosphatization varies between as well as within taxa. This suggests that the phosphatization process relied primarily on an intrinsic source of phosphate. We speculate that the abundant microbial mats in Sirius Passet may have contributed to the high frequency of phosphatization by acting as barriers of diffusion in the sediment.

Global marine beta diversity in the early Palaeozoic

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After the appearance of many new phyla during the Cambrian (~541–521 Ma), the Ordovician radiation (~485–445 Ma) was an unprecedented increase in global marine biodiversity at lower taxonomic levels. The early Palaeozoic has been conceptualized as a time of increasingly specialized communities, often on the basis of regional-scale studies. We expected this to lead to an increase in the global spatial heterogeneity of fossil assemblages (average beta diversity). To generate global diversity curves, we divided

Cambrian to Silurian marine animal fossil occurrences into stage-level time bins, and assigned occurrences to squares on a global grid by palaeogeographic location. We could then track alpha (within-square), gamma (global) and average beta diversity through time. While our method shows the expected increases in alpha and gamma diversity, beta diversity declines from Cambrian to Silurian. This apparent contradiction may be explained by an increase in the spatial packing of taxon geographic ranges, leading to more shared taxa between grid squares. We suggest that tracking beta diversity at global and regional scales may be important in understanding the drivers of early Palaeozoic diversification.

Ecologically distinct Silurian ostracod faunas from a single horizon in Spain

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For several decades now, the Silurian myodocope ostracod fauna has been recognized as the first planktonic component of the group. Although the colonization event during the middle Silurian (Wenlock–Ludlow) is becoming well documented all around the world, the evolution of this fauna during the late Silurian (Pridoli) still remains unstudied. Here we describe, for the first time, two ecologically distinct myodocope ostracod faunas from the same horizon in the late Pridoli (possibly *Istrograptus transgrediens* Biozone) of central Spain (Alcaracejos, Córdoba district). The first fauna comes from altered black shales and comprises five myodocope species associated with orthoconic cephalopods, bivalves and graptolites. The second fauna was recovered from large dark-reddish calcareous nodules containing five myodocope species associated with the planktonic crinoid *Scyphocrinites elegans*, orthoconic cephalopods, phyllocarids and bivalves. Although the shales and nodules share two myodocopes species, these two faunas seem to have had different ecologies, with the shales' association representing the background planktonic fauna, while the nodules' association would have lived in the vicinity of the *Scyphocrinites* 'floating islands'. These two faunas may have been living in different parts of the water column.

Surf n' turf: evolution of tetrapod skull shape and mechanics across the water–land transition

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The conquest of the land by vertebrates was a landmark event in the history of life marked by dramatic evolution of skull shape across the water–land transition. These changes are inferred to reflect shifts in jaw muscle anatomy, feeding mechanism or environmental constraints. We explore the anatomy and mechanics of fossil tetrapod skulls spanning the transition – from the Late Devonian to Early Triassic – as well as extant bracketing taxa. Computed tomography was used to capture skull shape in half a dozen fossil taxa spanning the transition and scan data processed to remove damage and deformation, resulting in new three-dimensional reconstructions of iconic fossil tetrapod skulls. Contrast-enhanced

scanning was used to obtain skeletal and soft tissue morphology in the heads of extant relatives, including basal ray-finned fish, lungfish and salamanders. We compare sutural morphology in living and fossil taxa to predict load regimes across the fish-tetrapod transition. Osteological correlates and information from digital dissections of extant taxa are used to reconstruct the major jaw-closing muscles of early tetrapods for the first time. These data shed light on the evolution of the tetrapod head and changes in feeding mode during the water–land transition. Furthermore, our reconstructions form the basis for ongoing biomechanical modelling.

Interrelationships of land plants and the nature of the ancestral embryophyte

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The origin of land plants (embryophytes) transformed both the planet and the evolution of life. These changes included the development of soil, changes to long-term carbon dioxide patterns and the expansion of habitats for fungi and animals. However, our understanding of this formative episode is mired in the uncertainty associated with the phylogenetic relationships among the earliest land plant lineages: bryophytes (hornworts, liverworts, and mosses) and tracheophytes (vascular plants). Here we attempt to clarify this problem by analysing a large amino acid transcriptomic dataset with models that allow for compositional heterogeneity between sites. All analyses, including concatenated sequence analyses that can explicitly accommodate site-specific compositional heterogeneity, support a mosses–liverworts clade 'Setaphyta'. Both maximum-likelihood analyses that compare the fit of each gene tree to proposed species trees and Bayesian supertree estimation support bryophyte monophyly. Our results imply that the ancestral embryophyte was more complex than has been envisaged based on topologies recognizing liverworts as the sister lineage to all other embryophytes. This requires many phenotypic character losses and transformations in the liverwort lineage, diminishes inconsistency between phylogeny and the fossil record, and prompts re-evaluation of the phylogenetic affinity of early land plant fossils.

FossilJ: a palaeontologically focused plugin for image analysis software ImageJ

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ImageJ is an open source image analysis software developed by the US National Institutes of Health (NIH). This software is frequently utilized by biologists and palaeontologists alike; however, without a dedicated plugin, the user must manually process each image, potentially resulting in methodological inconsistencies. To address these problems, a plugin

named FossilJ has been created. FossilJ introduces a user friendly, versatile and efficient method to count and gather morphometric data on bivalves semi-automatically. The systematic nature of this plugin makes data acquisition highly reproducible, eradicating latent user bias often observed in manual measurements. Images of numerous specimens can be batch-processed, even when inconsistent scale bars are present. Unique specimen and feature references are provided, alongside measurement verification images, background-cleaned images and data exported in CSV format. Collected data include length and width, valve chirality, complete/broken specimens, drillhole presence and diameter. Safety features ensure that the data produced are of high quality and prevents the need to reprocess images due to minor human error. FossilJ is demonstrated on several bivalve species which are associated with the Lessepsian Migration. Specimens were collected from death assemblages in the Mediterranean Sea, off the coast of Israel.

Out of the extra-tropics: origination and dispersal dynamics of Cenozoic marine plankton

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Several ecological and evolutionary hypotheses have been proposed to explain the latitudinal diversity gradient. The "out of the tropics" hypothesis posits the tropics as a cradle of biodiversity, with most clades originating in the tropics and then expanding their ranges towards temperate regions through dispersal. This study analyses the diversity gradient of planktonic microfossil groups (foraminifera, coccolithophores, diatoms and radiolaria) over the Cenozoic. The aim is to investigate if origination and dispersal events are more prominent in and to tropical or extratropical regions using fossil data compiled in the Neptune database. The tropical region here is defined as the region between -30 ° to 30 ° latitude band. Log odds ratio comparing origination in the tropics *vs* extratropics as well as proportions exported to and from each region were calculated. Our findings showed that plankton exhibited a slight predilection for origination in the extratropics during the Cenozoic. Diatoms and foraminifera preferentially originated in the extratropical region, mainly in the early Palaeogene for the latter. On the other hand, coccolithophores were more likely to originate in the tropics and radiolarians in both regions. Overall, the tropical region was more notable at exporting diversity although proportions exported varied among the different groups.

Preparation alters chemistry of fossil melanosomes: a case study from the Messel biota

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Fossil melanosomes, organelles containing the pigment melanin, have been reported from soft tissues of various vertebrates from Messel. Our recent study on extant and fossil taxa revealed that the trace element inventory of melanosomes is controlled strongly by tissue type. Exceptionally-preserved fossil vertebrates from the Messel biota (48 Ma, Germany) are often transferred to resin blocks for museum curation. Although this practice does not affect the skeletal elements, the impact on the trace element chemistry of soft tissues

is unknown. We used synchrotron X-ray fluorescence analysis to test the impact of resin transfer on the trace element chemistry of melanosomes preserved in six fossil specimens from the Messel biota. Multivariate analysis reveals that the trace element chemistry of the resin is always significantly different to that of the fossil melanosomes. There are, however, significant differences between the chemistry of these melanosomes and those associated with Messel fossils that are still hosted in the sedimentary matrix. Fossils in resin are thus not ideal for study of trace element chemistry of melanosomes but remain of great importance for other palaeontological studies and museum exhibitions.

Quantitative analysis of species distribution of the *Zaphrentis delanouei* group

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The *Zaphrentis delanouei* group has been logged in the Vale of Glamorgan, South Wales and concurrent species have been correlated within beds of the Friars Point Limestone to provide an updated ontogeny and phylogeny. Markov chain analysis and branching processes with immigration provide the likelihood of occurrence of *Zaphrentis* species in different types of limestone based on the number of species found concurrently. The results show the distribution of species within the Friars Point Limestone is both consecutive with a probability of 0.81 and concurrent with a probability of 0.19, with *Zaphrentis delanouei* the most commonly occurring species estimated provisionally at 35 %. This study will lead to a revision of the mechanisms controlling the trends of evolution within the *Zaphrentis delanouei* group and a quantification of the probability of coexistence of multiple species within a given horizon. This study will intend to make a morphometric quantification of the *Zaphrentis delanouei* group to justify revisions to ontogenic and phylogenetic mechanisms.

Graptolites from Silurian (Llandovery Series) sedimentary deposits attributed to a forearc setting, Co To Formation, Co To archipelago, northeast Vietnam

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The lower Palaeozoic graptolite-bearing strata of Vietnam have been noted since the time of the French colonial era, yet most of the assemblages are yet to be illustrated. More recently, Vietnamese and Japanese geologists have examined the Vietnamese lower Palaeozoic succession in detail, including the Co To Formation that crops out over 40 islands and islets of the Co To Archipelago in northeast Vietnam. The Co To Formation is more than 1,000 m thick and regionally has been considered to be of Late Ordovician and Silurian age, though only strata of Silurian age have been recognized in our study. Newly collected graptolites identify strata that are lower Silurian and further constrain the biostratigraphical age of part of the formation to the *Torquigraptus proteus* Subzone of the *Spirograptus turriculatus* Biozone, and the *Oktavites spiralis* Biozone, both of the Telychian Stage. The material likely includes at least one new graptolite species.

Insights into the neurosensory evolution of thalattosuchian crocodylomorphs

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Thalattosuchia are ancient crocodylomorphs that thrived from the Early Jurassic to the Early Cretaceous. They originated in shallow marine environments, but one subclade, Metriorhynchidae, evolved into pelagic dolphin-like forms with paddle shaped limbs and a vertically orientated tail fluke. Hence, they underwent a major evolutionary transition. Besides the obvious osteological changes, understanding the shifts in their cephalic sensory organs will be key to understanding how these ancient animals adapted to a radically new ecosystem. Based on micro-CT scans and digitally segmented endocranial features we address the basal condition of these ancient crocodylomorphs with *Pelagosaurus typus* and *Steneosaurus* cf. *gracilirostris*. Our early results support the hypothesis that thalattosuchians adapted to an aquatic lifestyle early in their evolution. Compared with extant crocodylians they had reduced cranial pneumaticity, with the loss of numerous pharyngotympanic diverticula. Furthermore, they had enlarged carotid and orbital arteries, and pituitary fossae. Our examination of metriorhynchid micro-CT scans shows further reduction of the sinus system and similar semicircular canal adaptations seen in cetaceans. We hypothesize a mosaic evolutionary pattern to thalattosuchians adaptations to aquatic environments, with neuroanatomical shifts occurring prior to large scale osteological changes.

posters

Fluctuating asymmetry in Ordovician trilobites from the Builth-Llandrindod Inlier, central Wales

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Fluctuating asymmetry refers to small, random deviations from perfect bilateral symmetry. Ten trilobite genera from the *Teretiusculus* Biozone show some asymmetric development of pygidial ribs. In most genera, 10–30 % of specimens are asymmetric, although this rarely exceeds half a rib. For example, in 630 specimens of *Ogygiocarella* with countable ribs both sides, 25.7 % are asymmetric: 24 % have an asymmetry of half a rib and 1.7 % have an asymmetry of one whole rib. In each genus the asymmetry is itself symmetrically disposed – the higher number of ribs is equally likely to be on the left side or the right. *Cnemidopyge* is exceptionally asymmetric: 53.5 % of 904 specimens. 23.4 % have an asymmetry of ≥1 rib and 1.5 % have an asymmetry of two ribs. In living animals, fluctuating asymmetry is often taken to indicate that a population is under stress – environmental and/or genetic. However, *Cnemidopyge* is abundant and persistent, occurring at 63.9 % of 380 sampling horizons, with an average contribution to the trilobite fauna of 49.8 %. The degree of fluctuating asymmetry appears to have changed little through the biozone and its significance is unclear. Perhaps *Cnemidopyge* thrived despite the stress of dysaerobia or repeatedly recovered after countless (unresolvable) stressful episodes of local extinction.

Wear, tear, and systematic repair: testing growth dynamic models in euconodonts

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Conodont elements are the earliest mineralized vertebrate dental tools and the only ones capable of extensive repair. Two models of conodont growth, as well as the presence of a larval stage, have been hypothesized. We analysed normally and pathologically developed elements to test these hypotheses and identified three ontogenetic stages characterized by different anisometric growth and morphology. The distinction of these stages is independently corroborated by differences in tissue strontium content. The onset of the last stage is marked by the appearance of wear resulting from mechanical food digestion. At least five episodes of damage and repair could be identified in the normally developed specimen. In the pathological element, function was compromised by development of abnormal denticles. This development can be reconstructed as addition of new growth centres out of the main growth axis during an episode of renewed growth. Our findings support the model of periodic retraction of elements and addition of new growth centres. Changes in strontium content coincident with distinct morphology and lack of wear in the early life stage indicate that conodonts might have assumed their mature feeding habit of predators or scavengers after an initial larval stage characterized by a different feeding mode.

A morpho-functional study of archosauromorph herbivory and the faunal turnovers of the Late Triassic and Early Jurassic

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The evolution of herbivorous archosaurs has long been seen as a key part of the Late Triassic terrestrial faunal turnovers that fostered dinosaur terrestrial supremacy through the remainder of the Mesozoic. Despite extensive attention, the principal drivers of these turnovers remain hotly debated with competition, increased volcanism and bolide impacts suggested as potential triggers. Recent studies have identified the Carnian Pluvial Event (CPE) and affirmed the Central Atlantic Magmatic Province (CAMP) eruptions as key factors in the progression from archosauromorph to archosaur-dominated faunas and the rise of the dinosaurs. Nonetheless, the underlying reasons for dinosaur success remain poorly resolved and we lack a clear idea of the ecological dynamics within these changing faunas. Here we apply functional morphometric and multivariate, phylogenetic comparative methods to infer patterns of trophic ecology and evolution in herbivorous archosauromorph clades. We compare mandibular functional morphology to identify the niches and potential ecological interactions of rhynchosaurs, aetosaurs, sauropodomorphs and ornithischians. Our results support the significance of the CPE, and reveal a degree of niche separation and potential intrinsic influences. Furthermore, we find that dinosaur dietary generalism may have enabled their survival and success through the environmental upheavals of the Late Triassic.

Progress report on the coverage of rudists in the revised Bivalvia '*Treatise Online*'

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The background to the coverage of rudists in the ongoing complete revision of the Bivalvia volumes of the '*Treatise on Invertebrate Paleontology*' will be summarized, progress on publication reported and plans for further work outlined. Three introductory chapters on rudists have already been published in '*Treatise Online*' (University of Kansas, Paleontological Institute **<http://paleo.ku.edu/tronline/toparts/n.html>**) and their content will be briefly reviewed. Future work on the taxonomic descriptions of genera will be illustrated with a synoptic example.

Colour patterns in the stem upupiform *Messelirrisor*

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The Eocene deposits of Messel have yielded an important array of extinct bird taxa, many of which represent stem members of extant clades. One of these is the stem upupiform *Messelirrisor*. Like many of the Messel birds, specimens of *Messelirrisor* have exceptional soft tissue preservation including feathers, with some showing original colour patterns. Thanks to the discovery that integumentary structures such as feathers are often preserved due to the pigment melanin, original colouration can be predicted through quantitative comparison to modern bird melanosomes. Here we analyse melanosome morphology from multiple *Messelirrisor* specimens and use a comprehensive new database of feather colours from extant Upupiformes and successive outgroups to predict a likely colouration of mixed blacks and greys, as well as a striped black and white tail. The extant members of Upupiformes, the hoopoes and wood hoopoes, show different colouration to one another likely related to their respective feeding habitats. Of the two extant clades, *Messelirrisor* shows more similarity to the wood hoopoes which are specialist arboreal feeders. The colour predictions therefore match the presumed forested environment of Messel and the predicted perching habit of *Messelirrisor*, although there is no evidence that the iridescence of wood hoopoes was present in *Messelirrisor*.

Constraints and adaptations in crocodilian skull form and function

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Extinct crocodilians display a diverse range of skull morphologies, yet extant crocodilians possess primarily flattened, broad 'platyrostral' snouts. Platyrostral shape is considered to

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be sub-optimal for resisting feeding loads and represents the conflicting demands of feeding optimization and drag reduction in semi-aquatic taxa. Numerous Mesozoic crocodilians possessed tall, narrower 'oreinirostral' skulls, thought to be more optimally constructed for resisting loads. Here we assess differences in feeding mechanics between extinct and extant taxa to test whether terrestrial crocodilian skulls, freed from aquatic constraints, are more efficient at resisting feeding induced loads. We used beam analysis and finite element analysis for evaluating resistance to feeding-induced loads, bite forces and muscle efficiency in Mesozoic taxa *Baurusuchus salgadoensis*, *Montealtosuchus arrudacamposi* and *Caipirasuchus paulistanus* with highly oreinirostral skulls, compared to extant *Alligator mississippiensis*, *Crocodylus niloticus*, *Paleosuchus palpebrosus* and *Gavialis gangeticus*, with platyrostral skulls. Results show that oreinirostral morphologies are better-suited for resisting higher stresses under various biting scenarios. Bite force estimates were independent of rostral shape, instead scaling positively with body size. Oreinirostral taxa show increased mechanical advantages due to differences in musculoskeletal architecture. Overall, fossil taxa with oreinirostral morphologies show skull structures remarkably optimized for feeding, enabling a singular mapping of form and function.

Preserved pigmentation of the Bolca fishes: the first assemblage palaeo-colour investigation – assessing variability in fish pigmentation between ecosystems

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Organismal colour patterns can be indicative of habitat. We take an ecosystems approach to marine fish colour patterns to infer the collective ecology of the teleost-dominated Eocene (Ypresian) fauna from the Bolca Lagerstätte. The Bolca fishes are widely interpreted as the first reef-fish assemblage of modern character. However, the level of association between the fish community and coral reefs is disputed. Using preserved pigmentation patterns, we test the hypothesis that the Bolca fishes are representative of a shallow-marine community most similar to that of a modern tropical coral reef. We note that there is a bias due to fishes with thick squamation obscuring preserved colour patterns. Nine categories of melanin-based pigmentation patterns were defined from those observed in extant faunas and the Bolca fishes. We identified eight pattern types preserved in 47 fossil specimens, representing 30 fossil species. Comparative study of melanin-based pigmentation patterns in the Bolca fishes alongside modern ecosystems indicates that the Bolca fauna represents a coral-associated ecosystem, with some pelagic influence. This may be suggestive of a unique ecosystem identity from the Eocene 'reef gap'. Our data indicate that ecosystem-wide colour pattern compositions have some ecological signature.

The ecophysiological implications of early Palaeozoic climate models

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Correlating geochemical proxy data with trends in the fossil-record is increasingly commonplace; however, mechanistic approaches to evaluating how environmental change might impact marine ecosystems on geologic timescales are underexplored. The emerging view of early Palaeozoic marine environments is one of elevated seawater temperatures and

poorly oxygenated oceans relative to the modern Earth system. Oxygen, temperature and pH are known to be key environmental stressors today, and ecophysiological research has recently provided metrics to link changes in these environmental parameters to biological response. Here we use the cGENIE Earth systems model and methods from ecophysiology to investigate the implications of early Palaeozoic atmospheric reconstructions for marine ecosystems. We use a compilation of atmospheric pCO_2 and pO_2 estimates from the Cambrian and Ordovician geochemical record to generate a range of corresponding ocean models with cGENIE. We then evaluate the impact of early Palaeozoic climate scenarios on the metabolic index and oxygen supply index (emerging proxies for evaluating the synergistic impacts of oxygen and temperature on aerobic metabolism and environmental oxygen availability), and carbonate saturation state, to interrogate the potential impacts of environmental stressors during the diversification of Palaeozoic animal ecosystems.

Ground-truthing models of trace-fossil applications in palaeoenvironmental analysis with a modern submarine canyon

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Submarine canyons are often biodiversity hotspots; yet any life in submarine canyons is subject to episodic, highly energetic sediment transport events such as turbidity currents. We considered the effects of turbidity currents on benthic communities by analysing the traces that modern organisms leave behind in the sedimentary record of Monterey Canyon. A unique dataset of 87 precisely located vibracores was collected along six cross-channel transects using a remotely operated vehicle (ROV). Statistical analysis reveals that altitude above the local thalweg affects the distribution of lithofacies and bioturbation index, whereas water depth affects the distribution of specific biogenic sedimentary structures and their relational associations (ichnofabrics). The effect of water depth on ichnofabric distribution is likely controlled by dissolved oxygen and the frequency of energetic turbidity currents. Whilst the availability of particulate organic matter may also play a role in explaining the observed ichnofabric distributions, the simple traces observed in shallow water and more complex burrow systems created in deeper water are thought to relate to the colonization window. This new understanding enables validation of models of the applicability of trace fossils in palaeoenvironmental analysis and permits better reconstruction of water depth and altitude in ancient submarine canyon systems.

New locality (Merek-Chesme) of late Miocene marine mammals in Crimea

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Three nearly complete skeletons and isolated postcranial fragments were found along the right bank of the Merek-Chesme river (5 km to the northwest of Kerch city) in September

2018. The skeletal fragments were preliminarily determined as representatives of a very small species of Cetotherium-like whale. Taphonomy of the new locality is similar to the Polevoe locality in Adygea (Ciscaucasia; Tarasenko 2013; 2014). In contrast to the situation in Polevoe, the skeletons and fragments had been subjected to erosion and partial water abrasion before being completely covered with deposits. The burial of bones in clay was synchronous with the formation of the reef, so parts of bones stick out of the reef limestone. The bioherm reef formed with bryozoans and blue-green algae. The reef massive axes are elongated to the northwest. The eastern edge of the lagoon was separated from the sea by a reef. Moreover, the bones of another whale skeleton and isolated bones of pinnipeds were found in the tobacco-coloured clay of the lagoon deposits.

Do Sr/Ca ratios hold clues to determining the trophic position of conodonts?

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Conodonts are small marine vertebrates known primarily from tooth-like elements from the Cambrian to the end of the Triassic. Often found in carbonate rocks and shales, conodonts are frequently used for biostratigraphic analysis due to their abundance, rapid evolution and diversity of morphology. Despite being studied for well over a century, little is known about the ecology of conodonts, including what they may have fed upon. This is further complicated by the common occurrence of multiple conodont taxa in the same samples. These taxa often have radically different morphologies, suggesting differing sources of nutrition between them. One potential tool to resolve this question is the use of Sr/Ca ratios preserved in the apatite of the conodont elements. In terrestrial environments (and to a lesser extent marine environments), this ratio can be used as a proxy for trophic level, as lower Sr/Ca values are produced at higher trophic levels. Here we have analysed Sr/Ca ratios in a number of conodont taxa from time-equivalent strata in the Silurian Gotland succession in Sweden. Variability of Sr/Ca ratios between taxa should be indicative of differences in diet, while homogeneity would suggest variations in morphology have little impact on diet.

Recent insight into the Permian–Triassic macroevolutionary history of echinoids

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The Permian–Triassic bottleneck has long been thought to have drastically altered the course of echinoid evolution. However, recent fossil finds of stem group echinoids from the Middle Triassic of France and China are revising the scenario for the extinction of echinoids during the end-Permian extinction. Here we present results using phylogenetic analyses of stem group and crown group echinoids from the late Palaeozoic and early Mesozoic to document a revised macroevolutionary history of echinoids during the end-Permian mass extinction. We show that stem group echinoids did survive into the Early Triassic, and were not limited in their occurrence to the Palaeozoic Era. We propose that stem group echinoids exhibited the Lazarus effect during the latest Permian and Early Triassic, implying mass rarity, restricted distribution, low diversity or all of these conditions in the post-Palaeozoic stem group. Crown group echinoids, however, were comparatively diverse in the Early

Triassic. The crown group and stem group echinoids thus overlap over 20 million years in their stratigraphic ranges, and the initial post-Palaeozoic diversification of the crown group echinoids accompanied the decline of the echinoid stem group.

Giants in the hot tub? Sclerochronology of Pliocene brachiopods of the southeast UK

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Atmospheric CO_2 last exceeded 400 ppmv during the Pliocene, which is commonly invoked as a potential analogue for future change. The shallow marine fauna of the Pliocene Coralline Crag Formation of southeast England includes brachiopods of unexpectedly large size (*Pliothyrina maxima*), which may exceed 10 cm in length. Given the relationship between body size and temperature, the expectation is that *P. maxima* lived in cold waters. Although some studies estimate that the Coralline Crag sea was cooler than the present-day southern North Sea, others suggest subtropical conditions. If giant *Pliothyrina* really inhabited very warm waters then there are significant implications for our understanding of the general relationship between body size and temperature. To address this, we undertook morphometric and geochemical analyses of complete and well-preserved specimens. Laser ablation ICP-MS was used to determine the trace element chemistry of their shells, and concentrations of Al, Sr and Mn were used to screen individual datapoints for potential diagenesis. Palaeotemperatures were estimated from Mg/Ca ratios. Mean seawater temperatures from nearby locations presently range from 5–6 °C in winter to 18–19 °C in summer. Results from the fossil brachiopods show that both winter and summer temperatures were several degrees warmer than the present day, but were not subtropical.

New marine snakes (Palaeophiidae) from the early Palaeogene of Morocco, and adaptive radiation of the Palaeophiidae

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The Cretaceous–Palaeogene (K-Pg) boundary is associated with a major extinction of marine reptiles, which had dominated the Mesozoic seas. However, many groups survived this mass extinction and recovered in the new Cenozoic world, including snakes. The Palaeophiidae are a family of highly specialized marine snakes that shed light on patterns of recovery among marine vertebrates in the post-mass extinction seas. Here we describe a new palaeophiid from the Ypresian (Lower Eocene) phosphates of the Oulad Abdoun Basin in Morocco, and describe a species previously unknown from Morocco, *Palaeophis* cf. *toliapicus*. These deposits preserve a diverse Early Cenozoic marine vertebrate fauna, bridging an important gap between Cretaceous and modern faunas. The new taxon differs from early Palaeophiid snakes, exhibiting aquatic adaptations such as hypertrophied neural spines and tall pterapophyses. Palaeophiid size correlates with latitude, larger snakes are present at lower latitudes, and occurrence data indicate a sudden appearance in the Paleocene with fossil occurrences remaining constant throughout the Eocene. Time-calibrated phylogenetic and morphological disparity analyses suggests that Palaeophiidae underwent a major adaptive radiation in the late Paleocene or early Eocene,

likely in response to the extinction of Cretaceous marine reptiles and Paleocene–Eocene global warming.

Hyperostosis in bone in the vertebral column of the Devonian placoderm fishes *Millerostus minor* (Miller, 1858) and *Eastmanosteus calliapsis* (Dennis-Bryan, 1987)

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Traditionally, it has been perceived that bone enlargement processes including hyperostosis and pachyostosis only occur in endochondral bone (that which replaces cartilage) and dermal bone, including bone of the early cetacean *Ambolucetus natans* and dermal bone of the teleost *Platax*. However, the arthrodiran placoderm *Millerosteus minor*'s vertebral column comprises hyperostotic neural and haemal arches, which were ossified perichondrally (the cartilage precursor was not replaced). Additionally, *Eastmanosteus calliapsis* vertebrae show growth and histology similar to *M. minor*. *M. minor* vertebrae are larger and more bulbous than in other arthrodiran placoderms, such as *Coccosteus cuspidatus*. Growth and development of *M. minor* vertebrae, along with their histology, were probably influenced by one or more of the following: environmental factors; ontogeny; genetic factors; and taphonomy. *M. minor* and *E. calliapsis* vertebral histology are comparable to taxa possessing endochondral bone, especially semi-aquatic osteicthyans. The Middle Devonian Mey Beds (Caithness, Scotland) demonstrate well-preserved *M. minor* histology, which shows particular similarity to taxa including *Rodhocetus kasranii* (early cetacean), *Carentonosaurus mineaui* (squamate) and *Caranx* (carangid fish). *E. calliapsis* histology is reminiscent of *Pachyvaranus crassispondylus* (squamate) and *Kutchicetus minimus* (early cetacean). Such investigations question the placement of bone enlargement processes on the phylogenetic tree, and questions current understanding of perichondral bone.

It's all in your head – or is it? A new actinopterygian braincase from the Upper Carboniferous coal measures of the UK and the role of neurocranial characters in actinopt relationships

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The deep evolutionary history of the Actinopterygii has been mired in controversy due to the paucity of character-rich endoskeletal specimens. Recent advances in tomographic imaging of exceptionally-preserved fossils have begun to clarify relationships between extinct and extant clades of the group. Adding to these advances, we present an exceptionally-preserved neurocranium and parasphenoid of an Upper Carboniferous actinopterygian from Readycon Dean, Oldham, UK. Tomographic reconstruction reveals extensive details of posterior myodomes, the trigeminofacial chamber and jugal canal, with associated nervous and vascular tracts. These data prompt a re-evaluation of endoskeletal characters in previously published specimens, as well as the role of neurocranial information in recent analyses examining the relationships between extant (*e.g.* Polypteriformes) and extinct clades.

Biomechanics of kangaroo feet: hopping for a better resolution

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Bipedal hopping in large kangaroos (*e.g.* the grey kangaroo *Macropus giganteus*, Macropodinae, ~60 kg) provides a highly energy-efficient means of fast locomotion; however, there are limitations. Bone and tendon stresses indicate hopping animals are likely to have a body size limit of 150 kg, which would likely make hopping problematic for a range of Pleistocene macropods that exceeded this weight, such as the giant short-faced kangaroo *Sthenurus stirlingi* (Sthenurinae, ~150–205 kg). Based on this size constraint and previous anatomical observations, *Sthenurus stirlingi* is hypothesized to have employed bipedal striding as an alternative gait to hopping. Using CT datasets, we quantify resistance to bending and torsion, and cortical bone distribution in the calcanea and metatarsals and first and second phalanges of the fourth digits, and show that *Sthenurus stirlingi* has considerably higher hindlimb bone resistance to bending and torsion than does *Macropus giganteus*. There are also considerable differences in cortical bone distribution: *Sthenurus stirlingi* exhibits medial thickening of the bone, not observed in *Macropus giganteus*, which is associated with alternate leg weight-bearing in primates. These results suggest that *Macropus giganteus* and *Sthenurus stirlingi* were locomoting in different manners, and support previous hypotheses of bipedal walking in *Sthenurus*.

Constraining the Late Triassic mass extinction using the fossilized birth-death range model

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The Late Triassic extinction event led to a substantial loss of biodiversity, but the underlying drivers appear complex and it remains unclear whether this was a sudden or a gradual event. We address this question using the fossilized birth-death (FBD) range model and global stratigraphic range data for 14 marine invertebrate classes. The FBD process is a phylogenetic model that incorporates species diversification and fossil sampling processes explicitly. The model can be applied to the analysis of stratigraphic ranges and used to estimate speciation, extinction and fossil recovery rates during different geological intervals. We introduce an extension of the model that allows for the possibility that we may only know whether a given taxon was sampled or not during each interval, but not the frequency or precise time points the taxon was sampled (presence/absence data sampling). We assess the performance of our modelling framework using simulations and demonstrate that we can recover reliable estimates of diversification and fossil recovery. We apply the new model to the analysis of the Triassic–Jurassic extinction interval, for which presence/absence data are only available at the sub-stage level, and we re-examine the diversification dynamics across this important and turbulent episode in Earth's history.

Macroevolutionary patterns of tetrapod evolution during the Carboniferous–Permian transition: evidence from the fossil footprint record

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The ichnofossil record is an under-utilized resource in studies of palaeodiversity. Occurrence datasets compiled for diversity analyses frequently ignore footprint records due to difficulties in correlating them with valid body fossil taxa. We aimed to see if the ichnofossil record can act as a complementary resource to the body fossil record. To test hypotheses relating to tetrapod diversity from the Bashkirian to the Kungurian, we devised the first comprehensive database of Carboniferous–Permian terrestrial tetrapod ichnofossils and quantified ichnodisparity. The number of ichnogenera fluctuated throughout the tested time range, plummeting in the Asselian before gradually increasing towards the end of the Kungurian. There was a statistically significant correlation between the number of formations sampled, the number of ichnogenera and the number of localities (indicating a strong sampling bias). An overall decrease of amphibians (relative to amniotes) occurred from the Bashkirian to the Kungurian. A combined ichnodisparity analysis in R revealed that there is no significant change in ichnodisparity during the time interval. There was no significant increase in body size although a trend of increasing maximum body size was observed. These new analyses demonstrate the potential for the ichnofossil record to complement the body fossil record in macroevolutionary studies.

Globally discordant Isocrinida (Crinoidea) migration confirms asynchronous Marine Mesozoic Revolution

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Increased predation pressure as a result of the Marine Mesozoic Revolution (MMR, starting ~200 Ma) shaped the ecological structure of benthic sea floor communities from the Mesozoic to the Recent. It has been argued that less mobile groups such as stalked isocrinids moved out of shallow water environments by the Late Cretaceous (100–66 Ma) to evade increased predation pressure. Newly collected and described taxa from Antarctica and Australia, supplemented by data gathered from the literature, demonstrate a substantial Southern Hemisphere fossil record of stalked isocrinid crinoids (Order Isocrinida), which inhabited shallow water until the Eocene–Oligocene boundary (~34 Ma). These occurrences, from often overlooked isolated crinoid columnals, as well as newly discovered articulated crinoid fossils, challenge the perceived notion that the majority of stalked crinoids became restricted to deep water in the mid-late Mesozoic. The delayed migration of the Southern Hemisphere isocrinids to deeper waters after the Eocene–Oligocene boundary may have been due to intra-order competition from the more motile comatulids, which became dominant in the Southern Hemisphere following major ocean circulation changes including the onset of the Antarctic Circumpolar Current.

A basal turtle shows its teeth: possible evidence of dental microwear on the palatal denticles of *Proganochelys quenstedti* (Testudinata; Late Triassic)

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The palaeoecology of the basal turtle *Proganochelys quenstedti* has been open to debate. Whereas it was first described as semi-aquatic/aquatic, anatomical and histological data support adaptation to a terrestrial habitat. Our objective is to explore whether the palatal denticles of basal turtles could contain evidence of dental microwear. Two *Proganochelys* skulls were sampled (MB1910.45.2 and SMNS16980; Halberstadt and Trossingen quarries respectively, Late Triassic, Germany). The palatal denticle-bearing areas were cleaned, moulded and examined under a stereoscopic microscope. The SMNS skull did not yield any microwear evidence, possibly because of taphonomic alteration. Contrariwise, the denticles of the MB skull displayed clear microwear-like features (scratches and pits). We argue that food transport using the tongue under a jaw prehension mechanism could have left these marks on the denticles. Unfortunately, the absence of a modern analogue with palatal teeth does not allow testing of our interpretation. When compared with the microwear signal of a semi-aquatic piscivore (*Lutra lutra*) and a terrestrial herbivore mammal (*Tragulus javanicus*), the signal of *Proganochelys* more closely resembles a browsing terrestrial herbivore. The positive evidence of dental microwear in *Proganochelys* opens new lines of research in basal tetrapods, especially if similar results are found in other taxa with similar palatal denticles.

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Fossil Giraffidae (Mammalia, Artiodactyla) from the early Turolian of Kavakdere (Central Anatolia, Turkey)

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The fossiliferous site of Kavakdere is one of numerous important late Miocene fossil mammal-bearing localities of Anatolia. It is located approximately 65 km north-northwest of Ankara, Turkey, and has been known to palaeontologists for more than 50 years. Previous taxonomic studies have revealed a plethora of taxa. However, the fossil Giraffidae from this locality are poorly documented, with *Bramatherium* being the only comprehensively described taxon. Here we present newly excavated dental and postcranial material of Giraffidae from Kavakdere. The new fossils are hosted in the collections of the Natural History Museum of Ege University, Izmir, Turkey. Despite the small number of specimens, the fossils suggest the co-occurrence of five different giraffid taxa: *Bramatherium perimense*, *Helladotherium duvernoyi*, *Palaeotragus rouenii*, *Samotherium boissieri* and *Samotherium major*. The faunal composition agrees with previous chronostratigraphic assumptions that placed Kavakdere in the early Turolian (MN11). *Helladotherium* fossils are the most abundant at Kavakdere. Contrariwise, *S. major* is represented only by two postcranial elements, suggesting the species was a rare faunal element during the early Turolian. *Samotherium major* is mostly from the middle Turolian (MN12) of Greece and Turkey. Thus, the occurrence of the taxon in the fossil record of Kavakdere constitutes one of the earliest records of this taxon.

Distinguishing euarthropod tergites from radiodont head sclerites

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Tauricornicaris from the Chengjiang biota was recently described as a hurdiid radiodont based on some isolated sclerotized plates comparable with the head carapaces of hurdiids. However, articulated specimens indicate that the sclerites of *Tauricornicaris* are indeed euathropod tergites. Here we show several similar articulated specimens, presenting evidence that reinforces an euarthropod affinity of *Tauricornicaris*, such as a pygidium and typical euarthropod biramous appendages. Integrated information from all known specimens and their detailed morphology indicate that *Tauricornicaris* bears a large head shield with paired facial sutures and free cheeks, more than ten wide tergites with median sutures and a pygidium. Such a body composition, together with its biramous appendages, indicates that *Tauricornicaris* is an artiopodan euarthropod, which is supported by a phylogenetic analysis. A reappraisal of the similarities and differences between the tergites of *Tauricornicaris* and the head carapaces of radiodonts is presented, and taxonomic significance of the morphology of sclerites in stem arthropods is discussed.

Identifying a unique body plan in the problematic *Conicula* from the Cambrian Chengjiang biota

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The enigmatic *Conicula striata* from the Chengjiang biota has been described as a lophophorate of uncertain affinity primarily based on the eight tentacles identified in the only known specimen. The body plan of *C. striata* could be simply divided into a conical area and a column on the top. Here we present a redescription of the morphology of *C. striata* based on 39 newly collected specimens. It is revealed that the column bears more than eight, probably 18, longitudinal ridges and tentacles together with an oval saccular structure. Within the conical area is a central tube-like structure that expands into a dark stain on the top. Such a body plan of *C. striata* is not consistent with any known living animal phylum. However, its conical area, longitudinal ridges and attached tentacles prompt a comparison with some spiralian fossils, as well as some contemporaneous fossil coelenterates such as *Xianguangia*, *Dinomischus* and *Archisaccophyllia*. It is proposed that *Conicula* might capture the early divergence of major spiralian groups, or more radically, document a transitional stage from a coelenterate-like ancestor to stem bilaterians.

New data on *Arthropterygius* Maxwell, 2010 shows that it is not rare, but a most abundant ichthyosaur genus of the Late Jurassic and earliest Cretaceous

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The ichthyosaur genus *Arthropterygius* has heretofore been considered as rare and poorly known. Recently excavated unique material from the Berriasian of the Russian Extreme North and examination of historical collections in Russian museums provided numerous specimens referable to *Arthropterygius*. The new data, combined with examination of ichthyosaurs from Svalbard, give us reason to refer most of the Svalbard ichthyosaur genera to *Arthropterygius*. Therefore, we recognize four species within the genus: *Arthropterigius chrisorum* (Russell, 1993), *A. volgensis* (Kasansky, 1903) comb. nov., *A. hoybergeti* (Druckenmiller, Hurum, Knutsen, Narkem, 2012) comb. nov. and *A. lundi* (Roberts, Druckenmiller, Sætre and Hurum, 2014) comb. nov. Three of the species are found in both European Russia and the Arctic. This, together with the evidence of the presence of *Arthropterygius* in the Southern Hemisphere, allows the suggestion that *Arthropterygius* was probably the most common and widespread ichthyosaur genus in the Late Jurassic and earliest Cretaceous. Our phylogenetic analysis places the clade of *Arthropterygius* species close to the base of Ophthalmosauridae as a sister group either to ophthalmosaurines or to platypterygiines. Although its position is still uncertain, this is the most well-supported clade among ophthalmosaurids (Bremer support value of 5, Bootstrap exceeding 80) that further augments our taxonomic decision.