

**The
Palaeontological
Association**

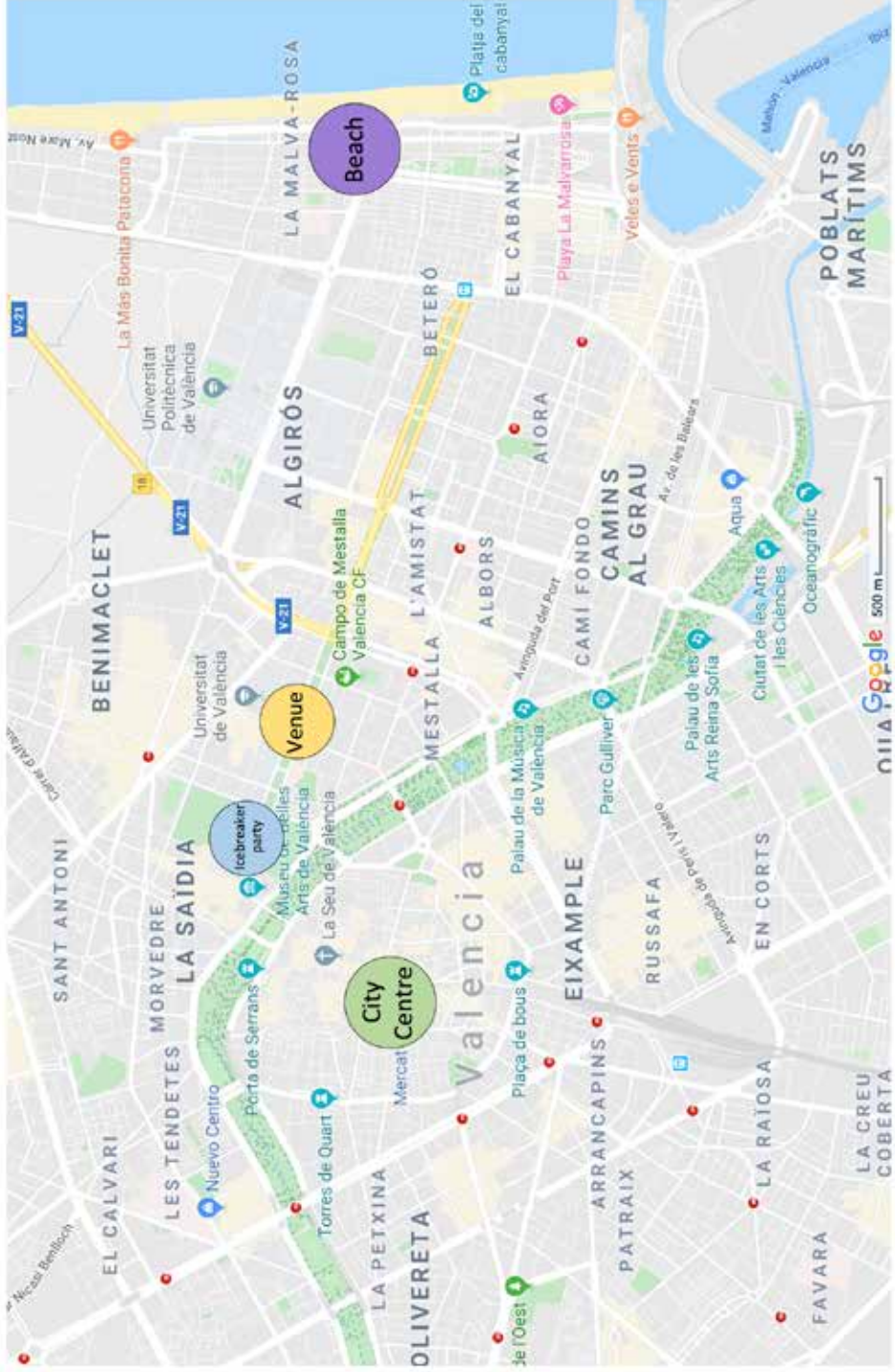
63rd Annual Meeting

**15th–21st December
2019**

*University of Valencia,
Spain*

**PROGRAMME
ABSTRACTS
AGM papers**



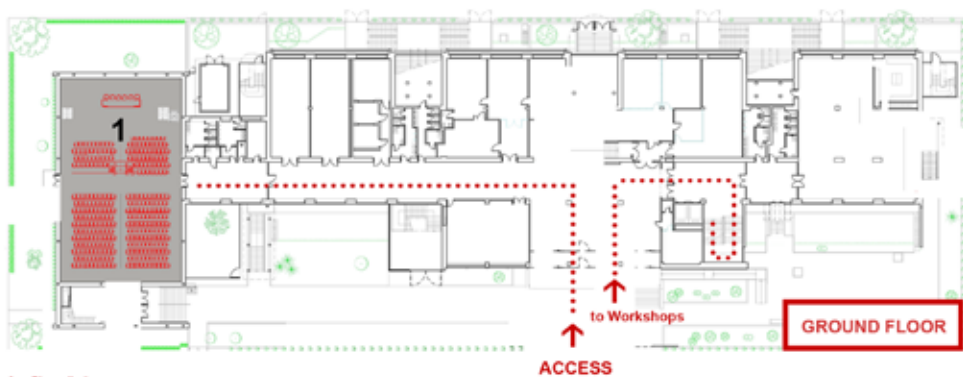




MUSEUM-FACULTIES VENUES



FACULTY OF PHILOLOGY



1

ORAL PRESENTATIONS

Conference Hall Manuel Sanchis Guarner

CONFERENCE VENUES

- 1 Faculty of Philology**
- Conference Hall Manuel Sanchis Guarner
- 2 Faculty of Philosophy**
- Conference Hall of Philosophy
- Annual Dinner meeting point
- Natural Science Museum**
- W56 First steps into Geometric Morphometrics
- Icebreaker venue

Route between venues

PUBLIC TRANSPORT



BUS

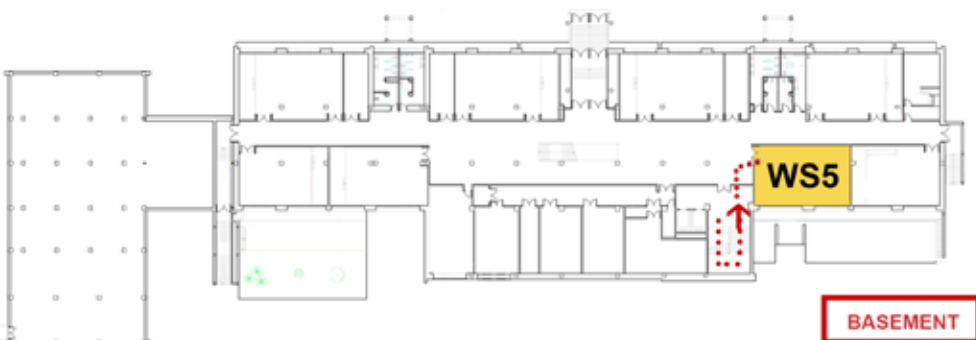
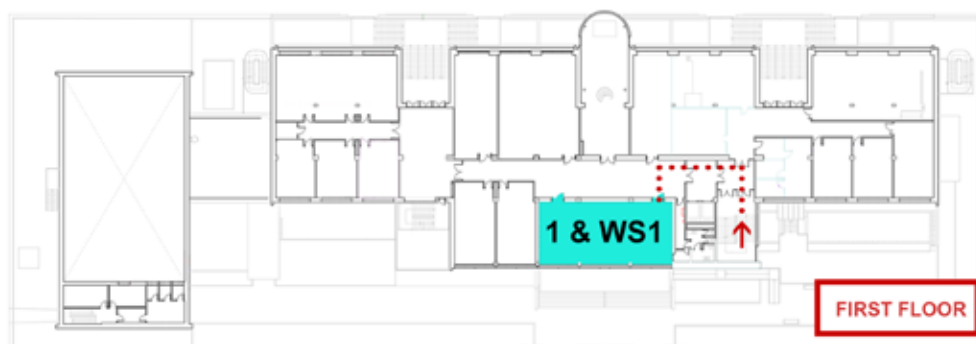
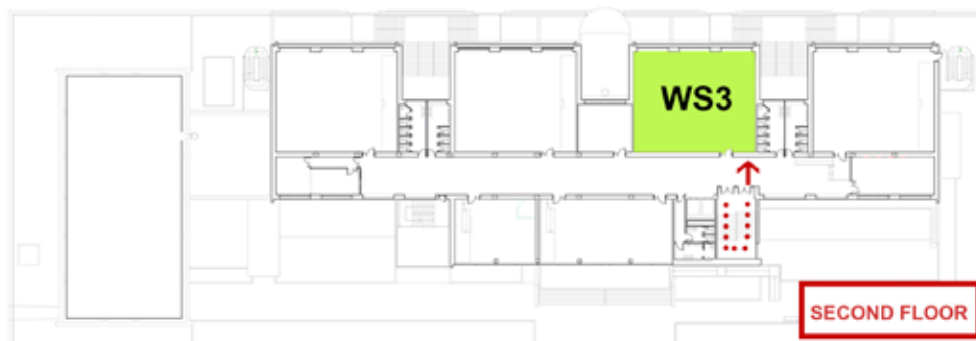


UNDERGROUND

1. Blasco Ibañez-Gascó Ollag
10 12 79 89 N89
2. Blasco Ibañez-Ciutat Universit ria
12 31 30 71 79 81
89 N89
3. Blasco Ibañez-Hospital
12 31 71 79 81
4. Blasco Ibañez-Jaume Roig
31 71 79 81

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FACULTY OF PHILOLOGY



1

DIVERSITY MEET-UP
Salon de Grados Enric Valor

WS3

Using phylogenies in
palaeontological studies

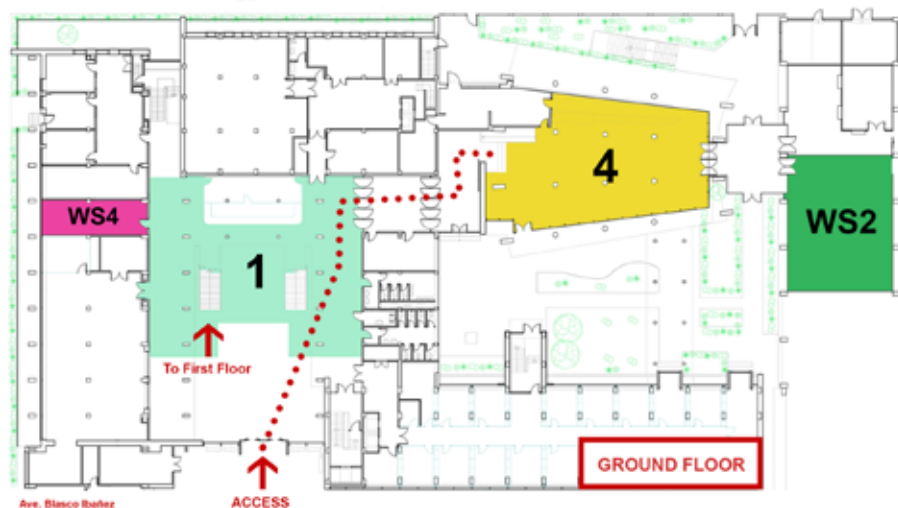
WS1

Introduction to
biomechanics and Finite
Element Analysis

WS5

Introduction to 3D data
visualization & segmen-
tation using Avizo

FACULTY OF PHILOSOPHY



1 POSTER SESSION

4 COFFEE BREAK

2 CONFERENCE HALL PHILOSOPHY
A. Registration Desk
B. Oral sessions

WS2 Essentials of Anatomical
Network Analysis

3 EXHIBITORS

WS4 Introduction to graphic design
for scientists





The Palaeontological Association

63rd Annual Meeting

15th–21st December 2019

University of Valencia

The programme and abstracts for the 63rd 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 in the faculties of Philosophy and Philology on the Blasco Ibañez Campus of the University of Valencia. The Symposium will take place in the Salon Actos Manuel Sanchis Guarner in the Faculty of Philology. The main meeting will take place in this and a nearby lecture theatre (Salon Actos, Faculty of Philosophy). There is a Metro stop just a few metres from the campus that connects with the centre of the city in 5-10 minutes (Line 3-Facultats). Alternatively, the campus is a 20-25 minute walk from the 'old town'.

Registration

Registration will be possible before and during the Symposium at the entrance to the Salon Actos in the Faculty of Philosophy. During the main meeting the registration desk will continue to be available in the Faculty of Philosophy.

Oral Presentations

All speakers (apart from the symposium speakers) have been allocated 15 minutes. It is therefore expected that you prepare to speak for no more than 12 minutes to allow time for questions and switching between presenters. We have a number of parallel sessions in nearby lecture theatres so timing will be especially important. All lecture theatres have an AV projector linked to a large screen. All presentations should be in PowerPoint or PDF format. Those not submitted prior to the meeting to Carlos Martínez Pérez must now be uploaded to the local system and checked. This should be done as soon as possible, and at least an hour before the allotted time for the presentation.

Poster presentations

Poster boards will accommodate an A0-sized poster presented in portrait format only. Pins to affix your poster to the boards are available. Posters are displayed in the Faculty of Philosophy. Please put up your posters either on Wednesday afternoon or first thing Thursday morning (between 08.00 and 08.45).

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

Accessibility

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

Valencia

Valencia is located on Spain's eastern coast, on the shores of the Mediterranean Sea in the centre of the Gulf of Valencia. Its architecture dates from the first century BC to the most futuristic 21st century designs, combining history, tradition and modernity in an unusual way. Beaches bathed by the Mediterranean Sea are just 15 minutes from the city centre, near to the Marina Real Juan Carlos I, where an abundance of restaurants, pubs and music await. In addition, the city boasts wide-ranging environmental aspects due to its proximity to the Albufera nature reserve (cradle of the most famous Spanish dish, 'la Paella') and more centrally its green lung, located in the old Turia riverbed that crosses the city centre from east to west. Valencia is a city experienced in accommodating all kinds of events, with a reputation as one of the most complete and versatile destinations on the continent. We hope you enjoy your stay.

Sponsors

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

- Instituto Cavanilles de Biodiversidad y Biología Evolutiva
- Facultad de Ciencias Biológicas
- Generalitat Valenciana
- Transmitting Science
- Instituto Geológico y Minero de España
- Thermo Fisher Scientific
- The Geological Society Publishing House
- Taylor and Francis Group
- Combined Academic Publishers Ltd
- Sociedad Española de Paleontología
- Ajuntament de València
- *Nature Ecology and Evolution*
- Museo de Ciencias Naturales de Valencia
- The Paleontological Institute
- Royal Society Publishing
- *Biology* — MDPI
- Museu de la Universitat de València: Història Natural





The Palaeontological Association thanks the Organizing Committee:

Co-Chairs:

- Dr Carlos Martinez-Perez
- Dr Hector Botella Sevilla

Committee:

- Dr Hugo Corbi
- Prof. Jose Ignacio Valenzuela Rios
- Dr Samuel Zamora
- Prof. Philip Donoghue
- Dr Humberto Ferron
- Prof. Emily Rayfield
- Dr Soledad De Esteban-Trivigno
- Dr Jau-Chin Liao
- Dr Alice Giannetti
- Dr Rachel Warnock
- Mrs Esther Manzanares




Student-collaborators:

- Castor Armañanzas Alpuente
- Alvaro Simarro Cano
- Fernando Antonio Martín-Arnal
- Oscar Caballero Chorda
- Rafel Matamales
- Belen Roqueta
- Maria Victoria Paredes Aliaga
- Jose Luis Herraiz
- Sergio Álvarez Parra
- Mireia Costa Perez
- Gonçalo Gomes Silvério
- Adrian Martinez Campoy

Recently published by the *Geological Society of London*

- **Regurgitalites – a window into the trophic ecology of fossil cephalopods.**
By Hoffmann, R., Stevens, K., Keupp, H., Simonsen, S. & Schweigert, G.
Read now: doi.org/10.1144/jgs2019-117
- **The Herefordshire Lagerstätte: fleshing out Silurian marine life.**
By Siveter, De. J., Briggs, D. E. G., Siveter, Da. J. & Sutton, M. D.
Read now: doi.org/10.1144/jgs2019-110
- **New theropod dinosaur teeth from the Middle Jurassic of the Isle of Skye, Scotland.**
By Young, C. M. E., Hendrickx, C., Challands, T. J., Foffa, D. Ross, D. A., Butler, I. B. & Brusatte, S. L.
Read now: doi.org/10.1144/sjg2018-020

Find out more on the Lyell Collection
www.lyellcollection.org.uk

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Summary of Schedule

Sunday 15th to Tuesday 17th December: Pre-conference field-trip

A three-day pre-conference field-trip will visit the Palaeozoic series of the Iberian Range, visiting numerous palaeontological sites ranging from the Lower Cambrian to the Middle Devonian in the neighbouring provinces of Teruel and Zaragoza. This trip will depart on 15th December early in the morning from Valencia, and return on the 17th late in the afternoon, arriving in time to check in and relax before the beginning of the Annual Meeting. The field-trip fees include three days of meals, transport, the field-trip guide and all accommodation for the duration.

Field-trip leader: Samuel Zamora.

Wednesday 18th December: Workshops, Symposium and Reception

The morning of 18th December features six workshops led by specialists from Transmitting Science on the application of analytical techniques for the study of fossils. See below for more details.

The meeting will begin with a symposium entitled “Virtual Palaeontology”. Registration will be available from 12.00 to 17.30 in the Faculty of Philosophy.

Following the symposium there will be an icebreaker reception from 18.00 to 21.00 at the Natural Sciences Museum of Valencia at Jardines del Real.

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

Registration will be open from 08.00 in the Faculty of Philosophy.

The conference will start at 09.00 in the faculties of Philology and Philosophy. Talks will be held in double and single sessions in two lecture theatres, Salon Actos Manuel Sanchis Guarner in Philology and Salon Actos in Philosophy, which are close to one other. The Annual General Meeting (AGM) will be held at 14.45 followed by a brief coffee break, returning for the Annual Address at 16.00. Posters will be set up in the Faculty of Philosophy where lunch and coffee breaks will also be held.

Please note that lunch and refreshments are included in the registration fee. An informal Diversity in Palaeontology meet-up will be held during the Thursday lunch break and anyone is welcome to attend.

The afternoon will have a dedicated poster session (17.00–18.00) in the Faculty of Philosophy where drinks will be served.

The Annual Dinner will be held at the Albufera nature reserve, beginning at 20.00. The dinner will feature a three-course meal accompanied by drinks, an open cash bar and the venue is ours until 01.00. The meeting point for transport to the venue is at the Faculty of Philosophy at 19.30. Coaches will drop people back there starting return trips from around 23.30 onwards.

**Friday 20th December: Conference and prizes**

Registration will be open from 08.00 in the Faculty of Philosophy.

Talks will begin at 09.00 in double and single sessions in the same two lecture theatres as on the previous day. Coffee breaks and lunch will be served at the Faculty of Philosophy, where posters will be on display. Talks will end by 17.30, 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.

Saturday 21st December: Post-conference field-trip

We will visit the Miocene of the Province of Alicante, taking in the ichonological record of the Cabo de las Huerta close to Alicante, the Messinian coral reef of Santa Pola and the unique Palaeontological Museum of the province in Elche. The field-trip will depart from Valencia in the morning and return there during the evening. Lunch in Elche is included.

Departure time is 08.00 from the Faculty of Philology. We are expecting to arrive back in Valencia around 19.30 but will be able to stop in at Alicante Airport en route around 17.00–17.30 if needed.

Field-trip leader: Hugo Corbí.



Schedule of events and timetable of presentations

Sunday 15th to Tuesday 17th December

Pre-conference field-trip

The pre-conference field-trip will depart from Valencia on 15th December early in the morning, and return on the 17th late in the afternoon.

Field-trip leader: Samuel Zamora.

Wednesday 18th December

Pre-meeting workshops

Participants must be pre-registered as spaces are limited.

09.00 – 12.30 Introduction to biomechanics and finite element analysis

Instructor: Jordi Marcé-Nogué

Salon de Grados, Philology

09.00 – 12.30 Essentials of anatomical network analysis

Instructors: Borja Esteve-Altava and Diego Rasskin-Gutman

Crystal Room, Philosophy

09.00 – 12.30 Using phylogenies in palaeobiological studies

Instructor: Juan L. Cantalapiedra

Room 202, Philology

09.00 – 12.30 Introduction to graphic design for scientists

Instructor: Oscar Sanisidro

Professors Meeting Room, Philosophy

09.00 – 12.30 Introduction to 3D data visualization and segmentation using Avizo

Instructors: John Cunningham and Carlos Martínez Pérez

Room S03, Philology

09.00 – 12.00 First steps into geometric morphometrics

Instructor: Soledad De Esteban-Trivigno

Museum Natural Sciences Valencia

REGISTRATION

12.00 – 17.30 Faculty of Philosophy



Symposium: “Virtual Palaeontology”

Salon Actos Manuel Sanchis Guarner, Faculty of Philology

13.30 – 13.45 Welcome address

13.45 – 14.15 **Digitizing the vertebrate palaeontology collection of the Museum für Naturkunde of Berlin: preserving our natural history heritage by assessing different digitization techniques**

Verónica Díez-Díaz

14.15 – 14.45 **Virtual footprints: simulation and digitization elucidate deep track formation**

Peter L. Falkingham and Stephen M. Gatesy

14.45 – 15.15 **Synchrotron X-rays: new developments to reveal fossil bone microstructures in three dimensions**

Sophie Sanchez

15.15 – 16.00 Tea/coffee break

16.00 – 16.30 **Computational fluid dynamics as a tool for testing functional and ecological hypotheses in fossil taxa**

Imran A. Rahman

16.30– 17.00 **Finite elements, morphometrics, extant animals and accuracy**

Jen A. Bright

17.00 – 17.30 **Multibody dynamics analysis (MDA) as a tool to reconstruct the function and palaeobiology of extinct organisms**

Stephan Lautenschlager

REGISTRATION

Registration will be possible before and during the Symposium. During the main meeting a registration desk will be available in the Faculty of Philosophy.

Reception

18.00 – 21.00 Natural Science Museum of Valencia



Thursday 19th 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 Faculty of Philosophy

Session 1A (in parallel with session 1B)

Salon Actos Manuel Sanchis Guarner, Philology Chair: Emily Rayfield

09.00 – 09.15 **Success of early archosauromorphs: a case of positive phenotypic selection?**

*Armin Elsler, Suresh Singh, Michael J. Benton, Marcello Ruta and Alexander M. Dunhill

09.15 – 09.30 **Reconstructing diets of extinct reptiles from the Solnhofen Archipelago using dental microwear texture analysis**

*Jordan Bestwick, David M. Unwin and Mark A. Purnell

09.30 – 09.45 **Lagerstätte effect on notosuchian palaeodiversity (Crocodyliformes, Notosuchia)**

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

09.45 – 10.00 **Palaeogene–Neogene squamates and their spatial and temporal relationships with climatic drivers and sampling biases**

*Terri J. Cleary, Alex Farnsworth and Richard J. Butler

10.00 – 10.15 **A late Barremian food web through fossil faeces: an isotopic insight on the ecology of the Las Hoyas fossil site (Cuenca, Spain)**

*Sandra Barrios-de Pedro, Karyne M. Rogers, Paloma Alcorlo and Ángela D. Buscalioni

Session 1B (in parallel with session 1A)

Salon Actos Philosophy Chair: Sarah Gabbott

09.00 – 09.15 **Evolution of trilobite development and global ecosystem changes**

Lukáš Laibl

09.15 – 09.30 **Reconstructing the feeding apparatus of Amplectobeluidae (Radiodonta: stem Euarthropoda)**

Peiyun Cong, Jin Guo, Gregory D. Edgecombe, Allison C. Daley and Xianguang Hou

09.30 – 09.45 **Aluminosilicate haloes fossilize complex life over 800 million years ago**

Ross P. Anderson, Nicholas J. Tosca, Gianfelice Cinque, Mark Frogley, Ioannis Lekkas, Austin Akey *et al.*

09.45 – 10.00 **Global climate changes account for the main trends of conodont diversity but not for their final demise**

Samuel Ginot and Nicolas Goudemand



10.00 – 10.15 **An innovative synchrotron approach to access the chemical nature of carbon in 2D or 3D in large organic fossils**

Pierre Gueriau, Rafaella Georgiou, Christoph J. Sahle, Sylvain Bernard, Alessandro Mirone, Romain Garrouste *et al.*

10.15 – 11.00 **Tea/coffee break and posters**

Session 2A (in parallel with session 2B)

Salon Actos Manuel Sanchis Guarner, Philology Chair: Duncan Murdock

11.00 – 11.15 **Biogeography of conodonts in the Early Triassic**

*Pauline Guenser, Gilles Escarguel and Nicolas Goudemand

11.15 – 11.30 ***Albalimulus*: the oldest limulid**

*Russell D. C. Bicknell and Stephen Pates

11.30 – 11.45 **Biogenic iron liberated during decay initializes highly detailed soft tissue pyritization in Burgess Shale-type biotas**

*Farid Saleh, Allison C. Daley, Bertrand Lefebvre, Bernard Pittet and Jean Philippe Perrillat

11.45 – 12.00 **Soft tissue associations reveal the influence of preservation on biodiversity in Burgess Shale-type fossil deposits**

Allison C. Daley, Farid Saleh, Bertrand Lefebvre, Bernard Pittet, Lukáš Laibl, Francesc Perez Peris *et al.*

12.00 – 12.15 **A giant sediment-sifting hurdiid from the Burgess Shale illuminates hurdiid carapace diversity and highlights competition for prey resources**

Jean-Bernard Caron and Joseph Moysiuk

Session 2B (in parallel with session 2A)

Salon Actos Philosophy Chair: Soledad de Esteban-Trivigno

11.00 – 11.15 **A finite element model on vibrations of Weberian ossicles of cypriniform fish using harmonic analysis**

Jordi Marcé-Nogué and Juan Liu

11.15 – 11.30 **Stable isotopes of rodent tooth enamel provide new evidence on Miocene ape environments in the Vallès-Penedès Basin (Catalonia)**

Isaac Casanovas-Vilar, Yuri Kimura, Lawrence J. Flynn, David Pilbeam, Salvador Moyà-Solà and David M. Alba

11.30 – 11.45 **Untangling the fossil record of Rhinocerotidae**

Oscar Sanisidro Morant and Juan L. Cantalapiedra

11.45 – 12.00 **The nature, evolution and ecology of nonavian and avian egg colour**

Jasmina Wiemann

12.00 – 12.15 **The impact of the resurgence of carbonate platforms on the re-diversification of level-bottom faunas after the end-Permian mass extinction**

Evelyn Friesenbichler, Michael Hautmann and Hugo Bucher



12.15 – 13.30 **Lunch, poster session and Diversity in Palaeontology meet-up**

Session 3

Salon Actos Manuel Sanchis Guarner, Philology Chair: Soledad Domingo

13.30 – 13.45 **Exploring the topological impact of palaeontological data in phylogenetic hypotheses**

*[Nicolas Mongiardino Koch](#) and Luke A. Parry

13.45 – 14.00 **Disentangling taphonomic and ecological signals in fossil food webs**

*[Jack Shaw](#), Kate Wootton, Emily Coco, Dries Daems, Andrew Gillreath-Brown and Anshuman Swain

14.00 – 14.15 **Poor spatial sampling coverage obscures our understanding of the latitudinal biodiversity gradient in deep time**

[Lewis A. Jones](#), [Christopher D. Dean](#), Philip D. Mannion and Peter A. Allison

14.15 – 14.30 **Unique locomotor habits in Early Palaeogene mammals provides ecomorphological insight into evolution after the end-Cretaceous mass extinction**

[Sarah L. Shelley](#), Stephen L. Brusatte and Thomas Williamson

14.30 – 14.45 **The early diversity dynamics of the great evolutionary floras**

Elliott Capel, Christopher J. Cleal, Philippe Gerrienne and [Borja Cascales-Miñana](#)

Annual General Meeting

Salon Actos Manuel Sanchis Guarner, Philology

14.45 – 15.30 **Annual General Meeting**

Faculty of Philosophy

15.30 – 16.00 **Tea/coffee break and posters**

Annual Address

Salon Actos Manuel Sanchis Guarner, Philology

16.00 – 17.00 **Not just skin deep: probing the secrets of fossil melanin using taphonomic experiments and analytical chemistry**

Maria E. McNamara

Faculty of Philosophy

17.00 – 18.00 **Poster session with refreshments**

Reception & Annual Dinner

Albufera nature reserve

19.30 Transport from Faculty of Philosophy

20.00 – 20.30 **Reception**

20.30 – 01.00 **Annual Dinner**



Friday 20th December

Conference & poster session

Session 4A (in parallel with session 4B)

Salon Actos Manuel Sanchis Guarner, Philology Chair: Javier Alvaro

- 09.00 – 09.15 **The origin of modern birds: new information from the Cretaceous stem bird *Ichthyornis***
*[Juan Benito](#), Bhart-Anjan S. Bhullar, David Burnham, Laura E. Wilson and Daniel J. Field
- 09.15 – 09.30 **Comparison of modern and fossil Forcipulatacea (Asteroidea, Echinodermata) skeletal ossicles reveals the early diversification of this major order**
*[Marine Fau](#), Loïc Villier and Timothy A. M. Ewin
- 09.30 – 09.45 **To the bitter end: do planktonic foraminifera actively change their niche habit prior to extinction?**
*[Adam D. Woodhouse](#), Sophie Jackson, Philip F. Sexton, Paul N. Pearson, Stewart Knott, Alexander M. Dunhill *et al.*
- 09.45 – 10.00 **Phylogenetics of true crabs, and the early origins of crab-like forms**
*[Javier Luque](#), Heather D. Bracken-Grissom, Javier Ortega-Hernández and Joanna M. Wolfe
- 10.00 – 10.15 **Interpreting colour patterns in aquatic vertebrates: decay-induced changes to the distribution and morphology of melanosomes throughout pigmented tissues**
*[Christopher Nedza](#), Mark A. Purnell, Jakob Vinther and Sarah E. Gabbott

Session 4B (in parallel with session 4A)

Salon Actos Philosophy Chair: Kenneth de Baets

- 09.00 – 09.15 **The Cambrian evolution of chelicerates**
[Rudy Lerosey-Aubril](#) and Javier Ortega-Hernández
- 09.15 – 09.30 **The forgotten latest Cambrian nautiloid cephalopods from Black Mountain (NW Queensland, Australia)**
[Alexander Pohle](#), Peter A. Jell, Yong-Yi Zhen and Christian Klug
- 09.30 – 09.45 **Prey fractionation in the Archaeocyatha and its implication for the ecology of the first animal reef systems**
[Jonathan B. Antcliffe](#), William Jessop and Allison C. Daley
- 09.45 – 10.00 **Somatic versus reproductive investment in *Antarctothoa tongima* over two million years**
[Emanuela Di Martino](#) and Lee Hsiang Liow
- 10.00 – 10.15 **Brachiopod shell thickness links environment and evolution**
[Uwe Balthasar](#)



10.15 – 11.00 **Tea/coffee break and posters**

Session 5A (in parallel with session 5B)

Salon Actos Manuel Sanchis Guarner, Philology Chair: Mike Benton

11.00 – 11.15 **Was complex life excluded from tropical latitudes in the aftermath of the Permo–Triassic mass extinction?**

*[Bethany J. Allen](#), Paul B. Wignall, Daniel J. Hill, Erin E. Saupe and Alexander M. Dunhill

11.15 – 11.30 **Aragonite–calcite sea effects on calcifying organisms and reefs**

*[Kilian Eichenseer](#), Uwe Balthasar, Christopher W. Smart, Julian Stander, Kristian A. Haaga and Wolfgang Kiessling

11.30 – 11.45 **New insights into the vital effect during brachiopod shell formation and its relevance to the geochemical record**

*[María del Mar Simonet Roda](#), Andreas Ziegler, Erika Griesshaber, Daniela Henkel, Vreni Häusermann, Anton Eisenhauer *et al.*

11.45 – 12.00 **The phylogenetic history of the armoured dinosaurs (Ornithischia, Thyreophora)**

*[Thomas J. Raven](#), Paul M. Barrett and Susannah C.R. Maidment

12.00 – 12.15 **Bone fusion and morphological change: an unexplored relationship in tetrapod macroevolution**

[Aitor Navarro Diaz](#), Diego Rasskin Gutman and Borja Esteve Altava

Session 5B (in parallel with session 5A)

Salon Actos Philosophy Chair: Alex Liu

11.00 – 11.15 **Arm waving in stylophoran echinoderms: insights into the function of the aulacophore through 3D imaging and digital modelling**

[Elizabeth Clark](#), John R. Hutchinson, Peter J. Bishop and Derek E. G. Briggs

11.15 – 11.30 **Juvenile skeletogenesis and implications for body plan evolution in echinoids**

[Jeffrey Thompson](#) and Paola Oliveri

11.30 – 11.45 **Constraining morphological disparity in rangeomorphs**

[Charlotte Kenchington](#), Frances S. Dunn, Alexander G. Liu and Philip R. Wilby

11.45 – 12.00 **Ediacaran life close to land: coastal and shoreface environments of the Ediacara biota of South Australia**

[William McMahon](#), Alexander G. Liu and Maarten Kleinans

12.00 – 12.15 **The Ediacaran–Cambrian transition: the emerging record from small carbonaceous fossils (SCFs)**

[Ben J. Slater](#), Thomas H. P. Harvey, Romain Guilbaud, Sebastian Willman, Graham E. Budd and Nicholas J. Butterfield

**Faculty of Philosophy**

12.15 – 13.30 **Lunch and poster session**

Session 6

Salon Actos Manuel Sanchis Guarner, Philology Chair: Christian Klug

13.30 – 13.45 **Overcoming the challenges of studying the earliest macrofossils: a case study from the middle Ediacaran (pre-Gaskiers) of Newfoundland**
Alexander G. Liu and Benjamin H. Tindal

13.45 – 14.00 **Tracking the origin of an ancient genome duplication in teleost fishes using fossilized bone cell spaces**
Donald Davesne, Armin D. Schmitt, Matt Friedman, Per E. Ahlberg, Vincent Fernandez, Sophie Sanchez *et al.*

14.00 – 14.15 **Breathing new life into the earliest soft-bodied animals: computed tomography of early Cambrian fossils from South China**
Joanna M. Wolfe, Javier Ortega-Hernández, Dayou Zhai and Yu Liu

14.15 – 14.30 **Molecular developmental genetics, homology and ancestral organisms: what about fossils and morphology?**
Arsham Nejad Kourki, Jakob Vinther and Philip C. J. Donoghue

14.30 – 14.45 **Moms: how to measure occupancy in multidimensional space (disparity)?**
Thomas Guillerme, Mark Puttick, Ariel Marcy and Vera Weisbecker

14.45 – 15.00 **A novel Bayesian phylodynamic approach to estimating diversity from the fossil record**
Rachel C. M. Warnock, Marc Manceau, Timothy G. Vaughan and Tanja Stadler

15.00 – 15.15 **New insights into early terrestrial environments using high resolution 3D imaging and chemical techniques**
Christine Strullu-Derrien, Alan R. T. Spencer and Paul Kenrick

15.15 – 16.00 **Tea/coffee break** (take down posters)

Session 7

Salon Actos Manuel Sanchis Guarner, Philology Chair: Laura Domingo

16.00 – 16.15 **Putting the AI into Palaeontology: using new methods of machine learning to capture evolutionary history**
Jennifer Hoyal Cuthill and Nicholas Guttenberg

16.15 – 16.30 **A time to be born and a time to die: the life and death of stem groups**
Graham E. Budd and Richard P. Mann

16.30 – 16.45 **Will marine animals become smaller with continued global warming? Deep time tests of the 'shrinking seafood' hypothesis**
Richard J. Twitchett



16.45 – 17.00 **Early Palaeozoic diversifications and extinctions in the marine biosphere: onwards and upwards**

David A. T. Harper, Borja Cascales-Miñana and Thomas Servais

17.00 – 17.15 **Should meristic characters be ordered in phylogenetic analysis?**

Neil Brocklehurst and Yara Haridy

17.15 – 17.30 **Evolutionary simulations demonstrate punctuated equilibrium**

Mark D. Sutton, Nicole L. Barnes and Russell J. Garwood

Closing business

Salon Actos Manuel Sanchis Guarner, Philology

17.30 – 18.00 Presentations from the organizing committees of PalAss 2020 (Manchester) and Progressive Palaeontology 2020 (Leeds/York)

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

Saturday 21st December

Post-conference field-trip

Departure time is 08.00 from the Faculty of Philology. We are expecting to arrive back in Valencia around 19.30 but will be able to stop at Alicante Airport en route around 17.00–17.30 if needed.

Field-trip leader: Hugo Corbí.



The Palaeontological Association

Registered Charity Number: 1168330

Code of Conduct for Palaeontological Association meetings

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

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

Behavioural expectations: It is the expectation of the Palaeontological Association that meeting attendees behave in a courteous, collegial and respectful fashion to each other, volunteers, exhibitors and meeting facility staff. Attendees should respect 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 in 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 Carlos Martínez Pérez (<Carlos.Martinez-Perez@uv.es>) and/or a designated member of the Palaeontological Association Council (Executive Officer Dr Jo Hellawell, <executive@palass.org>; President Prof. Charles Wellman, <c.wellman@sheffield.ac.uk>; Vice-Presidents Prof. Thijs Vandenbroucke or Dr Caroline Buttler, <Thijs.Vandenbroucke@UGent.be>, <Caroline.Buttler@museumwales.ac.uk>; ProgPal representative Bethany Allen, <eebja@leeds.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 112. Those witnessing a potential criminal act should also take actions necessary to maintain their own personal safety.



Abstracts of symposium presentations:

Virtual Palaeontology

Finite elements, morphometrics, extant animals and accuracy

Jen A. Bright

University of Hull, UK

Since becoming part of the virtual palaeontology toolbox in the early 2000s, finite element (FE) analysis is now a widespread feature of many studies exploring the relationship between form and function in extinct animals. However, two major criticisms are often directed at FE models: firstly, they take considerable time, money and experience to build; and secondly, it is difficult to test for accuracy in the model outputs, especially when the original biological material under study has turned to rock. The application of geometric morphometrics potentially solves the first problem by rapidly generating new model geometries with which to directly compare relationships between function and form, but it also increases the levels of assumption (and therefore doubt) in model outputs. This means that we must carefully frame our questions in order to provide a problem that the FE method is equipped to answer, and utilize validation and sensitivity analyses on extant specimens to help highlight and bracket modelling problems. I illustrate these concepts with a series of examples from extant birds informing an FE model of cranial kinesis in the late Cretaceous bird, *Hesperornis*.

Digitizing the vertebrate palaeontology collection of the Museum für Naturkunde of Berlin: preserving our natural history heritage by assessing different digitization techniques

Verónica Díez-Díaz

Museum für Naturkunde, Berlin, Germany

Digitization of natural history collections is becoming a major focus of museum programmes. The importance of digital collections is not only related to research projects, but also has high curatorial and outreach significance. Besides the 3D models (also called cybertypes) created for each physical specimen, an impressive quantity of metadata is obtained, and must be saved in close relation with the former. Consequently, a curator of digital collections should be considered as a new position, as these collections need to be organized, updated and cared for, as is the case for the physical ones. The Museum für Naturkunde (MfN), Berlin is a partner of the German Natural Sciences Collections as an Integrated Research Infrastructure (DCOLL in German), which aims to bring the digitization and usage of natural science collections in Germany to an unprecedented level. Germany's public research museums, universities and institutes house more than 150 million scientific objects (at the MfN about 30 million objects), but only about five percent is digitally registered. In the MfN we are assessing different digitization techniques and methods, taking into account the external features of the physical specimens, the final quality and use of the cybertype, budget and time.



Virtual footprints: simulation and digitization elucidate deep track formation

Peter L. Falkingham¹ and Stephen M. Gatesy²

¹*Liverpool John Moores University, UK*

²*Brown University, USA*

Whilst bones present a static view of extinct animals, fossil footprints are a direct record of the activity and motion of the trackmaker. Deep footprints are a particularly good record of foot motion; however, such footprints rarely look like the feet that made them. Because of this, such tracks are often overlooked or dismissed in preference for more foot-like impressions. However, the deeper the foot penetrates the substrate, the more motion is captured in the sediment volume. Unfortunately, sub-surface deformations in both modern and fossil tracks are obscured by the opacity of the sediment and the transient nature of the foot–sediment interaction. We combine imaging and simulation techniques to visualize track formation. Using XROMM, we have recorded motion of the feet of birds as they walk over soft substrates, and we have incorporated these motions into particle simulations to study the formation of sub-surface structures during and after the track-making process. Not only does this workflow shed light on how individual feet moved, but our ability to digitally look inside the footprint throughout its formation process (a process we have dubbed ‘track ontogeny’) has enabled us to identify emergent sedimentary features common to certain motions and foot morphologies.

Multibody dynamics analysis (MDA) as a tool to reconstruct the function and palaeobiology of extinct organisms

Stephan Lautenschlager

University of Birmingham, UK

Over the last three decades, novel computational applications and technologies have increasingly found their way into palaeontological and biological sciences. Digital visualization techniques, such as computed tomography (CT) scanning, have substantially changed the way fossil organisms can be studied and characterized in unprecedented detail. The potential of these methods to generate highly detailed and accurate 3D digital models has itself triggered a further surge in downstream analyses to study the functional morphology and biomechanical behaviour of fossil and extant taxa. While some techniques, such as finite element analysis (FEA), have become mainstream in palaeontological research, multibody dynamic analysis (MDA) has so far rarely been used. MDA is a computational method widely used in engineering and biomedical sciences to simulate and study the kinematic behaviour of mechanical systems. However, its potential for reconstructing the function and palaeobiology of fossil organisms remains relatively unused. In order to facilitate the dissemination and application of MDA in palaeontology, the fundamentals and main steps involved in this technique will be presented. General requirements and possible research applications based on case studies will be introduced and advantages and disadvantages will be discussed.



Computational fluid dynamics as a tool for testing functional and ecological hypotheses in fossil taxa

Imran A. Rahman

Oxford University Museum of Natural History, UK

Palaeontologists have long been fascinated with how ancient organisms moved and fed, but it has proved difficult to address these questions in ways that allow specific hypotheses to be tested. As a result, endeavours in the field are sometimes dismissed as unscientific ‘just-so’ stories. However, the increasing availability of techniques for visualizing and analysing fossils digitally and in three dimensions has provided a framework for testing specific hypotheses in extinct taxa. One such method is computational fluid dynamics, or CFD, a tool for simulating flows of fluids and their interaction with solid surfaces. In this talk, I will present case studies of CFD used to test functional hypotheses in fossil taxa, shedding light on the ecology and evolution of a range of ancient organisms.

Synchrotron X-rays: new developments to reveal fossil bone microstructures in three dimensions

Sophie Sanchez

Uppsala University, Sweden

The first thin sections of fossil hard tissues for microscopic observations were published by Owen in 1840. Since then, many technical advances have occurred in the field of microscopy. New techniques such as serial grinding, confocal and electron microscopy created new possibilities for understanding fossil mineralized microstructures in three dimensions. Because some of these techniques were destructive and others could not entirely penetrate the fossil samples, new developments were needed. X-ray synchrotron microtomography was recently developed to compensate for this. Based on phase contrast, this is one of the most powerful techniques to reveal fossil 3D mineralized tissues in large fossil samples with no damage. The combination of synchrotron X-ray microtomography and diffraction further opened up the possibilities to reveal the mineralized matrix crystallite structure in 3D. Based on case studies, I propose to show the potential of this technique applied to vertebrate palaeohistology.



Abstract of Annual Address

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

Not just skin deep: probing the secrets of fossil melanin using taphonomic experiments and analytical chemistry

Maria E. McNamara

University College Cork, Ireland

The research landscape in palaeobiology has been transformed in recent years by the recovery of evidence of melanin in diverse fossil taxa from the Carboniferous to the Pliocene. This has facilitated the first evidence-based interpretations of the original hue and/or pattern of integumentary tissues in ancient organisms, with important implications for the evolution of behaviour and ecology in key animal groups. Studies of fossil melanin have also yielded somewhat unexpected insights into the taxonomic affinities, physiology and internal anatomy of fossil animals, confirming that ancient melanin has broad applications beyond reconstructions of original colour. New advances in this developing field are underpinned by a strong analytical and multidisciplinary approach, including data from modern analogues of fossil taxa and controlled laboratory experiments investigating the taphonomy of melanin. Despite intense interest in this rapidly expanding field, certain fundamental aspects of melanin biology, preservation and evolution are incompletely understood. Here I will review progress and challenges in the study of fossil melanin, incorporating a synthesis of best practice in study design and an emerging model for melanin evolution.



Abstracts of oral presentations

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

Underlined author denotes designated speaker.

Was complex life excluded from tropical latitudes in the aftermath of the Permo-Triassic mass extinction?

***Bethany J. Allen**¹, **Paul B. Wignall**¹, **Daniel J. Hill**¹, **Erin E. Saupe**² and **Alexander M. Dunhill**¹

¹University of Leeds, UK

²University of Oxford, UK

The modern-day latitudinal diversity gradient (LDG) is a general trend of increasing biodiversity from the poles to the equator. Our understanding of the underlying processes that drive LDGs is limited, and it remains unclear whether this pattern was consistent throughout the Phanerozoic. One approach to answering these questions is to examine spatial biodiversity patterns in the geological past, under different global climate regimes and continental configurations. The Late Permian–Middle Triassic (~260 – 237 Ma) is characterized by large-scale volcanic episodes, continental aggregation, and mass extinctions and recoveries. Extremely high equatorial temperatures could have rendered the lower latitudes uninhabitable for complex animals, producing a bimodal LDG with temperate peaks. To test this, we used a global fossil database to reconstruct Late Permian–Middle Triassic LDGs for tetrapods, brachiopods and bivalves. Permo-Triassic terrestrial tetrapods exhibited a bimodal richness distribution, with northern low and southern mid latitude peaks, while marine reptiles were only found in northern mid latitudes. In contrast, brachiopods and bivalves possessed a unimodal distribution, with peak latitudinal diversity moving northwards across the equator during the Induan. These results indicate that Permo-Triassic terrestrial LDGs may have been driven by changes in precipitation, or more influenced by extreme temperatures than marine LDGs.

Aluminosilicate haloes fossilize complex life over 800 million years ago

Ross P. Anderson¹, **Nicholas J. Tosca**¹, **Gianfelice Cinque**², **Mark Frogley**², **Ioannis Lekkas**², **Austin Akey**³, **Gareth M. Hughes**¹, **Nicholas J. Butterfield**⁴, **Andrew H. Knoll**³ and **Derek E. G. Briggs**⁵

¹University of Oxford, UK

²Diamond Light Source, Didcot, UK

³Harvard University, USA

⁴University of Cambridge, UK

⁵Yale University, USA

Although molecular estimates for metazoan antiquity commonly extend into early Neoproterozoic time, the first metazoan body fossils do not appear until ~570 Ma. This disconnect is commonly attributed to taphonomic bias, whereby unidentified physico-chemical processes in early Neoproterozoic sedimentary environments prevented early metazoan fossilization. However, Cambrian Burgess Shale-type (BST) deposits preserve decay-prone metazoans without hard mineralized skeletons. Are there really no older



deposits with similarly favourable fossilization conditions? We interrogated fossilization within eukaryotic microfossil-bearing shales of the ~1,000 Ma Lakhanda (Siberia) Group and ~800 Ma Svanbergfjellet and Wynniatt (Svalbard and Arctic Canada) formations, and compared it to BST fossilization. Fossilized material was extracted from bedding parallel thin-sections by focused-ion-beam milling. SEM-EDS chemical mapping and synchrotron-based FTIR together revealed that microfossils are commonly surrounded by aluminium-rich and kaolinite-rich haloes relative to the surrounding substrate. Kaolinite is known to slow the growth of bacterial degraders and has been implicated in BST fossilization by recent mineralogical analyses of Cambrian BST deposits. Neoproterozoic deposits lack metazoan fossils even though they share fossilization conditions with younger BST deposits. Thus metazoans, at least those typically preserved in BST faunas, were likely absent from Tonian sedimentary environments.

Prey fractionation in the Archaeocyatha and its implication for the ecology of the first animal reef systems

Jonathan B. Antcliffe¹, William Jessop² and Allison C. Daley¹

¹*University of Lausanne, Switzerland*

²*University of Oxford, UK*

Archaeocyaths are the most abundant sponges from the Cambrian period, forming the first animal reef communities. The Archaeocyatha are well-known index fossils yet their ecology remains incompletely explored. They strongly competitively interact unlike modern sponges and despite being suspension feeders that filtered prey through pores in their outer wall. Here we outline a new method to estimate the prey sizes that could be consumed by an archaeocyath during life. The archaeocyaths examined were predominantly feeding on nanoplankton and microplankton such as phytoplankton and protozooplankton. Size-frequency distributions of pore sizes from six different Siberian assemblages (Tommotian to Botoman age), reveal significantly different upper limits to the prey consumed at each locality. Some of the assemblages contain specimens that could have fed on larger organisms extending into the mesoplankton including micro-invertebrates. This shows that during the establishment of the first animal reef systems, prey partitioning was established as a way of reducing competition. This method helps in understanding the construction and the functioning of the first reef systems, and could be applied to nutrient flow and prey partitioning in modern reef systems and fossil Phanerozoic reef systems, as well as more broadly informing reef development through time and space.

Brachiopod shell thickness links environment and evolution

Uwe Balthasar

University of Plymouth, UK

Secreting a shell comes at a metabolic cost and shell secretion should balance the needs for protection and structural support against the available energy budget. Within ecologically similar groups and similar environments, variation in shell thickness should thus reflect the metabolic efficiency of shell secretion. Here I present shell thickness data for 123 specimens of 57 Ordovician/Silurian and 9 Cenozoic genera and interpret them in the context of Ordovician–Silurian diversification and extinction events. In order to compare shell thickness across a large variety of different groups, shell thickness was measured across the anterior half of the shell only, which is structurally broadly homologous across most



groups. The results suggest that energy-efficient shell secretion was probably a selective advantage across the end-Ordovician mass extinction with an overall drop in shell thickness followed by a sustained increase throughout the early Silurian. Furthermore, orders that dominated the Great Ordovician Biodiversification Event but suffered particularly strongly in the end-Ordovician extinction had significantly thicker than average shells, whereas thin-shelled taxa had an initially modest diversity but showed no sustained drop in diversity across the mass extinction.

A late Barremian food web through fossil faeces: an isotopic insight on the ecology of the Las Hoyas fossil site (Cuenca, Spain)

***Sandra Barrios-de Pedro**¹, **Karyne M. Rogers**², **Paloma Alcorlo**¹ and **Ángela D. Buscalioni**¹

¹Universidad Autónoma de Madrid, Spain

²GNS Science, New Zealand

Las Hoyas is an upper Barremian continental Konservat-Lagerstätte located in Cuenca (Spain). The exceptional preservation of fossils has allowed the description of 12 morphotypes from the coprolite association, which are mostly composed of apatite group compounds. A total of 54 coprolites with different morphologies were analysed for stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}_{\text{org}}$), using their preserved primary isotopic signals. The $\delta^{15}\text{N}$ values allowed us to define up to three different trophic levels (assuming a trophic enrichment factor of 2.5 ‰), and to differentiate between drier and wetter periods within the ecosystem. The largest coprolites demonstrated that there was no correspondence between size and $\delta^{15}\text{N}$ values. The $\delta^{13}\text{C}_{\text{org}}$ values indicated that the most common food sources used by animals from Las Hoyas were freshwater sourced. The overlap in the isotopic signatures of coprolites when the covariation of $\delta^{15}\text{N}$ was expressed against $\delta^{13}\text{C}_{\text{org}}$ indicated that animals occupied similar trophic positions and competed for the same food resources.

The origin of modern birds: new information from the Cretaceous stem bird *Ichthyornis*

***Juan Benito**^{1,2}, **Bhart-Anjan S. Bhullar**³, **David Burnham**⁴, **Laura E. Wilson**⁵ and **Daniel J. Field**²

¹University of Bath, UK

²University of Cambridge, UK

³Yale Peabody Museum of Natural History, USA

⁴University of Kansas Natural History Museum, USA

⁵Sternberg Museum of Natural History, USA

The postcranial morphology of the Late Cretaceous toothed bird *Ichthyornis dispar* 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 morphological evolution prior to the great radiation of the avian crown group. Here we present high-resolution scans of new, exquisitely preserved three-dimensional specimens of *Ichthyornis* from the Late Cretaceous of Kansas. These correspond to a partial skeleton from a single individual, and include a complete sternum and shoulder girdle with evidence of extensive pneumatization. Given the absence of some previously proposed autapomorphies of *I. dispar*, the new material may represent a previously unknown species, or it could indicate greater morphological variation within *I. dispar*. Phylogenetic analyses



incorporating our new data corroborate recent results recovering a grade of predominantly marine taxa close to the origin of crown birds. *I. dispar* is recovered stemward of Hesperornithes and *Iaceornis marsbi*, which is recovered as the sister taxon to crown birds. Additional information on the crownward-most portion of the avian stem group will help confirm these results and provide critical information on the ancestral ecology of the crown bird radiation.

Reconstructing diets of extinct reptiles from the Solnhofen Archipelago using dental microwear texture analysis

***Jordan Bestwick, David M. Unwin and Mark A. Purnell**

University of Leicester, UK

The Late Jurassic Solnhofen Archipelago, Germany, is a renowned Lagerstätte for its exceptionally preserved skeletons of extinct reptiles from several biotopes. Marine reptiles include Crocodyliformes and ichthyosaurs, terrestrial reptiles include theropod dinosaurs and rhynchocephalians, and aerial reptiles include pterosaurs and the first bird, *Archaeopteryx*. Reconstructing the diets of Solnhofen reptiles is therefore vital for characterizing their ecological role(s) within this palaeoecosystem and for determining whether taxa competed for, or partitioned, food resources. Current dietary hypotheses for Solnhofen reptiles, however, are poorly constrained as hypotheses are largely based on descriptive evidence that is difficult to explicitly test. Here, we constrain the diets of Solnhofen reptiles by applying dental microwear texture analysis to their non-occlusal tooth surfaces and by comparing their microwear textures with data from modern crocodylians and monitor lizards (including insectivorous, piscivorous and carnivorous species). We show subtle niche partitioning between *Archaeopteryx* and pterosaurs; *Archaeopteryx* as a 'softer' invertebrate consumer and pterosaurs as piscivores or consumers of 'harder' invertebrates. We also show dietary overlap between Crocodyliformes *Cricosaurus* and *Geosaurus* (mixed carnivorous-piscivorous diets), which casts doubt on the hypothesis that these taxa partitioned resources. Lastly, we provide the first evidence that the theropod dinosaur *Juravenator* had a mixed carnivorous-insectivorous diet.

Albalimulus: the oldest limulid

***Russell D. C. Bicknell¹ and Stephen Pates²**

¹*University of New England, Australia*

²*Harvard University, USA*

Horseshoe crabs have a fossil record which spans over 450 million years, but only one extant family: Limulidae. The origin of this family has been somewhat debated. The first limulid was thought to have arisen in the Triassic (*c.* 250 million years old) but here we challenge this paradigm with the discovery of a new limulid from the Lower Carboniferous (Tournaisian stage, *c.* 350 million years) of Scotland: *Albalimulus bottoni*. This discovery demonstrates that the three major Mesozoic group horseshoe crab families had a Palaeozoic origin. We present a systematic description of the taxon and a comprehensive phylogenetic analysis illustrating the placement of the taxon close to the base of Limulidae. Furthermore, landmark- and semilandmark-based geometric morphometric analyses illustrate two major pulses of xiphosurid evolution between the Upper Ordovician and today. The first reflects the rise of belinurids and palaeolimulids, and the presence of marine and non-marine groups, and the second the diversification of Limulidae. We



conclude that continued study of such rare specimens is needed to thoroughly understand the evolutionary history experienced by these iconic chelicerates.

Should meristic characters be ordered in phylogenetic analysis?

Neil Brocklehurst¹ and Yara Haridy²

¹*University of Oxford, UK*

²*Museum für Naturkunde, Berlin, Germany*

Use of ordered characters in phylogenetic analysis has been inconsistent through research history, but some have advocated that all characters representing continuous or meristic traits should be ordered as a matter of course. Using the example of dental evolution, we examine two factors that may impact whether meristic characters actually evolve in an ordered manner: the regulatory hierarchy governing the development of teeth that allows large sections or the entire tooth-row to be suppressed in a single transition, and regionalization of the tooth-row where different modules have a degree of independence in their evolution. Ordered and unordered models of evolution of such characters are fit to molecular phylogenies. In a clade with largely homodont dentition the characters evolve in an ordered manner, but when dentition has regionalization their evolution better fits an unordered model. In simulations of tooth-row evolution designed to incorporate changes in region size and multiple levels of developmental control, dividing the row into independently evolving modules leads to characters covering multiple modules better fitting an unordered model. We advise not following a single policy when deciding whether to order meristic traits but basing the decision on the evolution and developmental biology of the clade under study.

A time to be born and a time to die: the life and death of stem groups

Graham E. Budd¹ and Richard P. Mann²

¹*Uppsala University, Sweden*

²*University of Leeds, UK*

Stem groups are an essential feature of the modern understanding of the past diversification of life. However, little attention has been paid to what they might look like. How quickly do stem groups diversify, and when do they go extinct? Here we model their expected diversity using a birth–death model. Under a wide range of conditions, stem groups briefly diversify until they deliver their crown group, at which point they rapidly go extinct. The only exceptions are those stem groups that diversify as if they were a crown group, only to be eliminated by a mass extinction. Crown groups, conversely, diversify rapidly without any cryptic phase, and usually appear early in the history of the total group. Huge mass extinctions can force crown groups to emerge later; the least likely time for a crown group to emerge, however, is just before a mass extinction. These results are robust under a wide range of conditions, and match many patterns seen in the fossil record. In turn, this suggests that the fossil record is often recording genuine patterns of diversification, contrary to the view that molecular clock estimates are more reliable in determining the timing and nature of major living groups.



The early diversity dynamics of the great evolutionary floras

Elliott Capel¹, Christopher J. Cleal², Philippe Gerrienne³ and Borja Cascales-Miñana⁴

¹Université de Lille, France

²Amgueddfa Cymru – National Museum Wales, UK

³University of Liège, Belgium

⁴CNRS UMR 8198, Université de Lille, France

Data from a new comprehensive megafossil-based compilation of early plant genera are analysed via a Q-mode factor analysis. The compilation ranges from the Silurian to lowest Carboniferous and illustrates the key vegetation changes in the configuration of early terrestrial ecosystems. Results reveal that only four factors are needed to account for more than 90 % of the data. These factors are interpreted as reflecting the major evolutionary phases of the first floras: a first Eotracheophytic flora (Silurian-Lochkovian) dominated by basal eutracheophytes and rhyniophytoids, an early Eophytic Flora (Early Devonian) dominated by zosterophylls and basal euphyllophytes, a transitional late Eophytic Flora (Middle Devonian–Tournaisian) mainly dominated by lycopsids, cladoxyloids and progymnosperms, and finally, the earliest phase of Palaeophytic Flora (Frasnian/Famennian boundary–Tournaisian) dominated by the first seed plants. These floras present different but complementary patterns, which help us to understand the whole trajectory of plant diversity and its composition. Results further show how the maximum peaks of diversity appear linked to the rise of each new flora, but interestingly such a rise is not associated with any exponential decline of the previously dominant flora. This new four-phase diversification model probably reflects the key steps of the early Earth's greening.

A giant sediment-sifting hurdiid from the Burgess Shale illuminates hurdiid carapace diversity and highlights competition for prey resources

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

¹Royal Ontario Museum, Canada

²University of Toronto, Canada

Cambroraster falcatus, a sediment-sifting hurdiid arthropod (Radiodonta), was recently described from the Burgess Shale's Marble Canyon locality in Kootenay National Park, British Columbia (Canada). A second and much rarer hurdiid, inferred to have shared a similar feeding ecology based on its rake-like claws, is also present at Marble Canyon. The H-element is the largest known from any Cambrian hurdiid and bears a blunt anterior spine and short posterolateral processes. Each process terminates in a large spine and bears a second smaller spine pointing inward. The pair of P-elements are connected anteriorly by short necks, each possessing a downward-pointing spine. Both types of carapaces show a reticulated pattern with distinct crenulated longitudinal striations. The new taxon is recovered in a derived hurdiid clade with *Cambroraster* and *Zhenghecaris*; its precise phylogenetic position varies depending on whether discrete characters or landmark configurations are used to describe carapace shape. This taxon, together with other undescribed material from the Burgess Shale, underscores the diversity of carapace morphologies and size variations attained by Cambrian hurdiids. This find also highlights levels of resource overlap between sympatric hurdiid species, and we hypothesize that body size differences could have been a primary factor in benthic prey resource partitioning.



Stable isotopes of rodent tooth enamel provide new evidence on Miocene ape environments in the Vallès-Penedès Basin (Catalonia)

Isaac Casanovas-Vilar¹, Yuri Kimura², Lawrence J. Flynn³, David Pilbeam³, Salvador Moyà-Solà¹ and David M. Alba¹

¹*Institut Català de Paleontologia Miquel Crusafont, Spain*

²*National Museum of Nature and Science, Japan*

³*Harvard University, USA*

Extant apes are the relicts of a much more diverse group that originated in Africa around the Oligocene/Miocene boundary and dispersed into Eurasia by the beginning of the Middle Miocene where they experienced a notable evolutionary radiation. Generally rare, this group is well represented in the Vallès-Penedès Basin (Catalonia, NE Spain) with several different genera and species occurring at multiple sites. Here we use stable isotopes of molar enamel of murid rodents to reconstruct the climate and vegetation in Vallès-Penedès sites ranging from 12.5 to 9.1 Ma. Carbon isotope values indicate pure C3 diets throughout the interval. The $\delta^{13}\text{C}$ values are also used to estimate mean annual precipitation and environment after correcting for biological fractionation, altitude, latitude and variations in $\delta^{13}\text{C}$ of atmospheric CO_2 over geologic time. Results show that ape-bearing sites consistently represent more humid environments than those where apes are absent. Most ape-bearing sites are in the isotopic range of tropical deciduous forests, particularly during the Middle Miocene, while a few correspond to evergreen warm mixed forests. Therefore, most ape species inhabited less humid and more seasonal environments than their extant relatives.

Arm waving in stylophoran echinoderms: insights into the function of the aulacophore through 3D imaging and digital modelling

Elizabeth Clark¹, John R. Hutchinson², Peter J. Bishop² and Derek E. G. Briggs¹

¹*Yale University, USA*

²*Royal Veterinary College, UK*

Pentamer symmetry is a key innovation for omnidirectional locomotion, exemplified by the unique locomotion strategies employed by living echinoderms. Determining how fossil echinoderm taxa locomote is important in resolving the steps underlying the evolution of pentamer symmetry and the history of echinoderm locomotion. Stylophorans are early fossil echinoderms that lacked the pentamer symmetry characteristic of the extant classes. Although most fossil echinoderms are considered to have been sessile, stylophorans have been found associated with trace fossils suggesting that they may have been capable of locomotion. Stylophorans have a flat body and a single jointed appendage (the aulacophore). We used micro-CT imaging to digitize a stylophoran and create a virtual model which revealed the range of motion of the aulacophore. Our results indicate that a previously hypothesized mode of locomotion in stylophorans is inviable and suggest that the stylophoran aulacophore was a compromise for movement and feeding.



Palaeogene–Neogene squamates and their spatial and temporal relationships with climatic drivers and sampling biases

***Terri J. Cleary**¹, **Alex Farnsworth**² and **Richard J. Butler**¹

¹*University of Birmingham, UK*

²*University of Bristol, UK*

Squamates are key components of modern terrestrial ecosystems, with over 10,000 extant species. There is much debate over how they will be affected by ongoing climate change. Some studies have examined their past diversity, alongside climatic variables, in order to determine if there is any relationship between the two, but few have taken into account the inherent biases in the fossil record, or explicitly considered spatial, as well as temporal, climate variation. We made statistical comparisons between spatial and temporal patterns of Palaeogene and Neogene (66–2.6 Ma) squamate richness and climatic variables from general circulation models. Through this interval the climate began to shift from a greenhouse to icehouse world, and many extant taxa emerged. Squamates are much better sampled in the Neogene compared to earlier times. Continental-level richness varies, with opposite patterns of increasing and decreasing diversity during the Miocene between Europe and both Asia and South America. At family level, many Miocene taxa display similar environmental preferences to their extant counterparts. Groups concentrated in the tropics today were found to have warmer-skewing temperature ranges than groups found at higher latitudes (*e.g.* Teiidae versus Lacertidae), indicating that the modern squamate distribution has been established for a long time.

Reconstructing the feeding apparatus of Amplectobeluidae (Radiodonta: stem Euarthropoda)

Peiyun Cong¹, **Jin Guo**^{1,2}, **Gregory D. Edgecombe**^{1,3}, **Allison C. Daley**^{1,4} and **Xianguang Hou**¹

¹*Yunnan University, China*

²*Management Committee of the Chengjiang Fossil Site World Heritage, China*

³*Natural History Museum, London, UK*

⁴*University of Lausanne, Switzerland*

Recent discoveries revealing diverse feeding strategies in Radiodonta (anomalocaridids and relatives) are supported by the description of complex feeding structures, including gnathobase-like structures (GLS) and accompanying tuberculate plates (TP) and smooth plates (SP) in Amplectobeluidae. GLSs are evidently appendicular and each pair of them is associated with a reduced transitional segment; however, the topological arrangement of TPs and SPs remains unclear. The only known pattern shows each SP preserved with several TPs, together forming a row or column. Recent reconstructions arranged the row/column in a square, with the slightly curved SPs at the outer edge, by comparison with the radial oral cones of Anomalocarididae and Hurdiidae. Here we show that SPs are hemisternite-like sclerites, probably corresponding with the reduced transitional segments in number, while the TPs bilaterally form a row, with their spines pointing inwards. The cuticle between the SPs and TPs bears dense tubercles, sometime with apical spines. Our new observations reinforce the idea that transitional segments of amplectobeluids are well integrated into feeding. The occurrence of hemisternites in amplectobeluids supplements the head carapace as a second example of body sclerites originating in the lower stem lineage before they were widely adopted in upper stem and crown-group euarthropods.



Soft tissue associations reveal the influence of preservation on biodiversity in Burgess Shale-type fossil deposits

Allison C. Daley¹, Farid Saleh², Bertrand Lefebvre², Bernard Pittet², Lukáš Laibl¹, Francesc Perez Peris¹, Lorenzo Lustri¹, Pierre Gueriau¹ and Jonathan B. Antcliffe¹

¹University of Lausanne, Switzerland

²Université Claude Bernard Lyon 1, France

Exceptionally-preserved fossil biotas of the Cambrian and Ordovician provide crucial data on early animal evolution, allowing for the reconstruction of stem lineages and informing on crown group character acquisition. However, a confounding factor to these phylogenetic analyses is information loss during fossil preservation. We compared the taphonomic signal of three Cambro–Ordovician Lagerstätten by classifying all eumetazoan genera based on presence/absence of different tissue types (biomineralized skeletons, sclerotized and unsclerotized cuticle, external and internal soft cellular tissue). Results show that preservation in the Ordovician Fezouata Shale is significantly different from the Cambrian Burgess Shale and Chengjiang Biota. In the Fezouata Shale, soft cellular structures are most commonly associated with partially mineralized and sclerotized tissues, which may be protecting the soft tissue, and soft, non-cuticularized organisms are unknown. Conversely, the Cambrian sites are remarkably similar, with both commonly preserving entirely soft cellular bodies and a higher diversity of tissue types per genus. This analysis allows for an exploration of the effects of taphonomic bias on phylogenetic analyses, which will be further constrained using decay experiments. Taken together, these approaches provide a coherent framework for reassessing biodiversity in Cambrian Lagerstätten and reanalysing character acquisition during the earliest evolution of animals.

Tracking the origin of an ancient genome duplication in teleost fishes using fossilized bone cell spaces

Donald Davesne¹, Armin D. Schmitt¹, Matt Friedman², Per E. Ahlberg³, Vincent Fernandez^{4,5}, Sophie Sanchez^{3,4} and Roger B. J. Benson¹

¹University of Oxford, UK

²University of Michigan Museum of Paleontology, USA

³Uppsala University, Sweden

⁴European Synchrotron Radiation Facility, Grenoble, France

⁵Natural History Museum, London, UK

Teleost fishes are a key model for genome evolution, because they experienced drastic changes in genome size in the course of their evolutionary history. Most notably, a whole-genome duplication occurred before the origin of modern teleosts, potentially triggering the evolutionary success of this enormous clade. However, exactly when in time and where in the phylogeny this occurred is unknown. Empirical quantitative studies have established a significant statistical relationship between the volume of osteocyte lacunae (spaces left by bone cells) and genome size. Since they fossilize easily, osteocyte lacunae have been used to infer genome size in a variety of fossil vertebrates, including non-avian dinosaurs and lungfishes. We assembled a dataset for teleosts and their close relatives, encompassing taxa with duplicated and non-duplicated genomes, Devonian to extant. Homologous bones have been CT-scanned with synchrotron light to three-dimensionally reconstruct osteocyte lacunae. This accounts for variations in cell shape and orientation, critical parameters not fully addressed by ‘classical’ 2D thin sections. Our results support an early occurrence of



the genome duplication in the teleost stem-group, in the Jurassic or Late Triassic. This has been followed by a significant decrease in genome size, which we are able to track within different teleost lineages

Lagerstätte effect on notosuchian palaeodiversity (Crocodyliformes, Notosuchia)

***Ane de Celis¹, Iván Narváez¹, Andrea Arcucci² and Francisco Ortega¹**

¹*Universidad Nacional de Educación a Distancia, Spain*

²*Universidad Nacional de San Luis, Argentina*

Identifying major biases in the fossil record is crucial to accurately reconstruct and interpret palaeodiversity patterns. More than half of notosuchian species described to date come from South America, and around one quarter of the total come from the Adamantina Formation (Bauru Group, Brazil). Therefore, it is expected that a bonanza, or Lagerstätte effect, might be distorting notosuchian palaeodiversity estimates. Visual inspection of palaeodiversity estimates, with and without the Adamantina Formation, suggests that notosuchian palaeodiversity peaks coincide with the presence of the Adamantina Formation. However, other factors might be contributing to the observed fluctuations of notosuchian palaeodiversity. Therefore, a modelling approach, in which several abiotic and sampling proxies were tested against notosuchian palaeodiversity, was performed. The results indicate that the observed notosuchian palaeodiversity is driven by a bonanza or Lagerstätte effect exerted by the Adamantina Formation.

Somatic versus reproductive investment in *Antarctothoa tongima* over two million years

Emanuela Di Martino and Lee Hsiang Liow

Natural History Museum, University of Oslo, Norway

Life history theory and quantitative studies on empirical systems largely focus on solitary organisms, while comparable research using colonial organisms as models is limited. Even less is known about how life histories vary in a species or lineage over macroevolutionary timescales. However, some morphological characters routinely preserved in the calcium carbonate skeleton of bryozoans can be meaningful approximations for the life history traits of colonies. In this study, we use the cheilostome bryozoan *Antarctothoa tongima* to track temporal dynamics in life history traits over more than two million years. *Antarctothoa tongima* is an ideal candidate for studying life history trait variation because of its polymorphic male, female and feeding zooids from which we can estimate investment in reproduction and somatic growth. Based on a suite of colony-level traits, including the density of feeding zooids, males and females and the size of zooids and ovicells (reproductive structures), we answer the following questions: 1) How temporally stable are trade-offs in life-history traits? 2) What combination of traits can best predict 'fitness' (female investment)? 3) Does variation in overgrowth competition affect 'fitness'? 4) Does female investment predict relative ecological abundance?



Aragonite–calcite sea effects on calcifying organisms and reefs

***Kilian Eichenseer¹, Uwe Balthasar¹, Christopher W. Smart¹, Julian Stander¹, Kristian A. Haaga² and Wolfgang Kiessling³**

¹University of Plymouth, UK

²University of Bergen, Norway

³University of Erlangen–Nuremberg, Germany

Phanerozoic changes in the oceanic Mg/Ca ratio and temperature gave rise to alternating episodes of abiotic aragonite and calcite precipitation. These aragonite–calcite sea conditions control the abiotic precipitation of calcium carbonate (CaCO₃) polymorphs. Experiments have demonstrated that aragonite–calcite sea conditions affect growth rates and skeletal secretion of some marine calcifiers, but questions remain on how these effects operate on ecological scales. Here we create a Phanerozoic model of aragonite and calcite sea conditions to test whether they affect marine calcification on a global scale. We find that aragonite–calcite sea conditions predict the ecological success of fossil calcifiers relative to their aragonitic or calcitic shell composition during the Ordovician–Middle Jurassic. The loss of coupling between shell mineralogy and environment coincides with the onset of deep sea CaCO₃ sedimentation and the advent of the modern carbon cycle. However, preliminary results from the distribution of reefs through time indicate that reef systems are affected differently.

Success of early archosauromorphs: a case of positive phenotypic selection?

***Armin Elsler¹, Suresh Singh¹, Michael J. Benton¹, Marcello Ruta² and Alexander M. Dunhill³**

¹University of Bristol, UK

²University of Lincoln, UK

³University of Leeds, UK

The success of archosauromorphs in the aftermath of the Permo-Triassic mass extinction event (PTME) and the rise to dominance of dinosaurs in the Late Triassic and Early Jurassic has been a long-standing debate in vertebrate palaeontology. It has been argued that early archosauromorphs and early dinosaurs merely ‘passively’ entered empty niches, that had been vacated after the disappearance of the previously dominating clades. Alternatively, a competitive replacement of the previous fauna has been proposed, with early archosauromorphs and early dinosaurs being biomechanically and physiologically ‘superior’ relative to their counterparts, ultimately resulting in their success. As part of this explanation it has been suggested that strong selective pressure led to the appearance of novel herbivore feeding adaptations in several early archosauromorph and early dinosaur clades. Using a phylogenetic comparative approach we test the hypothesis that positive phenotypic selection was acting on the lower jaw of early archosauromorphs. Contrary to previous suggestions, we find no evidence for strong selective pressure playing a major role in the evolution of feeding adaptations of early archosauromorphs and early dinosaurs. This result is consistent with an opportunistic non-competitive replacement model for the success of these clades.



Comparison of modern and fossil Forcipulatacea (Asteroidea, Echinodermata) skeletal ossicles reveals the early diversification of this major order

***Marine Fau**¹, **Loïc Villier**² and **Timothy A. M. Ewin**³

¹*University of Fribourg, Switzerland*

²*Sorbonne Université, France*

³*Natural History Museum, London, UK*

It is broadly accepted that all extant orders of the class Asteroidea emerged during the Jurassic period, and then had about 200 million years of independent evolutionary history. Jurassic fossils are therefore essential to understanding the initial diversification of the extant Asteroidea. The clade Forcipulatacea, comprised of about 400 extant species, is morphologically well-defined. However, its fossil record is relatively sparse with all representatives being assigned to two extant families (*i.e.* Asteroiidae and Zoroasteridae), whilst others are erroneously assigned to different orders. We investigate the anatomy of 29 extant forcipulatacean and 14 fossil forms, of which eight are from the Jurassic. Extensive observations including key details of the abactinal skeleton, ossicle spination and pedicellariae allowed us to derive more than a hundred phylogenetic characters, and perform the most comprehensive phylogenetic analysis based on morphological data for this group. The resulting phylogenetic tree shows a remarkable level of congruence with the most recent molecular analysis. The phylogenetic position of the fossils suggests an early diversification of the Forcipulatacea, during the Jurassic. The reanalysis of these fossils demonstrates that the early diversity of the Forcipulatacea was greater than previously thought and challenges existing perceptions of the evolutionary history of this major clade.

The impact of the resurgence of carbonate platforms on the rediversification of level-bottom faunas after the end-Permian mass extinction

Evelyn Friesenbichler, **Michael Hautmann** and **Hugo Bucher**

University of Zurich, Switzerland

The main recovery phase after the end-Permian mass extinction coincides with the resurgence of large carbonate platforms during the Middle Triassic. Did the resurgence of large carbonate platforms affect the diversification of level-bottom faunas? Which evolutionary changes have been involved in the colonization of this new habitat? In order to answer these questions, quantitative ecological analyses of level-bottom faunas from Middle Triassic carbonate platforms were performed and compared with Early Triassic faunas in terms of species richness and trophic composition. This comparison shows an increase in species richness that coincides with the main phase of recovery after the end-Permian mass extinction. This main phase of recovery was associated with a weakening of the dominance of bivalves in comparison to the Early Triassic, which reflects the proliferation of other invertebrate taxa, particularly gastropods. This shift in taxonomic composition is most notable in level-bottom faunas from carbonate platforms. We hypothesize that the increased environmental diversity associated with the newly-arising carbonate platforms and the co-evolution between carbonate producers and benthic faunas played an important role in the accelerated pace of recovery and the shift in taxonomic composition during the Middle Triassic.



Biogeography of conodonts in the Early Triassic

***Pauline Guenser**^{1,2}, **Gilles Escarguel**¹ and **Nicolas Goudemand**²

¹*Université Claude Bernard Lyon 1, France*

²*Institut de Génomique Fonctionnelle de Lyon, France*

Following the Permo-Triassic biotic crisis, corresponding to the largest Phanerozoic mass extinction, the Early Triassic has long been considered as a time of slow and delayed recovery. Since the end of the 2000s, geochemical, sedimentological and palaeontological studies focusing on marine diversity and biogeographic patterns showed that this epoch included several large-scale biotic events such as a mass extinction at the Smithian–Spathian boundary (Olenekian, late Early Triassic). In this context, ammonoids and conodonts were particularly studied, being among the best index fossils for that time interval. However, unlike for ammonoids, conodont biogeography has not yet been quantitatively studied. Examining conodont biogeography would help to better understand their post-crisis evolutionary dynamics, as any regional- to global-scale biotic perturbation would impact their geographic distribution through origination/extinction and migration phenomena. Their biogeographic patterns may also help to further characterize the biotic and abiotic drivers of the underlying Early Triassic environmental disturbances. To do so, a taxonomically homogenized incidence (presence/absence) data table of conodont species in major Early Triassic sedimentary basins was built for each Early Triassic sub-stage (Griesbachian, Dienerian, Smithian and Spathian), then quantitatively analysed using multivariate exploratory approaches including ordination, clustering and network analyses.

Global climate changes account for the main trends of conodont diversity but not for their final demise

Samuel Ginot^{1,2} and **Nicolas Goudemand**²

¹*Université Claude Bernard Lyon 1, France*

²*Institut de Génomique Fonctionnelle de Lyon, France*

Conodonts have a very complete fossil record ranging from late Cambrian to the end of the Triassic, going through many worldwide climatic and biotic changes. Despite this, the global diversity of conodonts has not been studied recently. Using up-to-date methods of diversity, origination and extinction estimation, applied to Paleobiology Database data, we computed global curves at the generic level. Conodont palaeogeographic extension was also studied. Our results confirm prominent events highlighted by older studies: Ordovician acme, Permian low and Triassic short recovery. Peaks of origination were found in the Early Ordovician and Early Triassic, while major extinctions were found in the Upper Ordovician and Pennsylvanian. Palaeogeographical extent of conodonts was impacted by the position of palaeocontinents, available continental shelf area and ice sheet expansion. Diversity trends were impacted by transitions between hothouse and icehouse ages, with glaciations co-occurring with major extinctions. The influence of sea level was less marked than that of temperature. Although several factors were not accounted for in our study, the absence of glaciation and unclear sea-level trend in the Middle Triassic support the view that the final demise of conodonts may be due to competition with Mesozoic taxa.



An innovative synchrotron approach to access the chemical nature of carbon in 2D or 3D in large organic fossils

Pierre Gueriau¹, Rafaella Georgiou^{2,3}, Christoph J. Sahle⁴, Sylvain Bernard⁵, Alessandro Mirone⁴, Romain Garrouste⁶, Uwe Bergmann⁷, Jean-Pascal Rueff^{3,8} and Loïc Bertrand^{2,3}

¹University of Lausanne, Switzerland

²IPANEMA, Gif-sur-Yvette, France

³Synchrotron SOLEIL, Gif-sur-Yvette, France

⁴European Synchrotron Radiation Facility, Grenoble, France

⁵Institut de Minéralogie, de Physique des Matériaux et de Cosmochimie (IMPMC), France

⁶Institut de Systématique Evolution Biodiversité (ISYEB), France

⁷SLAC National Accelerator Laboratory, USA

⁸Laboratoire de Chimie Physique–Matière et Rayonnement, Paris, France

Accessing the chemical nature of organic carbon-rich fossils in 2D or 3D imposes stringent constraints and is restricted essentially to ultra-thin or finely polished samples, but not entire fossils. We introduce X-ray Raman scattering (XRS)-based imaging at the carbon K-edge, an innovative synchrotron-based approach that has allowed us to form 2D and 3D images of the carbon chemistry in a Carboniferous fossil trunk fragment and a 53-million-year-old ant trapped in amber. The 2D XRS imaging of the trunk reveals a homogeneous chemical composition with micrometric ‘pockets’ of preservation, likely inherited from its geological history. The 3D XRS imaging of the ant exoskeleton displays an exceptionally well-preserved remaining chemical signature typical of polysaccharides such as chitin around a largely hollowed-out inclusion. Although the achieved resolution is far from that of X-ray microtomography, we could distinguish two degrees of preservation within the exoskeleton, the surface of the ant that was likely first brought into contact with resin appearing better chemically preserved than the areas covered later after the ant’s death. These results open up new perspectives for *in situ* chemical imaging of fossilized organic materials, with the potential to enhance our understanding of organic specimens and their palaeobiology.

Moms: how to measure occupancy in multidimensional space (disparity)?

Thomas Guillaume¹, Mark Puttick², Ariel Marcy¹ and Vera Weisbecker¹

¹The University of Queensland, Australia

²University of Bath, UK

Multidimensional analyses of traits are now a common tool-kit in macroevolution. Such analyses are based on datasets that summarize all observed and potential trait combinations (*e.g.* a morphospace). Researchers will then study how organisms occupy that trait-space using space occupancy metrics (*i.e.* disparity metrics) to investigate, for example, how the morphospace is occupied through time. Although there are a few (well-defined) metrics that are used in palaeobiology, we lack a general description of the majority of those metrics. This makes biological interpretation of trait-space occupancy sometimes vague which has consequences when linking changes in disparity to biological phenomena. For example, does a reduction in volume in the trait-space correspond to episodes of extinction or changes in traits distribution? Here we propose a broad classification of these space occupancy metrics into three categories: metrics that capture changes in volume, density or position of the trait-space. We analyse the behaviour of those different metrics through the textbook example of the radiation of mammals after the K-Pg event 66 million years ago.



Furthermore, we propose *moms*, a tool with a user-friendly graphical interface that allows researchers to test which metric is the most appropriate to their biological question.

Early Palaeozoic diversifications and extinctions in the marine biosphere: onwards and upwards

David A. T. Harper¹, Borja Cascales-Miñana² and Thomas Servais²

¹*Durham University, UK*

²*CNRS UMR 8198, Université de Lille, France*

A long-term radiation of marine life occurred during the Early Palaeozoic, aggregated by a succession of more discrete and regionalized radiations, across geographies and within phylogenies. It includes the Cambrian ‘Explosion’ and the Great Ordovician Biodiversification ‘Event’. Modern marine ecosystems were established during a continuous chronology of the evolution of organisms and ecological communities, developed during the ‘Cambrian substrate revolution’, ‘Ordovician plankton revolution’, ‘Ordovician substrate revolution’, ‘Ordovician bioerosion revolution’ and the ‘Devonian nekton revolution’. At smaller scales, different regional but important radiations are recognized geographically and some have been identified and named (*e.g.* those associated with the ‘Richmondian Invasion’ during the Late Ordovician in Laurentia and the contemporaneous ‘Boda Event’ in parts of Europe and Gondwana). Datasets remain incomplete for many other geographical areas, but also for particular time intervals (*e.g.* during the late Cambrian ‘Furongian Gap’). Early Palaeozoic biodiversification was a long-term process, modulated by bursts of significant diversity and intervals of inadequate data; its progressive character will become increasingly clearer with more complete datasets, better global coverage, and more advanced analytical techniques.

Putting the AI into Palaeontology: using new methods of machine learning to capture evolutionary history

Jennifer Hoyal Cuthill^{1,2,3} and Nicholas Guttenberg²

¹*University of Essex, UK*

²*Tokyo Institute of Technology, Japan*

³*University of Cambridge, UK*

The ‘second wave’ of AI technology is upon us, bringing new methods such as deep learning capable of analysing very large and complex datasets. As custodians of the most extensive data on biological diversity, palaeontologists therefore have new opportunities to capture life’s evolutionary history. This talk will provide an overview of new machine learning methods with particular promise for evolutionary analysis, including demonstrations from a study of databased fossil occurrences across the Phanerozoic. Methods and applications to be discussed will include the following: 1) Use of neural networks to create spatial embeddings that capture and visualize variation among biological or palaeontological data. 2) The wide range of palaeontological data analysable using such methods, including photographs, 3D scans, signal spectra and databased information. 3) Use of deep learning to produce automated, objective morphological phylogenies, as validated by our recent study of extant butterflies for which independent genetic data are available for comparison. Application of such methods to capture the probability of Phanerozoic fossil co-occurrences quantifies and visualizes the temporal structure of the fossil record. This embeds notable



events such as mass extinctions and diversifications within a unified continuous space, revealing and ranking their impacts on macro-ecology and evolution.

Poor spatial sampling coverage obscures our understanding of the latitudinal biodiversity gradient in deep time

Lewis A. Jones¹, Christopher D. Dean², Philip D. Mannion³ and Peter A. Allison¹

¹*Imperial College London, UK*

²*University of Birmingham, UK*

³*University College London, UK*

The latitudinal biodiversity gradient (LBG), where species richness decreases from tropical to polar regions, is a pervasive pattern of the modern biosphere. Whilst fossil data suggest that this pattern varied through deep-time, the reconstruction of palaeobiogeographic patterns is hampered by geological and anthropogenic biases. Using both real world and simulated data, we show that observed deep-time LBG trends in the marine realm are severely impacted by the geographic coverage of sampled outcrop. Through applying three geographic sampling methods, we establish that approximately 30 % of global homogenous sampling coverage is necessary to reconstruct today's LBG for zooxanthellate corals; however, mean average sampling coverage for the last 250 million years equates to less than 1 %. We also simulate shallow marine occurrences over the last 250 million years according to three LBG types (modern, flat, bimodal), then sample these by the geographic distribution of respective collections in order to reconstruct observed and subsampled biodiversity patterns in comparison to known simulated data. These simulations suggest that global coverage is often too poor to recover latitudinal biodiversity patterns, even after applying subsampling approaches. This suggests previous studies may have failed to recover the 'true' LBG type due to spatiotemporal biases.

Constraining morphological disparity in rangeomorphs

Charlotte G. Kenchington¹, Frances S. Dunn^{2,3}, Alexander G. Liu¹ and Philip R. Wilby³

¹*University of Cambridge, UK*

²*Oxford University Museum of Natural History, UK*

³*British Geological Survey, UK*

Avalonian Ediacaran successions (Newfoundland, Canada and Charnwood Forest, UK; *c.* 575–560 Ma) host the oldest known communities of complex multicellular organisms, including some of the best candidate early animals. Rangeomorphs dominate these communities, and are the most geographically and environmentally widespread of the Ediacaran clades. Although the gross morphology of rangeomorph taxa is broadly similar, some species bear structures that are unique or distinct among these groups, such as external sheath-like structures, novel eccentric growth architecture and different modes of growth. Diversity and species richness are critical parameters in studies of modern and fossil ecology. However, where these measures are influenced by changing opinions on classification, morphological disparity is not. Here we present an analysis of the disparity of rangeomorph taxa, across 20 communities, using non-metric dimensional scaling and multivariate analysis. Our analyses are coded to include intraspecific variation, which has recently been recognized in rangeomorph taxa. Our disparity framework provides a tool to test how species with unique features fit within the rest of the known rangeomorph



taxa. Finally, quantifying morphological disparity in rangeomorphs allows their levels of disparity to be compared to that of extant groups, and provides a quantitative assessment of the biotic composition of different communities.

Evolution of trilobite development and global ecosystem changes

Lukáš Laibl

University of Lausanne, Switzerland

Trilobites show enormous variability in their development. Enough well-preserved early developmental stages have now been described to evaluate this variation. I generated a database of 178 trilobite species across most of the major groups, for which the development is well known. Results show that phylogenetically and stratigraphically basal trilobites show development with little morphological change occurring between individual stages (direct development). Indirect development evolved independently in numerous lineages during the Cambrian and Ordovician, via modification of the earliest stages and acceleration of development. Some lineages evolved extended indirect development that contains multiple pre-metamorphic stages. During the Ordovician, many lineages with ancestrally indirect development lost their pre-metamorphic stage and evolved secondary direct development. All Cambrian taxa with primary direct development were replaced by lineages with secondary direct development during the Lower Ordovician. The origin of indirect development was rapid and started during the Cambrian Explosion; however, the main diversifications of lineages with indirect and extended indirect development are concentrated in the Furongian and Lower Ordovician (coinciding with the 'Ordovician Plankton Revolution'). Groups with indirect development dominated Ordovician ecosystems, but many of them went extinct during the late Ordovician extinction. The evolutionary history of trilobite development can be linked to global ecosystem changes.

The Cambrian evolution of chelicerates

Rudy Lerosey-Aubril and Javier Ortega-Hernández

Harvard University, USA

Extant chelicerates, such as spiders, scorpions and mites, form a megadiverse (>110,000 species) class of euarthropods with a profound influence on modern terrestrial ecosystems and human activities. They are unique in possessing pincer-like or jackknife-like claws rather than antennae, which they use to hold, crush and/or kill prey. A Cambrian origin of the clade is widely accepted based on both molecular and palaeontological data. Conversely, the relationships with other Cambrian euarthropods and the morphological changes characterizing early chelicerate evolution remain unclear, due to the paucity and lack of congruence of the anatomical data yielded by Cambrian fossils. Here we describe a new chelicerate-bearing euarthropod from the middle Cambrian of Utah, USA, which provides unambiguous data on the anatomy of early chelicerates. The large species features massive three-segmented chelicerae, followed by five prosomal pairs of non-chelate biramous appendages with stenopodous exopods, and at least eight opisthosomal pairs of opercula-bearing densely-packed lamellae. Phylogenetic analyses resolve this species within stem-group Chelicerata, alongside other controversial groups such as megacheirans and habeliidans. Our results support a unified phylogenetic model and allow a detailed depiction of the evolutionary morphological changes leading to the origin of Chelicerata.



Overcoming the challenges of studying the earliest macrofossils: a case study from the middle Ediacaran (pre-Gaskiers) of Newfoundland

Alexander G. Liu and Benjamin H. Tindal

University of Cambridge, UK

The island of Newfoundland, Canada hosts globally significant assemblages of late Ediacaran macrofossils, including candidate early animals. To date, all such impressions have been found in rocks dated to <580 Ma in age, lying above glaciogenic diamictites of the Gaskiers Formation. Here, macrofossils are reported from siliciclastic strata beneath the Gaskiers-equivalent Trinity Facies of the Rocky Harbour Formation, on the Bonavista Peninsula. The largest of these specimens, preserved as surface impressions, can be assigned to the probable protistan-grade taxon *Orbisiana*. Small (1–2 mm) circular, linear and ovate impressions also occur alongside the *Orbisiana* specimens. These simple structures are almost certainly biogenic in origin but possess very few morphological characters. An interpretive framework is presented here for the description of such problematic impressions, which are globally widespread but barely reported, to enable their incorporation into our understanding of the late Neoproterozoic rise of complex life.

Phylogenetics of true crabs, and the early origins of crab-like forms

***Javier Luque¹, Heather D. Bracken-Grissom², Javier Ortega-Hernández³ and Joanna M. Wolfe³**

¹*Yale University, USA*

²*Florida International University, USA*

³*Harvard University, USA*

True crabs or Brachyura are among the most ecologically dominant and economically significant group of arthropods that have conquered marine, freshwater and terrestrial habitats worldwide. Yet, the origins and phylogenetic relationships among – and within – the main brachyuran groups remain unresolved. This is in part because few early splitting branches have left living descendants, molecular data are currently unavailable for many key extant taxa, and useful fossils are rare or incomplete. Also, there is presently a lack of well-supported phylogenetic frameworks that combine molecular and morphological data for all crab-like groups, and include reliable fossils for time calibrations. We examine hypotheses about the early evolution of true crabs in light of new molecular, morphological and fossil data, and present several new Early and mid-Cretaceous body forms that challenge conventional views of crab evolution. Although several lineages have Jurassic origins, it is during the Cretaceous that true crabs underwent an adaptive radiation and morphological experimentation that we deem the ‘Cretaceous Crab Revolution’. Disentangling the phylogenetic relationships across extinct and extant crab groups is central to understanding the origins of body forms and novelties linked with the evolution of crab-like forms (carcinization), and even the multiple losses of these forms (decarcinization), through time.



A finite element model on vibrations of Weberian ossicles of cypriniform fish using harmonic analysis

Jordi Marcé-Nogué and Juan Liu

University at Buffalo, The State University of New York, USA

Weberian apparatus of cypriniform fishes including zebrafish conduct sound vibrations through a suite of Weberian ossicles, which give them high sensitivity and great frequency range of hearing. To understand the patterns of biomechanical performance of these hearing specialists, we used zebrafish to model the vibrations of Weberian ossicles using finite element analysis (FEA). Also, we applied the same methods to other cypriniforms including cyprinids and suckers. First, we performed harmonic analyses (ANSYS 17.1) using 3D reconstructed (Amira 2019) Weberian ossicles of an adult Zebrafish that was scanned using micro-CT (4.67 $\mu\text{m}/\text{voxel}$). The harmonic responses predict the expected amplitude and phase of the vibrations in zebrafish. Also, it is evident Weberian apparatus acts as a spring-transmitter at audible frequencies, permitting a coupling of gas bladder motion to the sacculus. Furthermore, we performed the same analysis using Weberian ossicles of other cypriniform fishes which were segmented from CT images of the 'Scan All Fish' project. Preliminary results show various amplitude and phase of vibrations present in cypriniforms. We conclude that our methods using harmonic response of FEA can be used to compare biomechanical performance of Weberian apparatus, and thus estimate hearing capability in different living and fossil cypriniforms.

Ediacaran life close to land: coastal and shoreface environments of the Ediacara biota of South Australia

William McMahon¹, Alexander G. Liu² and Maarten Kleinans¹

¹*Utrecht University, Netherlands*

²*University of Cambridge, UK*

The observed taxonomic composition of fossil assemblages of the Ediacaran macrobiota has been shown to be strongly linked to sedimentary facies. Comprehension of these facies is therefore fundamental to our broader understanding of the environments and ecosystems in which early animals thrived and radiated. We present new details on the sedimentology of the world-renowned Ediacara Member of South Australia, which hosts some of the most diverse assemblages of Ediacaran macrofossils. The most widely followed environmental models for the Ediacara Member place fossiliferous deposits in: 1) shelf environments below maximum (storm-weather) wave base; and 2) offshore environments between effective (fair-weather) and maximum wave base. A regional sequence stratigraphic framework combined with new observations of Ediacara Member sedimentology suggest that water depth has been considerably overestimated by such models. The Ediacaran macrobiota in South Australia occupied a range of environments along coastlines and the marine shoreface complex almost entirely above effective wave-base. Fossiliferous deposits grade landward into a complex of fossil-barren foreshore, backshore and coastal plain settings (emphasizing that the Ediacara biota remain definitively marine). Revised estimates of Ediacara Member bathymetry permit re-evaluation of the palaeoecology and taphonomic history of its biota, and detailed comparison with other global localities.



Exploring the topological impact of palaeontological data in phylogenetic hypotheses

***Nicolas Mongiardino Koch and Luke A. Parry**

Yale University, USA

Fossils constitute the most direct evidence of evolution across deep time. Incorporating the information preserved in the fossil record is therefore crucial for understanding macroevolutionary dynamics. Even though the relevance of palaeontological data for comparative palaeobiology has long been recognized, its role in inferring the tree of life itself remains controversial. Different studies have either dismissed the impact of fossils due to their incompleteness, championed their ability to bridge morphological gaps, or concluded their behaviour is indistinguishable from that of extant taxa. We have developed a series of taxon exclusion experiments to quantify the topological impact of fossil and extant taxa in morphological phylogenies. Applying this approach to a set of large empirical matrices, we find that fossils generally modify topologies to a higher degree and in significantly different ways than increasing sampling among extant lineages. We further attempt to explain this unique effect of fossils by exploring the determinants of a taxon's topological impact. Our quantitative analysis reveals topological impact has strong predictors, with morphological distinctiveness, missing data and number of autapomorphies showing the strongest effects. Our analyses have implications for the design of morphological matrices, providing intuitive guidelines for sampling of potentially impactful fossil taxa.

Bone fusion and morphological change: an unexplored relationship in tetrapod macroevolution

Aitor Navarro Diaz¹, Diego Rasskin Gutman¹ and Borja Esteve Altava²

¹*University of Valencia, Spain*

²*Universitat Pompeu Fabra, Spain*

During the evolution of tetrapods, the skull has experienced a net reduction in the number of bones from around 60 in early tetrapods to about 30 or less in birds and mammals. This macroevolutionary trend has been known as Williston's Law for more than a hundred years; two morphogenetic mechanisms are involved: the progressive loss of ossification centres and the fusion of ancestral bones. Even though the fossil record has provided numerous evidences of this macroevolutionary trend in the skull, no major analysis of the morphological implications has been carried out to date. Since the tetrapod skull achieved a wide range of morphological diversity throughout evolution, we consider the possible role that bone fusion could have played in shaping its morphology. Here we survey the literature on tetrapod evolution, focusing on bone fusions that occurred in each macroevolutionary transition, then we analyse the possible role of these fusion events in the morphological novelties that characterize each group. We show some illustrative examples where bone fusions could be the trigger of morphological change, highlighting an evolutionary relationship unexplored until now.



Interpreting colour patterns in aquatic vertebrates: decay-induced changes to the distribution and morphology of melanosomes throughout pigmented tissues

***Christopher Nedza¹, Mark A. Purnell¹, Jakob Vinther² and Sarah E. Gabbott¹**

¹University of Leicester, UK

²University of Bristol, UK

Melanin-based colour patterning serves several biological functions in aquatic vertebrates, such as camouflage, intra-species communication and display. Both melanin and melanosomes – pigment-producing organelles – preserve over geologic timescales, allowing palaeontologists to infer key developmental and ecological innovations in fossil taxa. However, how decay influences the shape and distribution of melanosomes prior to diagenesis is still equivocal. Here we test the hypothesis that the *in vivo* distribution and shape of melanosomes does not change with decay. Our analysis, based on several species of lamprey and teleost fish, allows us to determine whether patterns of pigmentation in fossils faithfully represent those of the living animal. We used taphonomic experiments coupled with morphometric analyses to track the changes in melanosome geometry and distribution during decay. Our results show that melanosomes from different tissues retain their morphology throughout decay, with the exception of eye melanosomes. Furthermore, we found that decay was responsible for reducing the definition of skin patterning in all species of fish, whilst also creating new, distinct patterns that were not originally present. This demonstrates that taphonomic processes affect the distribution of melanosomes within integument but not the fidelity of their morphology, crucial for the correct anatomical and ecological interpretations of fossils.

Molecular developmental genetics, homology and ancestral organisms: what about fossils and morphology?

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

University of Bristol, UK

Reconstructing ancient organisms has traditionally been a task for comparative morphologists, embryologists and palaeontologists. In the past few decades, a flurry of new molecular genetic approaches to understanding development have attracted a great deal of attention, often proposing revisions to generally accepted reconstructions of ancient organisms (e.g. Urbilateria, Ureumetazoa). Here we review some recent cases of conflict between morphological and developmental genetic approaches, elucidate the conceptual assumptions of such approaches, and argue that comparative morphology of extant and extinct organisms takes priority over molecular evidence due to the irreducibility of morphological traits to the molecular mechanisms underpinning them. Moreover, since this task of reconstruction consists of discerning homology from homoplasy – which is never straightforward using only evidence from extant taxa – we stress the further importance of palaeontological evidence due to its more direct connection with the ancient organisms in question. The resulting conceptual focus on morphological evidence, especially from fossils (when available), has implications for choice of research questions as well as epistemological and methodological approaches pertaining to the reconstruction of ancient life.



The forgotten latest Cambrian nautiloid cephalopods from Black Mountain (NW Queensland, Australia)

Alexander Pohle¹, Peter A. Jell², Yong-Yi Zhen³ and Christian Klug¹

¹University of Zurich, Switzerland

²The University of Queensland, Australia

³Geological Survey of New South Wales, Australia

Fossil remains of unequivocal Cambrian cephalopods are rather scarce with only North China yielding diverse assemblages. Additional sparse material is known from North America, possibly also Kazakhstan and Siberia. Here we present material from three distinct horizons in the latest Cambrian Mictosaukia zone of the Ninmaroo Formation at Black Mountain, north-west Queensland, Australia. These faunas, represented by several hundred specimens now in the Queensland Museum, were collected during the 1970s and 1980s by Mary Wade. Despite considerable preliminary work, Mary didn't manage systematic descriptions of these faunas before her death in 2005. Although she briefly mentioned the material in publications and in extensive correspondence between her and contemporaneous nautiloid experts, the modern literature appears to have ignored the occurrence of nautiloids in the Cambrian of Australia. This is especially striking as the Australian specimens are available in large numbers and are preserved as silicified internal moulds, thus providing a better understanding of three-dimensional morphology than the Chinese specimens, which are mostly known from thin sections. Additionally, these faunas fill an important gap in the fossil record of cephalopods, *i.e.* the supposed 'late Trempealeauan Eclipse', a time interval which was thought to be almost entirely devoid of cephalopods globally.

The phylogenetic history of the armoured dinosaurs (Ornithischia, Thyreophora)

***Thomas J. Raven^{1,2}, Paul M. Barrett¹ and Susannah C.R. Maidment¹**

¹Natural History Museum, London, UK

²University of Brighton, UK

The armoured dinosaurs (Ornithischia, Thyreophora) have been known since the early 1800s and include some of the most recognizable dinosaurs such as *Stegosaurus* and *Ankylosaurus*. The individual lineages, Ankylosauria and Stegosauria, have been studied thoroughly but there has never been a comprehensive whole-group cladistic analysis of Thyreophora. This has obscured character-state transformations at the base of the lineages, making the identification of basal taxa and clades problematic, and the degree of convergence difficult to assess. Here the first species-level phylogeny of Thyreophora is presented, including all valid species within Thyreophora, with 93 taxa and 327 characters. Analyses were performed under parsimony, and reductive and non-reductive coding techniques were compared. *Kunbarrasaurus* was found at the base of Nodosauridae and *Alcovasaurus* was found within Stegosauria for the first time. Evidence for a 'polacanthine' grouping was also found, with *Polacanthus*, *Hoplitosaurus*, *Mymoorapelta*, *Taobelong* and *Dongyangopelta* within the Nodosauridae, although symmetric resampling showed this to have weak support. Reductive character coding produced a lower resolution strict consensus tree than non-reductive coding, but with a lower tree length, suggesting less homoplasy. The phylogeny will become the framework for macroevolutionary studies of Thyreophora that will examine the mode and tempo of evolution of the group.



Biogenic iron liberated during decay initializes highly detailed soft tissue pyritization in Burgess Shale-type biotas

***Farid Saleh**¹, **Allison C. Daley**², **Bertrand Lefebvre**¹, **Bernard Pittet**¹ and **Jean Philippe Perrillat**¹

¹*Université Claude Bernard Lyon 1, France*

²*University of Lausanne, Switzerland*

During the last decade, experimental taphonomists have explained enigmatic structures in fossils from Burgess Shale-type biotas (BSTs) based on patterns of animal decay in laboratory aquariums. For instance, the fast decay of some features such as nervous systems contrasts with their discovery in Palaeozoic BST fossils. Given that many of the enigmatic structures are pyritized, or consist of an association of both pyrite and organic matter, we explored pyrite and organic matter distributions using Raman spectroscopy in unweathered sediments with soft-tissue BST preservation. Our investigations suggest that a highly reactive biogenic iron source may have played a role in initiating pyritization, as soon as decay started, independently from abiotic iron in the sediment. The model we propose suggests that little morphological information is lost from iron-rich tissues even if these structures are the most prone to decay. Based on chemical signatures of biological tissues, we hypothesize that extensive decay may lead, counterintuitively, to exquisite morphological preservation in some BSTs. It also resolves the apparent discordance between experimental taphonomy and descriptive palaeontology on the affinities of pyritized features in fossils from Burgess Shale-type biotas.

Untangling the fossil record of Rhinocerotidae

Oscar Sanisidro Morant^{1,2} and **Juan L. Cantalapiedra**^{1,3}

¹*Universidad de Alcalá, Spain*

²*University of Kansas, USA*

³*Museum für Naturkunde, Berlin, Germany*

Extant rhinoceros species represent but a vestige of the great diversity that the Family Rhinocerotidae attained during the Cenozoic. Recent taxonomic reviews permit an updated compilation of the first and last appearance data in order to estimate net diversity and turnover rates. Our results show several taxonomic replacements along seven main faunal turnovers have been described in detail, showing an episodic pattern of strong turnover pulses. Overall net diversity rates in Rhinocerotidae differ from continental results thus outlining different ecological and regional scenarios.



Disentangling taphonomic and ecological signals in fossil food webs

***Jack Shaw**¹, **Kate Wootton**², **Emily Coco**³, **Dries Daems**⁴, **Andrew Gillreath-Brown**⁵ and **Anshuman Swain**⁶

¹*Yale University, USA*

²*Swedish University of Agricultural Sciences, Sweden*

³*New York University, USA*

⁴*University of Leuven, Belgium*

⁵*Washington State University, USA*

⁶*University of Maryland, USA*

Ecological communities are complex systems, often composed of thousands of interacting species. Network analyses of those interactions have unlocked critical features of community structure, stability, and responses to perturbations (e.g. climate change). Similarly, studies of ancient interaction networks, as evidenced by fossils, reveal palaeoecological processes through Earth history. However, many of these analyses do not account for key differences between modern and ancient interaction data including the selective loss of pelagic and soft-bodied taxa during fossilization. We applied an information loss pipeline, modelled on fossilization processes, to modern trophic networks. A comparison of the structure of such 'artificially fossilized' networks to ancient trophic networks preserved in fossil deposits showed that the effects of artificial fossilization on network structure were highly dependent on initial structure and the characters of taxa within the network. Additionally, the removal of soft-bodied taxa impacts network structure more than the removal of pelagic taxa. Some metrics, such as trophic position and omnivory index, displayed unique responses to selective information loss whereas others, including connectance and degree, were indistinguishable from random loss. It is clear that specific taphonomic biases must be factored into analyses of the ecological structure of ancient food webs based on fossil evidence.

Unique locomotor habits in Early Palaeogene mammals provides ecomorphological insight into evolution after the end-Cretaceous mass extinction

Sarah L. Shelley¹, **Stephen L. Brusatte**² and **Thomas E. Williamson**³

¹*Carnegie Museum of Natural History, USA*

²*University of Edinburgh, UK*

³*New Mexico Museum of Natural History and Science, USA*

Mammals exhibit vast ecological diversity, including a panoply of locomotor behaviours. The foundations of this diversity were established in the Mesozoic, but it was not until after the end-Cretaceous mass extinction and the demise of the non-avian dinosaurs that mammals began to increase in body size, diversify into many new species and establish extant lineages. Comparatively little is known, however, about the palaeobiology of the Palaeogene mammals that diversified immediately after the extinction, which are often perceived as 'archaic' precursors to extant lineages. Using multivariate analyses, we show that tarsal measurements can infer locomotor mode in extant mammals, and demonstrate that Palaeogene mammals occupy a statistically distinctive region of locomotor morphospace relative to Cretaceous and extant species distinguished by their robust morphologies. Disparity analyses indicate that Palaeogene mammals attained comparable morphospace diversity as extant forms, supporting the hypothesis that mammals underwent a post-extinction adaptive radiation in locomotor behaviour. Palaeogene mammals,



therefore, should not be stereotyped as antiquated and generalized animals. Instead, they were products of a post-extinction radiation that combined a basic placental bauplan with inimitable anatomical and locomotor specializations, superlatively exemplifying their evolution in the global hot-house environments of the Palaeogene.

New insights into the vital effect during brachiopod shell formation and its relevance to the geochemical record

***María del Mar Simonet Roda**¹, **Andreas Ziegler**², **Erika Griesshaber**¹, **Daniela Henkel**³, **Vreni Häusermann**⁴, **Anton Eisenhauer**³ and **Wolfgang W. Schmahl**¹

¹Ludwig-Maximilians University of Munich, Germany

²University of Ulm, Germany

³GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany

⁴Huinay Scientific Field Station, Chile

The investigation of Thecideidine shell morphology and structure has been the subject of research for several decades and has revealed the distinctiveness of this group of brachiopods relative to species of other extinct and modern brachiopod genera. Shell microstructure and texture in modern brachiopod orders show that Thecideide brachiopod shells do not have an obvious mineral unit organization compared to that of modern rhynchonellide and terebratulide. In this study we trace the formation and evolution of thecideide shell microstructure and texture from their first appearance in the Late Triassic to modern times. We used two modern representatives (*Pajaudina atlantica* and *Kakanuiella chathamensis*) as control. They present a heterogranular microstructure consisting of highly irregularly-shaped mineral units with calcite being assembled with a low degree of co-orientation. We investigate with different techniques, such as EBSD and AFM, the relationship between fibrous, granular and acicular fabrics, thus, the progressive disappearance of fibres and the emergence of granules. We imaged and measured the shell microstructure and texture of selected taxa, differentiating the crystal morphologies within the individual microstructures and following their abundance through time. We observed major changes between the Jurassic and the Cretaceous.

The Ediacaran–Cambrian transition: the emerging record from small carbonaceous fossils (SCFs)

Ben J. Slater¹, **Thomas H. P. Harvey**², **Romain Guilbaud**³, **Sebastian Willman**¹, **Graham E. Budd**¹ and **Nicholas J. Butterfield**⁴

¹Uppsala University, Sweden

²University of Leicester, UK

³CNRS Géosciences Environnement Toulouse, France

⁴University of Cambridge, UK

The most striking signal in the fossil record is the rapid rise in diversity of metazoan-derived skeletal parts in early Cambrian strata. Along with the expansion of trace fossil diversity at this time, such shelly fossils form the most obvious expression of the Cambrian radiation. Rare Konservat-Lagerstätten, however, reveal that fossils of skeletonized taxa represent only a small proportion of total diversity, which largely comprised unmineralized forms. An alternate, but largely overlooked source of data on unmineralized taxa comes



from the emerging record of small carbonaceous fossils (SCFs). SCFs encompass a polyphyletic variety of fragmentary cuticular remains sourced from animals, algae and protists, and are beginning to reveal new aspects of Cambrian diversity from regions and time-windows devoid of Burgess Shale-type Lagerstätten. A new accounting of SCF records from Ediacaran–Cambrian successions on Baltica, Laurentia and elsewhere, reveals a clear temporal trend: early Cambrian (Stage 3–4) SCF assemblages are typically rich in metazoan diversity, including iconic taxa well known from Burgess Shale-type biotas elsewhere. Older, Terreneuvian assemblages are characteristically low in metazoan diversity and exhibit greater regional homogeneity. Despite an entirely different taphonomic pathway, this emerging signal broadly mirrors that recognized for the classical Cambrian radiation of ‘shelly’ fossils.

New insights into early terrestrial environments using high resolution 3D imaging and chemical techniques

Christine Strullu-Derrien^{1,2}, Alan R. T. Spencer^{1,3} and Paul Kenrick¹

¹Natural History Museum, London, UK

²Muséum national d’Histoire naturelle, Paris, France

³Imperial College London, UK

We employ a variety of high-resolution imaging and analytical techniques to investigate the biodiversity of early terrestrial environments in 407-million-year-old deposits from Scotland and France. Microbial elements preserved in historic thin sections of Rhynie chert (Scotland) were imaged using confocal laser scanning microscopy. The method has enabled the characterization of the earliest terrestrial fossil evidence of arcellinid amoebozoans, supporting the hypothesis that arcellinids colonized the land contemporaneously with plants. We are also documenting new species of Chlorophyta (green algae) that appear to be highly adapted to the special ecological conditions encountered in the Rhynie chert geothermal wetland. Advances in *in situ* geochemistry at high spatial resolution also complement our morphological research. We used propagation phase contrast synchrotron microtomography, and synchrotron-based scanning transmission X-ray microscopy coupled with X-ray absorption near edge structure (XANES) spectroscopy to document the structure and chemistry of the tracheids in the earliest woody plant from the Armorican Massif (France). This study characterized the structure of the vascular elements. Chemical analyses showed that although the fossils had undergone thermal maturation the chemical signal of lignin was not completely lost.

Evolutionary simulations demonstrate punctuated equilibrium

Mark D. Sutton¹, Nicole L. Barnes¹ and Russell J. Garwood^{2,3}

¹Imperial College London, UK

²The University of Manchester, UK

³Natural History Museum, London, UK

Punctuated Equilibrium (PE) holds that species initially evolve rapidly, then enter stasis. It remains controversial. We investigate PE using a computational model (REvoSim) in which organisms possess genomes comprising coding and non-coding sections, and adapt to environments of image sequences. We report genomic changes, tracked over the lifespans of simulated species in various environments and differing rates of environmental



change. PE patterns dominate in most scenarios and in both genomic sections; we discount potential artefacts. The preponderance of PE is not correlated with rates of environmental change. Punctuations result from initial adaptations in the coding genome, and non-coding variation ‘hitching’ on this selection through linkage disequilibrium. Genomic stasis, in both genomic sections, reflects stabilising selection: mutations reduce breeding likelihood. Coding-genome stasis is more prevalent in complex environments, so is additionally influenced by spatial effects (species track environments by moving rather than evolving). A reduction in non-coding genomic distance (from the initial genome) after the initial ‘punctuation’ arises from speciation events that preferentially excise faster-evolving sub-populations. We demonstrate, for the first time, that PE arises from simple simulations of spatially distributed populations; it is hence biologically plausible.

Juvenile skeletogenesis and implications for body plan evolution in echinoids

Jeffrey Thompson and Paola Oliveri

University College London, UK

In the history of life, some animal groups evolved numerous weird and wonderful body plans, while others have displayed marked morphological constraint for hundreds of millions of years. This is epitomized in the evolutionary histories of regular and irregular echinoids. The earliest regular echinoids in the fossil record look nearly identical to extant representatives living in the ocean today and many have exhibited marked constraint throughout their evolutionary history. Irregular echinoids, however, have undergone a massive morphological diversification. The differential morphological diversity of regular and irregular sea urchins has been attributed to differential strategies of skeletal growth, with regular echinoids growing primarily through (metameric) plate addition and irregular echinoids relying on remodelling and accretion onto pre-existing plates. The molecular and genetic underpinning of growth in post-metamorphic sea urchins, however, is far from well-understood. We surveyed the expression of a number of skeletogenic genes in the growth of the juvenile regular echinoid *Paracentrotus lividus*. EdU and calcein were used to determine sites of cell proliferation and biomineral deposition. The expression of these genes sheds light on the cellular and molecular mechanisms underlying post-metamorphic skeletogenesis in sea urchins, and will direct future research into differences in skeletogenesis between regular and irregular echinoids.

Will marine animals become smaller with continued global warming? Deep time tests of the ‘shrinking seafood’ hypothesis

Richard J. Twitchett

Natural History Museum, London, UK

One key prediction of current climate change is that during this century marine animals will become much smaller in size, with important consequences for food resources, ecosystem function and ocean productivity at local, regional and global scales. Environmental effects that are expected to cause a shrinking response are higher seawater temperatures and reduced levels of dissolved oxygen in the world’s oceans. Opportunities for directly testing this prediction in most extant marine animals are limited as the spatial and temporal scales are too large for direct experimentation. Fortunately, the present warming episode is not the first to have impacted marine ecosystems and body size is a key trait that is conserved during the fossilization process. The fossil records of past global change events therefore



provide an archive of data that can be used to test this hypothesis in taxa that cannot be directly studied *in vivo*; in natural ecosystems; and over longer, multi-generational, timescales. This study analysed the fossils of a range of marine animals, through several major episodes of past climate change, both warming and cooling. Resultant trends in body size consistently support the shrinking seafood hypothesis in most groups. Exceptions to the general trends are analysed and discussed.

A novel Bayesian phylodynamic approach to estimating diversity from the fossil record

Rachel C. M. Warnock, Marc Manceau, Timothy G. Vaughan and Tanja Stadler

ETH Zürich, Switzerland

Estimating the number of individuals or species through time allows us to test hypotheses at micro and macroevolutionary timescales. To date, approaches to estimating diversity or species richness have not incorporated explicit information about the underlying diversification and sampling processes. Here, we present a novel Bayesian phylodynamic framework that allows us to recover estimates of diversity through time in a statistically coherent way, with or without knowledge of the underlying tree. At the core of this approach are birth–death process models that provide the flexibility to infer diversity at different scales and under a wide range of scenarios. Within a Bayesian framework, we can incorporate multiple sources of palaeontological evidence and uncertainty, enabling us to take advantage of the maximum possible empirical evidence. We show using simulations that our approach leads to reliable estimates of diversity under a range of conditions, in comparison to alternative methods. We present an empirical case study and highlight the advantages of using a phylodynamic framework. This model-based approach creates the potential to take into account explicitly key features of the fossil record, including sampling biases and biogeographic structure, when inferring diversity.

The nature, evolution and ecology of nonavian and avian egg colour

Jasmina Wiemann

Yale University, USA

Birds are the only living amniotes with coloured eggs. However, both the nature of egg colour and its evolution are unknown. To trace egg colour evolution we designed a novel Raman microspectroscopy protocol for *in situ* detection of isolated and bound pigments in eggshell. Our analysis of fossil eggs representing the major clades of dinosaurs (= avian stem) reveals a single evolutionary origin of egg colour in eumaniraptorans, coinciding with the evolution of open nesting habits. Pigment surface maps show that nonavian eumaniraptoran eggs were speckled, a trait correlating with complex nesting behaviours. Eggshell pigment depth profiles demonstrate an identical mechanism of pigment deposition in nonavian and avian dinosaur eggs. Absence of colour in ornithischian and sauropod eggs represents a true signal rather than a taphonomic artefact. To test these findings, we conducted a survey of egg colours of extant avians ($n=180$) and performed an ancestral state reconstruction. The ancestral avian egg was coloured and patterned, confirming egg colour as an inherited trait. Egg colour has been lost several times within Aves along with the adoption of hidden nesting sites, suggesting that egg colouration may play a role as a visual stimulus in birds.



Breathing new life into the earliest soft-bodied animals: computed tomography of early Cambrian fossils from South China

Joanna M. Wolfe¹, Javier Ortega-Hernández¹, Dayou Zhai² and Yu Liu²

¹Harvard University, USA

²Yunnan University, China

The Early Cambrian Chengjiang biota of Yunnan, South China has revolutionized our understanding of the Cambrian explosion, as these deposits yield some of the earliest fossil evidence of exceptionally-preserved metazoan soft tissues. The majority of research on Chengjiang fossils, while revealing impressive structures such as the nervous and digestive systems of euarthropods, has employed traditional imaging techniques. Recently, our group has used micro-computed tomography (micro-CT) scanning to uncover unique, phylogenetically critical insights into the ventral morphology of several euarthropod taxa. These discoveries include differentiated tritocerebral antenna and trunk appendage epipodites, which together illuminate the early Cambrian stem group of pancrustaceans (and its concordance with molecular clock and developmental data); and exquisitely-preserved, biramous appendages that challenge the traditional view that arthropods lacked limb differentiation. The application of micro-CT to the study of Chengjiang fossils holds exceptional promise for reconstructing their morphological diversity, phylogenetic relationships and evolutionary history.

To the bitter end: do planktonic foraminifera actively change their niche habit prior to extinction?

***Adam D. Woodhouse¹, Sophie Jackson¹, Philip F. Sexton², Paul N. Pearson³, Stewart Knott⁴, Alexander M. Dunhill¹, Paul B. Wignall¹ and Tracy Aze¹**

¹University of Leeds, UK

²The Open University, UK

³Cardiff University, UK

⁴University of Bristol, UK

The extraordinary completeness of the planktonic foraminiferal fossil record permits a unique opportunity for assessing the ecological traits associated with extinction risk at high-resolution in continuous ocean sediments. Planktonic foraminiferal geochemistry, morphometry and biogeography can be utilized to determine changes in niche habit as potential indicators of looming-extinction. This study focuses on the planktonic foraminiferal species *Dentoglobigerina altispira*, which exhibits extinction at ~ 3.032 Ma within the palaeotropics. We present isotopically-tuned core data representing the interval covering not only the extinction horizon of *D. altispira*, but also the entirety of the mid-Pliocene warm period (mPWP). Through paired morphometric and geochemical analyses of *D. altispira* alongside select extant species with known bathymetric affinities, we interpreted the vertical profile of the water column to identify potential niche habit modification of *D. altispira* as it approaches extinction. Through the addition of a global series of isotopically-tuned ocean cores recording the extinction, we were able to document a stepwise longitudinal biogeographic range shift and hypothesize the external parameters that led to its demise. The mPWP exhibits global temperatures analogous to those expected by 2100 through anthropogenically-induced climate forcing, therefore the behaviour exhibited by *D. altispira* may shed light on marine extinction in future warmer worlds.



Abstracts of poster presentations

* indicates a poster eligible for the Council Poster Prize.

Underlined author denotes designated presenter.

Ecological responses to climate warming: shifts in diet of an archaic hoofed mammal are coincident with Paleocene hyperthermal dwarfing

***Neil F. Adams¹**, **Mark A. Purnell¹**, **Stephen L. Brusatte²**, **Thomas Williamson³** and **Ross Secord⁴**

¹University of Leicester, UK

²University of Edinburgh, UK

³New Mexico Museum of Natural History and Science, USA

⁴University of Nebraska–Lincoln, USA

Across the animal kingdom, and particularly among vertebrates, climate warming has been found to correlate with reductions in body size (or dwarfing). Observations of many extant animals suggest dwarfing is happening in response to anthropogenic climate change, but its drivers are often poorly constrained. Of the numerous possible causes of dwarfing, reduction in food quality and dietary change are frequently invoked. To test the hypothesis that dietary changes are coincident with dwarfing and rapid climate warming, we apply dental microwear texture analysis to the phenacodontid condylarth *Tetraclaenodon puercensis* (an early hoofed mammal or ‘archaic ungulate’) from the San Juan Basin, New Mexico, USA. Available data indicate that this taxon exhibited a dwarfing response to an early Paleocene hyperthermal event (the ‘Latest Danian Event’, LDE; ~62.2 Ma). Our analysis suggests dietary changes were coincident with the LDE. Microwear textures indicate a shift away from diets dominated by hard objects in response to floral community change, which likely occurred during the LDE, as demonstrated during other Palaeogene hyperthermals. Our results indicate that rather than resulting from simple biogeographic range shifts, hyperthermal dwarfing may involve complex ecological and dietary changes that can be linked to selective advantages favouring smaller body size.

Tackling ‘cryptogenesis’ from the bottom up: new data on the synapomorphies and higher phylogenetic structure of the trilobite orders Aulacopleurida and Olenida and the suborder Cheirurina

Jonathan M. Adrain

University of Iowa, USA

‘Cryptogenesis’ refers to the uncertain origin of major groups of post-Cambrian trilobites. Despite recent work on the phylogeny of Cambrian trilobites, the affinities of the great post-Cambrian groups remain as obscure as when Sir James Stubblefield coined the term in 1959. One approach to the problem is the development of new field data, particularly of trilobites preserved by silica replacement. Such faunas provide a wealth of information not normally available, especially on developmental morphologies. Recent discoveries reveal compelling and broadly conserved synapomorphies of order-level groups as well as clarifying higher level phylogeny. The Order Aulacopleurida is characterized by distinctive larvae and also by a broadly shared pattern of thoracic axial spines and tubercles, with more derived groups showing fixed modifications of the basic pattern. Early Ordovician taxa are resolved as several well supported family-level groups. The Order Olenida is



characterized by a distinctive larval type and a complex articulation of the inner edge of the cephalic doublure with the cranidium. Within Cheirurina, Encrinuridae is shown to lie within the phylogenetic structure of Pliomeridae. Together, the families form a clade sister to Cheiruridae, and the basal synapomorphies of either group are clarified.

Holocene fish death assemblages as a pre-industrial baseline for the Eastern Mediterranean

Konstantina Agiadi¹, Jonathan Belmaker² and Paolo G. Albano³

¹*National and Kapodistrian University of Athens, Greece*

²*Tel Aviv University, Israel*

³*University of Vienna, Austria*

The Eastern Mediterranean marine ecosystem (EMME) is undergoing massive modifications due to the invasion of non-indigenous species, overfishing, habitat deterioration and climate warming. Our ability to quantify these changes is severely hindered by the lack of an appropriate baseline. Here we compare living fish assemblages (1990–2012 trawl surveys) to Holocene (dated as far back as ~5,000 years BP) and fossil (Zanclean of Peloponnesus and the Gelasian of Rhodes, Greece) otolith assemblages to assess taxonomic and functional composition shifts. Our comparison between the death assemblages and the living assemblages confirms the occurrence of a massive shift in the composition and structure of fish assemblages that is due to the invasion of non-indigenous species in the Mediterranean. However, the death assemblages, rather than the living assemblages, present greater similarity to the fossil assemblages, suggesting that the ongoing changes in the EMME are unprecedented. Overall, the EMME today is characterized by a transformation of the marine fish fauna, which has not been seen since the early Miocene, when the Proto-Mediterranean was still connected to both the Atlantic and the Indo-Pacific Oceans. In this framework, the Holocene death assemblage provides a good baseline for assessing the rate and mechanisms of change.

Acritarchs from the Lower Ordovician of the Tazekka massif, eastern Morocco

Mustapha Akodad¹, Houcine Benachour^{2,3,4}, Imad El Kati⁵, Hicham El Messbahi⁵ and Thomas Servais²

¹*Université Mohamed Premier Oujda, Morocco*

²*CNRS UMR 8198, Université de Lille, France*

³*Université de Tlemcen, Algeria*

⁴*Université de Chlef, Algeria*

⁵*Université Sidi Mohamed Ben Abdellah, Morocco*

The Moroccan Ordovician played a major role in early acritarch research, with the establishment of numerous acritarch taxa first described during the 1960s and 1970s and subsequently widely recorded from many other localities around the world, such as *Barakella*, *Ericanthea*, *Marrocanium*, *Rugulidinium* (= *Striatotheca*), and others. After the original monographical works in the 1970s, many of the subsequent studies were only short reports and detailed investigations from the Ordovician of central and eastern Morocco have not been produced in the last three decades. Here we present the first results of new investigations from the Tazekka Massif, located in the western part of the eastern Meseta. Our new investigations concern the 'schistes de Tazekka' at the base of the



succession (lower part of the Bou Chfâa Formation). The acritarch assemblage recorded is typical of the peri-Gondwanan margin, including the palaeobiogeographical index taxa *Coryphidium* and *Striatotheca*. The investigated assemblage displays mostly taxa such as *Polygonium* and *Baltisphaeridium*, but also more age-diagnostic genera, such as *Barakella* and *Arkonina*, pointing to a Floian age of the base of the succession, below the levels with 'Llanvirn' graptolites in the upper part of the Bou Chfâa Formation.

Morphological disparity of the early ammonoids from Morocco: shell geometry and suture line shape evolution through the Lower and Middle Devonian

***Ninon Allaire^{1,2}, Samuel Ginot¹, Nicolas Goudehand¹ and Claude Monnet²**

¹Institut de Génomique Fonctionnelle de Lyon, France

²CNRS UMR 8198, Université de Lille, France

The Devonian ammonoids are particularly abundant and well preserved in the Anti-Atlas of Morocco. These rich faunas are well documented in the literature, and can provide an interesting record of the morphological disparity changes that characterize the macroevolution of the early Ammonoidea during the Devonian period. The present study aims to investigate the morphological evolution of the ammonoids from their origination in the early Emsian (Lower Devonian) to the end of the Givetian (Middle Devonian). Based on specimens from Morocco illustrated in the literature, we compile two exhaustive datasets, to respectively investigate the shell morphometry and the suture line shape. The shell geometry is here studied considering classical conch ratios based on standard linear measurements of the shells. Advances in geometric morphometrics provide a possible detailed quantification of two-dimensional shape diversity, thus we investigate the suture line shape using a geometric morphometrics approach based on the acquisition of semi-landmark coordinates. The analyses are performed at the species level and considering the ammonoid biozonation as temporal scale. Disparity indices (*e.g.* sum of ranges and variances) are used to quantify accurately the morphological disparity changes through time.

Cretaceous outcrops of fossiliferous amber from the Maestrazgo Basin (eastern Iberian Peninsula): state of the art and research perspectives

Sergio Álvarez-Parra¹, Enrique Peñalver² and Xavier Delclòs¹

¹Universitat de Barcelona, Spain

²IGME, Instituto Geológico y Minero de España, Spain

Cretaceous amber-bearing outcrops are abundant on the Iberian Peninsula and are located mainly in the Basco-Cantabrian Basin and the Maestrazgo Basin. Bioinclusions have been found in amber deposits mostly dated as Albian and occurring in the Escucha Formation. Around 25 Cretaceous amber localities are known in the Maestrazgo Basin, although only four of them have yielded bioinclusions to date: San Just, Arroyo de la Pascueta and Ariño in Teruel Province, and La Hoya in Castellón Province. San Just is the most studied locality in the basin and has provided a rich fossil collection of 14 arthropod orders, including new taxa. The collections from the other three sites are scarce and are still awaiting detailed study. Arroyo de la Pascueta is type locality of an evaniid wasp. The main palaeontological research perspectives are to increase the number of bioinclusions of these amber localities and to study their faunal contents, focusing on the insect orders Hymenoptera and Psocoptera. The recently discovered Ariño amber is very important



because it is older than the other three and is associated with dinosaur and other vertebrate bones. Ariño is especially notable from a taphonomic point of view, related to the origin of its amber concentration

Reassessing the Ediacaran–Cambrian boundary in the Iberian Peninsula

J. Javier Alvaro¹, Sören Jensen², Teodoro Palacios² and Pablo Valverde³

¹*Instituto de Geociencias (CSIC-UCM), Spain*

²*Universidad de Extremadura, Spain*

³*Instituto Geológico y Minero, Tres Cantos, Spain*

In Iberia the base of the Cambrian has been traditionally placed at the first occurrence of *Monomorphichnus lineatus* and *Treptichnus pedum* in the siliciclastic-dominated Pusa Formation. Independent age controls at this level are, however, poor and the Ediacaran–Cambrian boundary may be better constrained in the underlying Ibor Group. A multidisciplinary revision (including litho- and biostratigraphic studies and U-Pb laser ablation ICP-MS zircon dating) of the Villarta Formation (Ibor Group) has yielded a new scenario. The lower Villarta member exhibits numerous *Cloudina*-microbial reef complexes rich in *Cloudina* and *Simotubulites*. The middle member, dominated by sandstones and conglomerates, includes a tuffitic interbed dated at *c.* 537 Ma. This suggests a very latest Ediacaran age for *Cloudina* in the Villarta Formation. The upper member consists of alternating shale/shale couplets grading laterally into bedded carbonates, which include ichnofossils of Cambrian affinity. The first indisputable occurrence of *T. pedum* is placed a few metres above the Villarta carbonates, where a drowning surface is capped by the shale-dominated Arrocampo Formation (Ibor Group). The delayed occurrence of *T. pedum* may be related to significant facies and environmental controls on a Cadomian retro-arc basin reflecting a mosaic of differentially subsiding, fault-bounded crustal blocks.

Swimming in a closing ocean: Actinopterygii from the Cretaceous–Palaeogene of Pindos Unit, Eurytania, Greece

Thodoris Argyriou¹ and Donald Davesne²

¹*Muséum national d'Histoire naturelle, Paris, France*

²*University of Oxford, UK*

The K-Pg extinction event had a profound impact on marine actinopterygians, causing faunal restructuring and extinctions/diversifications on a global scale. These events are documented by both taxonomic and phylogenetic surveys, yet their mechanisms and timing remain conjectural, due to the scarcity of latest Cretaceous–Paleocene fossils. Pindos Unit exposures in Eurytania host continuous pelagic sedimentary successions deposited near the Gondwanan margin of the Tethys, and spanning the K-Pg boundary. Fish fossils from both sides of the boundary were discovered in the 1960s but have never been studied systematically. Extensive prospecting in the area led to the discovery of three late Maastrichtian fossiliferous localities and one Palaeogene locality. Late Maastrichtian actinopterygians come from thinly-bedded marly limestones, also containing ammonites and plants (Aceraceae). Aulopiformes, represented by at least three genera, are dominant. Additional taxa, including a possible elopomorph, are rare and poorly preserved. Palaeogene actinopterygians derive from dark clayey sediments of the Pindos flysch, and include a small clupeiform, and an enigmatic predatory teleost jaw. These localities/ occurrences constitute invaluable new additions to the poor record of K-Pg actinopterygians



at a global scale. Continued collection and research in these localities will offer important insights into the impact of the K-Pg extinction in pelagic ecosystems.

Cranial anatomy of the Paleocene snake *Helagras prisciformis*; early implications for crown macrostomatan snakes

***Roxanne Armfield**^{1,2} and **Jason J. Head**²

¹*Yale University, USA*

²*University of Cambridge, UK*

The majority of modern snake diversity falls within Macrostromata. The origin, timing and sequence of acquisition of macrostomatan characters remain disputed due to a lack of consensus of the interrelationships within the clade, and a Palaeogene fossil record deficient in diagnostic cranial material for crown group taxa. The North American Paleocene snake *Helagras prisciformis* was first described from isolated vertebral elements. *Helagras* has been alternately considered a boioid, erycine or a madtsoiid snake, but the evolutionary implications of the taxon for inferring crown macrostomatan history have not been previously explored. Recently-discovered specimens include partial skulls, providing the first opportunity to resolve this taxon's relationships. Segmentation of micro-CT data reveals braincase anatomy, palatomaxillary apparatus, jaw elements, as well as vertebrae and ribs. Morphological phylogenetic analysis recovered a position stemward of Booidea within crown Macrostromata, based on skull roof morphology. Addition of a molecular scaffold recovered the first anatomical support for synonymy of Alethinophidia with Macrostromata by joining *Helagras* with *Anilius scytale* and tropidophiids, based on stapedial and palatomaxillary morphologies. Our results provide the oldest unambiguous evidence for the dispersal of crown Macrostromata into northern continents, and indicate dispersal connectivity of the Americas between the Late Cretaceous and early Palaeogene.

Palaeogene polar plankton and productivity: a contribution to the Franco-German “Make Our Planet Great Again” research initiative

Gayane Asatryan, **David Lazarus**, **Johan Renaudie**, **Gabrielle Rodrigues de Faria** and **Volkan Özen**

Museum für Naturkunde, Berlin, Germany

Marine plankton species, key components of the carbon cycle, may be at risk of extinction from global warming. In a new project, we are studying this possibility via the interaction of climate, carbon capture and evolution/extinction of plankton in the Palaeogene where atmospheric $p\text{CO}_2$ and temperatures were close to what is predicted for our future. The research targets polar oceans, their role in carbon capture, and how these are related to the evolutionary history of the plankton, particularly diatoms as CO_2 regulators, and the radiolarians, as they are also important carbon exporters and excellent indicators of polar ocean currents and conditions in past times. Eighteen sites covering all ocean basins and latitudes have been selected for detailed new age-modelling and sampling. From these we will generate comprehensive biodiversity histories and multiple palaeoceanographic proxies to constrain computer-generated global simulations of ocean circulation and carbon capture. Initial results (age models, palaeoceanographic proxies and, in particular, new comprehensive taxonomic surveys of species) will be shown from two localities from the southeast Atlantic sector of the Southern Ocean: IODP Leg 177 Site 1090 from the Falkland Plateau and ODP Site 689 from the Weddell Sea.



The growth and development of osteoderms in the Liassic dinosaur *Scelidosaurus* from Charmouth, Dorset

***Isabelle Baker** and **David B. Norman**

University of Cambridge, UK

The armour-plating of thyreophoran dinosaurs has been described in the past by particular reference to the appearance and histology of the armour found in *Scelidosaurus*, because it is known to be one of the earliest dinosaurs to have exhibited any form of dermally derived body armour. However, the *Scelidosaurus* osteoderms used in these studies are isolated bones that show no context in relation to their position on the body, stage of growth or development. Recent work on this dinosaur has been able to demonstrate that the appearance, distribution, growth and development of the dermal armour of *Scelidosaurus* is far more complex than previously assumed. This poster will present research detailing the histological comparison of osteoderms from juvenile and adult scelidosaurids, using external examination, thin sections, and CT scans, to give further insight into the developmental processes of body armour in this species.

The Late Silurian–Early Devonian adaptive radiation (‘explosion’) of vascular plants

***Alexander C. Ball**¹, **Charles H. Wellman**¹, **Paul Kenrick**², **Stephen Stukins**² and **John B. Richardson**²

¹*University of Sheffield, UK*

²*Natural History Museum, London, UK*

The invasion of land by plants in the Middle Ordovician was a crucial event in the history of Earth’s biosphere. Almost immediately, plants began to have profound and far-reaching ramifications in terms of evolution and environment. Despite the rapid establishment of a global cosmopolitan flora by bryophyte-grade ‘cryptophytes’, evolutionary stasis reigned for some 40 Ma and they remained diminutive, simple and aerially limited. It was not until the Siluro-Devonian boundary that a major adaptive radiation characterized by high rates of diversity and disparity occurred. This adaptive radiation has been hypothesized to have been triggered by the emergence of vascular plants; however, much of this transformative evolutionary episode remains enigmatic. The land plant record of the classic Anglo-Welsh basin locality is the focal point for this investigation. The dispersed spore record will be quantitatively analysed in terms of diversity and disparity, alongside evolutionary turnover rates between cryptophytes and stem-tracheophytes. *In situ* spores will also be investigated, giving biological context to the diversification event. Ultimately, the project will shed light on the tempo of the shift in dominance from pioneering cryptophyte floras to stem-tracheophytes. Additionally, the project aims to clarify the biostratigraphy of the basin, including the *Apiculiretusispora* sp. E and *tripapillatus-spicula* biozones.

The basal sauropodomorph *Thecodontosaurus* from the Late Triassic of Britain: osteological re-description, limb musculature reconstruction and locomotion

***Antonio Ballell Mayoral**, **Emily J. Rayfield** and **Michael J. Benton**

University of Bristol, UK

Thecodontosaurus was the first sauropodomorph dinosaur ever named and one of the most basal members of this clade, making it crucial for the understanding of the early evolution of the group. Its fossils have been found in fissure fill localities of southwestern



Britain, with the type species *T. antiquus* holotype coming from the early Rhaetian deposits of Durdham Down in Bristol. Here we describe for the first time the numerous and well-preserved remains from Tytherington, southwest England. We find these specimens can be assigned to *T. antiquus*. The osteology of *Thecodontosaurus* is updated and new anatomical information of previously poorly-preserved or missing bones is added. We provide a revised diagnosis of the species and discuss its phylogenetic position. We also reconstruct limb muscle attachment sites from osteological correlates and inferences based on the extant phylogenetic bracket. From this we find that *Thecodontosaurus* possessed a plesiomorphic limb musculature arrangement for sauropodomorphs. Muscle attachment sites and functional morphology of the limb bones indicate that it was a biped with crouched hindlimbs and partially supinated forelimbs. Further biomechanical investigation is required to test whether it was an obligate or facultative biped, and more detailed aspects of locomotion.

Trilobite biodiversity fluctuations at a regional scale in the Late Palaeozoic from North Africa

***Valentin Bault, Catherine Cr nier and Claude Monnet**

CNRS UMR 8198, Universit  de Lille, France

Present in marine Palaeozoic habitats, trilobites were an amazing evolutionary success. During the ‘Devonian Nekton Revolution’, they experienced great diversification especially during the eustatic sea level rise of the Basal Pragian Event and the related climate warming. Nevertheless, little attention has been accorded to their late evolutionary history leading to their extinction; a period marked by important environmental changes. In this study we focused our investigations on biodiversity analyses of trilobite data gathered from North Africa, famous for its exceptional record. By using a newly compiled exhaustive dataset (*i.e.* 166 genera, 3,863 occurrences), we focus on the taxonomic component of biodiversity at the sub-stage temporal scale, in order to assess their distribution patterns through diversity curves in a palaeoenvironmental framework, to understand their fluctuations in time and space, and to increase insights into the Devonian extinction events. The evolution of trilobite diversity was characterized by a major decline resulting from extinction rates higher than origination rates during the Middle Devonian. After this major decline, a faunal turnover occurred especially in phacopid and proetid trilobites. In order to analyse the potential connections between trilobites and potential predators, a comparison with ammonoids from the same area has been done.

Using CT-scans to unveil the anatomy of *Tupandactylus navigans* (Pterodactyloidea, Tapejaridae)

***Victor Beccari Dieguez Campo¹, Felipe Pinheiro², Fabiana R. Costa³, Ivan Nunes⁴ and Luiz E. Anelli⁵**

¹NOVA University of Lisbon, Portugal

²Universidade Federal do Pampa, Brazil

³Universidade Federal do ABC, Brazil

⁴Universidade Estadual Paulista, Brazil

⁵Universidade de S o Paulo Brazil

Little is known about the post-cranial skeleton of tapejarids, a bizarre clade of huge-crested pterosaurs. In Brazil, remains of those flying archosaurs have been found in the



Paraná and Araripe Basins. In the latter, tapejarid fossils were recovered from the Early Cretaceous Romualdo and Crato formations. Here we describe an almost complete and articulated *Tupandactylus navigans* skeleton from the Crato Formation. Due to the flattened preservation of the specimen, which is characteristic of Crato Formation fossils, overpreparing the material to access data under the matrix can irreparably damage it. Therefore, we used both traditional methods and computer tomography to study the specimen and reveal important anatomical features, as well as to create a 3D model. CT data allow the access of numerous features overlapped by appendicular bones, sediment or with marks of erosion. Among the features only accessible by CT-scanning are the articular region of skull, occiput, all vertebrae and humeral head and deltopectoral crest, all invaluable information for studies of ecology and flight capability for this taxa. The use of CT-scanning to study Crato Formation fossils is so far scarce in the literature but is proving an excellent tool for the full examination of this specimen.

Resolving the pterosaur bauplan using quantitative taphonomy

***Rachel A. Belben** and **David M. Unwin**

University of Leicester, UK

The basic construction (bauplan) of pterosaurs, as defined by the extent of the wing membranes, remains unresolved. The current consensus is that in basal forms all four limbs were connected by the wing membranes, forming a single locomotor module in which the left and right sides of the body were linked, anatomically and functionally. By contrast, in derived forms (pterodactyls) the cruropatagium, a membrane that connected the hind limbs in basal pterosaurs, was separated along the midline, resulting in two discrete modules each incorporating a fore and hind limb. These models had fundamental implications for the terrestrial ability, ecology and evolution of pterosaurs, but the delineation of this basal-derived pterosaur divide is unclear. We applied a quantitative taphonomic approach to this problem, drawing on data that reflect the entire temporal and taxonomic range of pterosaurs, and a broad range of taphonomic pathways. Preliminary results that consider skeletal completeness, articulation and joint geometry for 100+ specimens suggest that there are distinct differences between basal pterosaurs and pterodactyls. The degree of articulation between the hind limbs, for example, shows significantly better correlation in basal forms, consistent with the presence of a continuous cruropatagium, and a relatively poor correlation in pterodactyls.

Lower Miocene rodents from Uganda and Namibia: palaeobiology and palaeoenvironmental interpretations

***Laura Bento Da Costa**^{1,2}, **Brigitte Senut**¹ and **Loïc Segalen**²

¹*Centre de Recherche en Paléontologie, Paris (UMR 7207), France*

²*Institut des Sciences de la Terre de Paris (UMR 7193), France*

Since the 1990s, expeditions conducted in Lower Miocene sites of Uganda and Namibia have led to the recovery of an abundant rodent fauna. The fossil remains of this study belong to four families: Bathyergidae, Diamantomyidae, Anomaluridae and Nonanomaluridae, which illustrate diverse adaptations, in particular in their locomotor habits (fossorial, terrestrial, gliders and arboreal). Despite the geographic distance between the sites, there are similarities in their respective faunas. Indeed, bathyergids and diamantomyids are found in both areas. Among the bathyergids, the species *Renefossor songhorensis* (Uganda) and *Bathyergoides neotertiarius* (Namibia) have comparable characteristics, probably indicating similar ecological niches (large fossorial rodent niche).



The main difference between the two regions is the presence of anomaluroid rodents only in the Ugandan sites. They are essentially found in forested environments, suggesting a more wooded habitat at Napak (Uganda) than in the Namibian sites. However, the presence of bathyergids and diamantomyids indicates a more open landscape, characterized by a mosaic environment in Uganda and humid woodland in Namibia, which is very different from the present-day desert. These interpretations are compared to stable isotope analyses ($\delta^{13}\text{C}_{\text{CO}_2}$, $\delta^{18}\text{O}_{\text{CO}_2}$), which are consistent with the palaeoenvironmental assumptions linked to the morphology.

Response of lamniform sharks to Cenomanian–Turonian warming: unlocking hidden data in historic collections to address key scientific questions

Emma Bernard¹, Sinjini Sinha², Wilfrid J. Pearson³, Liam T. Gallagher⁴ and Richard J. Twitchett¹

¹*Natural History Museum, London, UK*

²*The University of Texas at Austin, USA*

³*University of Birmingham, UK*

⁴*Network Stratigraphic Consulting Ltd, UK*

The fossil record of past global change events provides an archive of data that can be used to test predictions of the effects of current global warming; for example, that marine animals will shrink as temperature rises. The lamniform sharks of the English Chalk represent an ideal system to test this prediction as they span the Cenomanian–Turonian anoxic event (OAE 2) and Cretaceous Thermal Maximum. Shark teeth have been collected from the Chalk Group for more than 200 years and UK museums contain substantial archives of potential data. Unfortunately, many specimens were collected 100+ years ago and the variable quality of their associated stratigraphic data limits their usefulness. In order to improve this, we extracted nannofossils from the associated matrix of selected specimens to better constrain their relative ages and expand our dataset. Nannofossil biostratigraphy revealed that most museum specimens with original biozone information were correctly dated, although not all. Turonian lamniform shark teeth are rare in UK museum collections, and only one genus (*Scapanorhynchus*) was sufficiently abundant for individual analysis. Lamniform abundance does not appear to reflect rock record bias, so the post-Cenomanian decline either reflects collection failure and/or a real biological response to warming and associated extinction.

Twenty million years of decoupled functional-taxonomical assembly processes revealed by network analysis

***Fernando Blanco¹, Joaquin Calatayud², David M. Martín Perea^{3,4}, M. Soledad Domingo³, Iris Menéndez², Manuel Hernández Fernández³ and Juan L. Cantalapedra⁵**

¹*Museum für Naturkunde, Berlin, Germany*

²*Universidad Rey Juan Carlos, Spain*

³*Universidad Complutense de Madrid, Spain*

⁴*Museo Nacional de Ciencias Naturales – CSIC, Spain*

⁵*Universidad de Alcalá, Spain*

In the context of the current biotic crisis, one possible conservation strategy is to protect functional diversity with the hope that this will render ecosystems with higher resilience to eventual environmental disturbances. Palaeobiology can assess the resilience of



functionally-diverse systems over deep timescales. To do so, we investigate changes in the functional morphology of Neogene–Quaternary Iberian macromammals. We applied network analysis to study functional assembly processes of these faunas, identifying ten successive functional modules using network detection algorithms. Also, we estimated changes in several measures of functional diversity, and compared these functional trajectories with taxonomic diversity. We found that increases in functional diversity provoked system collapses due to the accumulation of species with similar functionality (redundancy). Collapses were followed by a substantial decrease in redundancy and diversity. We observed that taxonomical turnovers are seldom related to changes in functional assemblages. For example, between 20–11 Ma, taxonomic turnover in the regional pool was not paired by a detectable functional reassembly process at the community level. Moreover, community functional reassembly can take place in the absence of significant turnover of the regional species pool. This decoupling over deep time should be taken into account when defining protection plans based on functional diversity.

Use of new technologies in the revision of historical specimens of *Weichselia reticulata* from Bernissart (Barremian-Aptian of Belgium)

***Candela Blanco Moreno**¹, **Anne-Laure Decombeix**², **Cyrille Prestianni**³, **Bernard Gomez**⁴ and **Ángela D. Buscalioni**¹

¹Universidad Autónoma de Madrid, Spain

²CNRS Université Montpellier, France

³Royal Belgian Institute of Natural Sciences, Belgium

⁴Université Claude Bernard Lyon 1, France

Weichselia reticulata is a Mesozoic fern which has been thoroughly studied to date. A reconstruction of the plant based on stem and foliage material from the Barremian-Aptian locality of Bernissart (Mons Basin, Belgium) was performed by Alvin in 1971. Two of these stems have been revised and analysed by CT-scan imaging, providing new information on the internal anatomy and the external morphology of *Weichselia reticulata*. These results have implications on the systematic affinities of this fern, which place it closer to Marattiales. Also, some aspects of the autecology of the plant can be inferred, for example, the thick cortex and hair or scale insertions suggest an adaptation to extreme environments which were possibly subjected to recurrent wildfires. Additionally, the presence of structures in the base of roots and petioles that could be interpreted as nectaries or aerophores suggest interactions with animals or a necessity for extra ventilation of the leaf. Although a complete reconstruction of the plant is yet impossible, many aspects of the previous reconstructions of *Weichselia* do not agree with the new data obtained from the anatomical analyses.

Mantelliscan: 3D scanning an iconic British dinosaur specimen

***Joseph Bonsor**^{1,2}, **Susannah C. R. Maidment**¹, **Mark R. Graham**¹, **João V. Leite**^{1,3}, **Amy Scott Murray**¹ and **Emily Osterloff**¹

¹Natural History Museum, London, UK

²University of Bath, UK

³University College London, UK

The *Mantellisaurus atherfieldensis* holotype at the Natural History Museum, London is one of the most complete British dinosaurs known, described by Hooley in 1925. To make this important specimen available to researchers around the world, we used FARO 3D scanning



technology to produce a high-resolution model of each individual element of the skeleton currently on display in the Natural History Museum's main hall. The bones were relocated and scanned in a public gallery to enable scientific outreach. Once processed, the digital files will enable us to share these data with researchers who want to study the holotype but are usually prevented in doing so by it being on display. This project will form the basis of a redescription and morphological character analysis. Examination of the specimen has led us to identify several characters that were previously misdescribed in a large matrix by McDonald: the length of the pubis (a replica); a caudolateral notch on metatarsal III (fused together with MT IV); the shape of the sternal, and the acromion process. New characters were also created including the shape of the scapula (hook-like); and the angle of the transverse process on the dorsal vertebrae.

Body mass evolution of South American hystricognath rodents, and the role of climate

***Andrew R. Brinkworth^{1,2}, Julien Clavel² and Anjali Goswami²**

¹*University of Bath, UK*

²*Natural History Museum, London, UK*

Body size is a key biological and ecological trait of animal species, and variation in this trait is frequently linked to climatic and other environmental variables. In this study, using a combined phylogenetic and time-series modelling approach, we show evidence of a dependency between large-scale climatic changes, and both the rate and mode of body size evolution in caviomorph rodents (Rodentia: Hystricomorpha). We also apply a new model of continuous phenotypic trait evolution for the first time; an Ornstein–Uhlenbeck process in which the long-term trait optimum is dependent upon a continuous environmental variable. This study expands upon previous investigations performed in this group through the inclusion of fossil species data, which would be expected to improve the accuracy of results obtained through these approaches.

Using biomechanical modelling to investigate an adaptive radiation: a case study in Dinosauria

David J. Button¹, Laura B. Porro², Marc E. H. Jones² and Paul M. Barrett¹

¹*Natural History Museum, London, UK*

²*University College London, UK*

Adaptive radiations are central to understanding the history of life. However, the paucity of empirical studies comparing functional performance through clade history precludes a comprehensive perspective of radiation dynamics. Early dinosaur evolution, between 240–190 Ma, provides a case study. During this interval, dinosaurs increased greatly in diversity, size and abundance. Their varied craniodental morphologies have fuelled hypotheses linking this radiation to innovations in feeding apparatus and dietary ecology. However, anatomy alone is a poor indicator of functional performance, and biomechanical studies have been restricted to deeply-nested dinosaur taxa. Consequently, the functional morphology and feeding behaviour of early dinosaurs remains poorly understood. Here we restore the cranial osteology of early dinosaur taxa from CT-scan data, including representatives of Theropoda, Ornithischia and Sauropodomorpha. Retrodeformation procedures were used to repair taphonomic damage, and myology was reconstructed from osteological correlates.



Finite-element analyses were then executed to quantify biomechanical performance during simulated feeding behaviours. Results reveal cryptic functional diversity in early dinosaurs, with significant biomechanical differences between anatomically similar taxa. These differences are attributable to diet, indicating that ecological diversity was assembled prior to morphological diversification. This reflects an adaptive radiation into novel ecospace, illuminating the dynamics of early evolution of Dinosauria.

First probable indirect evidence of *Hyaena prisca* in the Middle Pleistocene of Spain

Irene Cambroner¹, Paloma Sevilla¹, Ana Mateos², Jesús Rodríguez² and César Laplana³

¹Universidad Complutense de Madrid, Spain

²Centro Nacional de Investigación sobre Evolución Humana, Spain

³Museo Arqueológico Regional de Alcalá de Henares, Spain

Modern techniques applied to fossil coprolites provide interesting information ranging from the identification of the producer and its diet, to diagenetic and palaeoenvironmental data. Indirect evidence of the presence of a particular species can also be obtained in some cases, as the producer need not be directly represented in the fossil assemblage. Here we present the results obtained after studying 59 coprolites collected between 2009 and 2018 at Villanueva-1 (Palencia, Spain), a late Middle Pleistocene karstic site in a Mesozoic outcrop located at the southern end of the Cantabrian Range. The specimens come from a thin detritic level, partially cemented, where coprolites appear grouped. Standard morphological methods were applied to describe the specimens preserved whole, and destructive methods (thin sections, pollen extraction and chemical analysis) were performed on fragments. Although the degree of diagenetic changes inferred from the chemical analysis was moderate, no pollen was obtained indicating the coprolites were deposited in the cave far from its opening. All evidence indicates hyenas were the producers; morphology, size and other physical characteristics correspond with coprolites of *Hyaena prisca*, a species reported in Middle and Upper Pleistocene sites of southern France and Portugal respectively, but so far unknown in Spain.

A reconstruction of the skull of *Dicraeosaurus hansemanni*

***Amy Campbell and Daniela Schwarz**

Museum für Naturkunde, Berlin, Germany

Dicraeosaurids are a group of unusual sauropod dinosaurs that are characterized by their small size, short necks with elongated neural spines, and robust skulls compared to other sauropod groups. Of the nine recognized species, five preserve cranial material, with *Dicraeosaurus hansemanni* being one of the most complete. The skull of *D. hansemanni* was first described by Werner Janensch in 1936 but a redescription is overdue. Since the original description, seven other dicraeosaurid taxa have been described. *Amargasaurus*, discovered in 1990, was only the second dicraeosaurid ever found; the long gap between the discoveries further cements the need for an updated description. Here we present a new reconstruction of the skull of *D. hansemanni*. Cranial elements from several specimens were digitized using an Artec Spider and rearticulated in 3D. Missing elements were mirrored from the opposite side or filled in and reconstructed based on skulls of other diplodocoid sauropods. As the number of dicraeosaurids that preserve skull material is high for a sauropod group, they offer a unique opportunity to understand the feeding



ecologies of these enigmatic dinosaurs. The novel 3D reconstruction builds the foundation for the comparison with the other dicraeosaurid taxa and enables future biomechanical and functional analyses.

The rise and fall of proboscideans' functional diversity

Juan L. Cantalapiedra¹, Oscar Sanisidro¹, María Teresa Alberdi², Jose Luis Prado³, Fernando Blanco⁴ and Juha Saarinen⁵

¹*Universidad de Alcalá, Spain*

²*Museo Nacional de Ciencias Naturales – CSIC, Spain*

³*Universidad Nacional del Centro de la Provincia de Buenos Aires (UNICEN), Argentina*

⁴*Museum für Naturkunde, Berlin, Germany*

⁵*University of Helsinki, Finland*

The history of the proboscidean lineage is one of success and decline. During their 60 million years of evolution, proboscideans evolved into a remarkable diversity of body sizes and cranio-dental adaptations, and have been common constituents of Cenozoic mammalian communities. Yet, today's proboscideans represent but a tiny fraction of their past diversity. We examine the tempo and mode of their functional evolution using extensive fossil information and phylogenetic methods. Based on 16 ecomorphological traits, we identify eight proboscidean functional types (FTs). During the early phase of their evolution (until ~40 Ma) only two of such FTs appeared. It wasn't until after speciation and extinction rates tapered off that the other six FTs evolved. The earliest Miocene witnessed the maximal functional disparity of the clade, as three new FTs appeared featuring zygodont and bunolamellar teeth with more cusps and lophs, as well as more derived patterns of mastication. The functional decay of the lineage started ~10 Ma, with extinction progressively being more selective with respect to function. Functional attrition peaked in the last two million years, and just three FTs survived until 100 kyr ago. We pick the signal of differential speciation and extinction rates across the functional space.

Women in Palaeontology: how are they represented at meetings?

Patricia M. Carro-Rodríguez^{1,2,3}, Elena Cuesta^{1,4}, María Ríos¹, Adriana Oliver¹, Sara Gamboa^{1,2,3}, Laura Domingo^{1,2,3,5}, Iris Menéndez^{1,2,3}, Verónica Hernández-Ballarín¹ and Ana Rosa Gomez Cano^{1,6,7}

¹*Colectivo Mujeres con los pies en la Tierra, Spain*

²*Universidad Complutense de Madrid, Spain*

³*Instituto de Geociencias (CSIC-UCM), Spain*

⁴*Fukui Prefectural University, Japan*

⁵*University of California Santa Cruz, USA*

⁶*Transmitting Science, Spain*

⁷*Institut Català de Paleontologia Miquel Crusafont, Spain*

Although the number of women in academic positions has increased over the past 20 years, they are still under-represented in postdoctoral and tenure positions. The factors behind this inequity, which impede and/or discourage women from entering the field, comprise the lesser encouragement of girls in school, the masculine culture of science, and the tendency for women to make positive choices of alternative fields. To examine the



equality/participation status of women in palaeontology-related careers, we have analysed the conference participation data for 55 editions of three palaeontological annual meetings held since 1985. We have considered the percentages of women giving contributions, the proportion of women who were featured as keynote speakers, and those who were part of the organization or scientific committee. Our results showed a strong trend in the last four years towards an almost equal representation in ‘first-stage’ conferences. However, for conferences that include a higher percentage of senior researchers, even as recently as 2018, only 21 % of women presented contributions, highlighting that women are still under-represented at palaeontological meetings. Organizing committees should be made aware of the situation and then be able to promote specific actions to solve the gender bias.

Geometric morphometric analysis on fossil cricetids mandibles

***Patricia M. Carro-Rodríguez^{1,2}, Paloma López-Guerrero¹, M. Ángeles Álvarez-Sierra^{1,2} and Pablo Peláez-Campomanes³**

¹Universidad Complutense de Madrid, Spain

²Instituto de Geociencias (CSIC-UCM), Spain

³Museo Nacional de Ciencias Naturales – CSIC, Spain

We aimed to quantify and compare the mandibular shape of three extinct genera of cricetids from the Miocene of Europe: *Cricetodon*, *Hispanomys* (tribe Cricetodontini) and *Megacricetodon* (tribe Megacricetodontini). Classically, the description and diagnosis of the mandibles of these cricetids is based on qualitative data that make differentiation and comparison between intermediate morphologies more difficult. To solve that, we digitalized 14 landmarks and seven curves formed by semilandmarks that define the most relevant parts of the mandibles. These landmarks and semilandmarks are equally distributed among the two main parts of the mandible: the alveolar and ramus regions. This equitable distribution avoids any sampling and analysis differentiation between the regions. Then, using geometric morphometric methodologies and analysis (PCA), we obtained summarized information about the total variance of the sample. The scatter plot for the PCA showed a clear difference between the two tribes and established two morphologies: one for *Cricetodon* and *Hispanomys* and another for *Megacricetodon*. Because the mandible is a structure where integration, modularity and biomechanics have been tested, this morphometric analysis will allow us to provide new information about extinct species.

Biochronology of the early Miocene mammal record of the Vallès-Penedès Basin (Catalonia)

Isaac Casanovas-Vilar¹, Miguel Garcés², Sílvia Jovells-Vaqué¹, Daniel DeMiguel^{1,3}, Israel García-Paredes¹, David M. Alba¹ and Lluís Cabrera²

¹Institut Català de Paleontologia Miquel Crusafont, Spain

²Universitat de Barcelona, Spain

³Universidad de Zaragoza, Spain

The early Miocene mammal record of the Vallès-Penedès Basin (Catalonia, Spain) had not been systematically studied until high-resolution litho- and magnetostratigraphic studies of the main sections were recently undertaken. The rodent succession shows multiple affinities to that from the Aragonian stage type area in the Calatayud-Montalbán Basin (Aragon, Spain), so that the same detailed local zonation may be used. Nevertheless, there are some



differences between the two records, such as the occurrence of Central European taxa and the significantly later extinction of certain rodent species in Catalonia. The Vallès-Penedès record ranges from zone A (MN3, Ramblian) to C (MN4, early Aragonian), with a minor hiatus corresponding to zone B. Contrary to the Aragonian type area, most of the Vallès-Penedès sites have also yielded large mammals, allowing for the calibration of major dispersal events in Western Europe, such as that of gomphotheres from Africa and the equid *Anchitherium* from North America.

Synchrotron-XRF analysis reveals fossil insect trace element chemistry retains a biological signal

Thomas Clements^{1,2}, Samuel Webb³ and Maria E. McNamara¹

¹University College Cork, Ireland

²University of Birmingham, UK

³Stanford Synchrotron Radiation Lightsource (SSRL), USA

Extant insects utilize both structural and pigmentary colouration and include some of the most striking and vibrantly coloured organisms on the planet. The fossilization process normally removes visible pigmentary colour from fossil insects, and because of this we have a poor understanding of the evolution of colour in this group. Recent work by our group has identified that different cuticular pigments exhibit distinctive taxonomic and pigment-specific trace element chemistry in some extant insect cuticles. Here we use synchrotron X-ray fluorescence (XRF) to examine the trace element chemistry of key groups of fossil insects (Coleoptera, Diptera and Hymenoptera) from several Lagerstätten. Linear discriminant analyses show that the trace element chemistry in fossil insects is influenced by environment and/or diagenesis. Despite this, different fossil insect groups retain distinct trace element chemistries. These data suggest that despite diagenetic overprint, an original biological signal can survive fossilization. Future work, combining an expanded fossil data set and taphonomic experiments, will confirm the validity of whether the biological signal in the fossils includes a pigmentary component.

Phylogenomics resolves early events in bacterial evolution

***Gareth A. Coleman¹, Gergely J. Szöllösi² and Tom A. Williams¹**

¹University of Bristol, UK

²Eötvös Loránd University, Hungary

A rooted tree of Bacteria is essential to reconstruct the early evolutionary history of life and the emergence of key geobiological interactions which affect us to this day. 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 probabilistic gene tree-species tree reconciliation methods. These hierarchical models integrate horizontal gene transfers (HGTs), gene duplications and gene losses into an overall model of genome evolution using amalgamated likelihood estimation, where patterns of gene family evolution contain information about the root of the tree. This rooting method also allows us to infer ancestral gene content and reconstruct ancestral



metabolisms for the internal nodes, including the last bacterial common ancestor, and to explore character evolution and rates of HGT over time. This provides insights into early bacterial evolution and key major evolutionary transitions, such as the evolution of photosynthesis, the double-membrane and terrestrialization.

3D scale geomodels of coral reefs: an opportunity to spread the palaeontological and geological heritage

Hugo Corbi¹, Francisco Asensio-Montesinos², Antonio Abellán³ and Javier Martínez-Martínez⁴

¹University of Alicante, Spain

²University of Cadiz, Spain

³University of Leeds, UK

⁴IGME, Instituto Geológico y Minero de España, Spain

The generation of accurate and realistic 3D models of entire geomorphic structures, such as coral reefs, can serve to promote the palaeontological heritage of a geosite. Here we show implemented 3D geomodels artistically recreating a coral reef (atoll-type), which can be useful to promote and disseminate the palaeo-scientific and didactic value of a geosite to both general and specialized audiences. We have selected the Messinian coral reef (atoll type) of Santa Pola cape, one of the most relevant geosites from the Neogene record of south-eastern Spain. It is located in the northern Bajo Segura basin, a western Mediterranean Neogene basin of the eastern Betic Cordillera. In this singular enclave, 3D scale geomodels have been developed at two different scales: the entire atoll structure, and the best representative outcrop where a high-resolution 3D model has been developed with the structure from motion (SfM) photogrammetric technique processing images carried out with remotely-piloted aircraft systems. Two different 3D models have been implemented for each selected scale: the first, reproducing the current relief (small mountain above the sea level); and the second, an artistically and geoscientific recreation attempting to simulate the sedimentary environments during the Messinian formation process.

Experimental diagenesis in coral skeletons in dry conditions: a reassessment of 'original' biomineral features in fossils

Ismael Coronado^{1,2}, Bartłomiej Januszewicz³, Maciej Mazur^{3,4} and Jarosław Stolarski¹

¹Institute of Paleobiology (PAN), Poland

²University of León, Spain

³Lodz University of Technology, Poland

⁴University of Warsaw, Poland

Coral skeletons, composed of aragonite, are commonly used palaeoclimate and palaeoenvironmental archives (based on geochemical proxies). Those fossil coral skeletons that still preserve primary biomineral structures contribute to reconstructing Earth's past climate and environments. Unfortunately, post-mortem diagenetic alteration can obliterate the biogenic features of biominerals and, therefore, compromise the record of geochemical signals. Here we focused on characterization of micro- and nano-structural, geochemical and crystallographic changes of the coral skeleton in experimental diagenesis (in dry conditions; by annealing of samples at 150°C and 275°C). The samples have been studied by TGA, SEM, AFM, EBSD, electron microprobe, Raman spectroscopy and X-ray diffraction. Two taxa representing different ecological groups (symbiotic *Stylophora*



pistillata and asymbiotic *Desmophyllum dianthus*) have been selected due to the significant structural and biogeochemical differences of their skeletons. Systematic structural (e.g. neof ormation), geochemical (in the ion partitioning) and crystallographic transformations (crystal lattice and orientation) have been observed due to water thermal loss, the organic matrix decomposition, the solid-state transformation of the aragonite to calcite and the subsequent stabilization of biogenic CaCO₃ amorphous phases. The observed skeletal transformations contribute to better understanding of selective preservation or diagenesis of skeletons of fossil corals and their use as palaeoenvironmental proxies.

Examination of the internal structure of the Cambrian paraconodont *Westergaardodina* reveals separate styles of growth in the earliest conodonts

***Will Crabbe¹, Thomas H. P. Harvey¹, Mark A. Purnell¹ and Duncan J. E. Murdock²**

¹University of Leicester, UK

²Oxford University Museum of Natural History, UK

Paraconodonts are a group of phosphatic tooth-like microfossil that ranged from the upper-middle Cambrian to the lower Ordovician and are a paraphyletic grade from which euconodonts derive, making them among the earliest vertebrates to possess a mineralized skeleton. This evolutionary scenario relies upon the microstructural continuity among coniform para- and euconodont elements. However, paraconodonts that differ from a coniform morphology, such as the U-shaped and W-shaped form-species of *Westergaardodina*, display apparently paradoxical growth patterns. Examination of the internal structure and growth patterning of these problematic forms will be crucial in resolving the early history of the vertebrate lineage. Here we present results collected from uniquely preserved carbonaceous *Westergaardodina* elements from the Deadwood Formation, Canada, as well as results from synchrotron radiation X-ray tomographic microscopy (SRXTM) of *Westergaardodina* elements from the Alum Shale Formation in Sweden and the Windfall Formation of Nevada, USA; together ranging from the Jiangshanian to Cambrian Stage 10. From these data we identify and describe three distinct growth styles within elements of *Westergaardodina*, demonstrating that these early conodonts were more structurally disparate than expected, rejecting previous hypotheses of shared growth styles in the earliest conodonts.

The soricids and heterosoricids (Eulipothypla, Mammalia) from the Ribesalbes-Alcora Basin

***Vicente Daniel Crespo Roures^{1,2,3}, Ana Fagoaga^{3,4}, Rafael Marquina-Blasco^{3,4}, Francisco Javier Ruiz-Sánchez^{3,4,5} and Plini Montoya⁴**

¹Museo de La Plata (UNLP), Argentina

²Museo Paleontológico de Alpuente, Spain

³Museu Valencià d'Història Natural, Spain

⁴University of Valencia, Spain

⁵Universidad Estatal Península de Santa Elena, Ecuador

The mammal fossil record from the Ribesalbes-Alcora Basin (Castellón, Spain) is distributed in 45 sites located in seven sections along the Campisano ravine of the Araia/Mas de Antolino outcrop. The presence of the rodents *Megacricetodon*, *Democricetodon* and *Ligerimys* allows us to assign an early Aragonian age (MN4, early Miocene) to these



localities, which can be correlated with local biozone C of the Calatayud-Montalbán Basin (Spain). In the early Miocene Iberian context, these sites have yielded a relatively rich assemblage of shrews, including *Oligosorex thauensis*, cf. *Soricella discrepans*, *Paenelimnoecus micromorphus* and *Heterosorex neumayrianus*. Biostratigraphically, a highlight is the presence of *O. thauensis* in localities from the MN4, this species being restricted until now to older deposits from the MN3 unit. With respect to palaeobiogeography, the record of *Paenelimnoecus micromorphus* in the Ribesalbes-Alcora Basin represents the first and, until now, only citation on the Iberian Peninsula. *Soricella discrepans* is a typical species from Central Europe (MN2-4); if its occurrence is confirmed, it would represent the only record of this species in MN4 from the Iberian Peninsula. Finally, while *Heterosorex neumayrianus* is relatively common on the Iberian Peninsula but always poorly represented, its fossil record in the Ribesalbes-Alcora constitutes the best Spanish collection described yet.

Distribution of extinct metatherians (Mammalia) in the Northern Hemisphere: state of the art

***Vicente Daniel Crespo Roures^{1,2,3} and Francisco Javier Goin¹**

¹*Museo de La Plata (UNLP), Argentina*

²*Museo Paleontológico de Alpuente, Spain*

³*Museu Valencià d'Història Natural, Spain*

We reconstructed the palaeogeographic distributions of all extinct metatherians from the Northern Hemisphere (Cretaceous to Miocene) known up to now. Poor sampling in Asia precludes a better understanding of their biogeographical patterns. Our preliminary observations are: 1) metatherians most probably originated in North America. 2) By the Cenomanian metatherians reach Eurasia, probably through a Beringian bridge. 3) Compared with eutherians, they were much better represented in North America than in Eurasia by the Late Cretaceous. 4) After the K-Pg extinctions, there is a disruption of the migrations between northern continents, together with an impoverishment of diversity. 5) In the Ypresian, metatherians increase their diversity and experience a great latitudinal expansion and intercontinental migration; they are first recorded in India and Africa, but are absent in Asia (sample bias?). 6) During the Lutetian there is a diversity peak in northern North America, while Asia shows its first post-Paleocene record. 7) During the Oligocene, metatherian diversity declines. 8) During the Middle Miocene Climatic Optimum there is a further impoverishment and, by the Middle Miocene, a final extinction of all lineages. Alternative arguments to global climate should be offered in order to explain the decline of metatherians in the Northern Hemisphere.

The first definitive carcharodontosaurian theropod from Southeast Asia (Khok Kruat Formation, Lower Cretaceous, Thailand)

Elena Cuesta¹, Soki Hattori^{1,2}, Duangsuda Chokchaloemwong³, Pratueng Jintasakul³, Masateru Shibata^{1,2} and Yoichi Azuma^{1,2}

¹*Fukui Prefectural University, Japan*

²*Fukui Prefectural Dinosaur Museum, Japan*

³*Nakhon Ratchasima Rajabhat University, Thailand*

Carcharodontosauria is a clade of theropods with a wide distribution in Laurasia and



Gondwana from the Late Jurassic to the Late Cretaceous. However, carcharodontosaurs have been poorly known so far in the Early to mid-Cretaceous of Asia. For the first time, a definitive carcharodontosaurian theropod is established from a series of autapomorphies among allosauroids observed in the isolated skeletal remains from the Lower Cretaceous Khok Kruat Formation in Thailand. Its basal phylogenetic position within Carcharodontosauria offers a new perspective on the palaeobiogeographical context of this group. The presence of basal carcharodontosaurs in Portugal and Tanzania during the Late Jurassic implies that this clade spread on both landmasses early in their evolutionary history. Under this scenario, the presence of this new taxon supports an extension of the record on the Laurasian landmasses during this evolutionary stage of Carcharodontosauria. Moreover, some of the unusual features observed in this new taxon are related to a striking pneumaticity, as the presence of pneumatic foramina in the surangular, camerate structures in the cervical vertebrae, and foramina perforating the bases of cervical and dorsal neural spines. These findings on the best-preserved carcharodontosaurian theropod in Southeast Asia shed new light on the early evolutionary history of Carcharodontosauria.

Late Permian ichthyofauna from the Zechstein Basin SW Poland

***Darja Dankina-Beyer¹, Andrej Spiridonov^{1,2} and Sigitas Radzevičius¹**

¹*Vilnius University, Lithuania*

²*Nature Research Centre, Lithuania*

The first detailed description of fish assemblages from Upper Permian (Lopingian Stage) strata assigned to Polish Zechstein Limestone (Ca1) deposits is presented here. The material described was obtained at the Nowy Kościół section in the outer part of the North-Sudetic Basin, southwest Poland. The outcrop studied comprises limestone-marl associations including spotted marls, copper-bearing marls and lead-bearing marls. Eleven carbonate samples were taken from three different sites at the outcrop, which is exposed in a 10-metre section at Nowy Kościół. The total weight of samples reached 124.8 kg. The acid-dissolved sample residue was dried and sieved. Rare fish microremains were handpicked and separated under a binocular microscope into microslides. In total, 134 isolated fish microremains were collected in the studied samples. Chondrichthyes are represented by 50 dermal denticles and two well-preserved teeth, while Osteichthyes are represented by 35 scales and 47 teeth. The majority of chondrichthyan dermal denticles belonged to euselachian-type sharks. Two teeth can be attributed to ?Protacrodontidae family. All material of bony fishes can be assigned to the subclass Actinopterygii. This study will increase our understanding of the evolution, palaeoecology and palaeogeographic distribution of fishes during the Upper Permian.

Frozen footprints: trace fossils from late Ordovician low-latitude glacial deposits (Pakhuis Formation, Table Mountain Group, South Africa)

Neil S. Davies¹, Anthony P. Shillito^{1,2} and Cameron R. Penn-Clarke^{3,4}

¹*University of Cambridge, UK*

²*University of Oxford, UK*

³*Council for Geoscience, South Africa*

⁴*University of the Witwatersrand, South Africa*

The Hirnantian Pakhuis Formation (Table Mountain Group) of South Africa comprises a suite of glacial and related facies, associated with a localized Gondwanan ice sheet that



existed at a palaeolatitude of *c.* 30° S. In the northernmost part of the Cape Basin, thin successions of Pakhuis strata rest directly on top of erosional and often glacially-scoured Precambrian basement. Here we report a diverse ichnofauna from a newly-recognized locality within these marginal glacial deposits. Trace fossils include at least six different vertical and horizontal burrows (most notably *Heimdallia* and *Metaichna*), some of which were excavated directly into glacial diamictites. Arthropod trackways are also relatively abundant and can be seen to have interacted with glacial sedimentary phenomena including striated and faceted dropstones and potential cryogenic surface textures. The ichnofauna sheds light on invertebrate life during an unusual equatorial Ordovician glaciation at sea-level, and is also notable for its stratigraphic position: immediately preceding the Soom Shale Lagerstätte (lower Cedarberg Formation).

Occupancy modelling of dinosaurs within the Late Cretaceous of North America

***Christopher D. Dean**¹, **Lewis A. Jones**², **Alfio A. Chiarenza**³ and **Richard J. Butler**¹

¹University of Birmingham, UK

²Imperial College London, UK

³Perot Museum of Nature and Science, USA

The availability of large-scale occurrence databases has revolutionized palaeobiology, allowing for investigation of diversity and macroecological trends through deep-time. However, the problem of data absence (*i.e.* does the lack of a fossil occurrence indicate genuine absence or imperfect detection?) has hindered studies, and potentially biased our understanding of the fossil record. Occupancy modelling, a commonly applied ecological technique that distinguishes between true (taxon genuinely absent) and false (taxon present, but not detected) absences, provides an avenue to explore spatiotemporal biases in the fossil record by producing independent and simultaneous estimates of both occupancy and detection probability. We use occupancy modelling to assess trends in occupancy and detection within three dinosaur groups (Tyrannosauridae, Ceratopsidae and Hadrosauridae) during the Late Cretaceous of North America, to establish whether their apparent decline towards the K-Pg boundary is a product of sampling bias or a genuine ecological signal. Preliminary results suggest that whilst occupancy remained stable, detection of dinosaur occurrences declines from the Campanian to the Maastrichtian, highlighting an increasing spatiotemporal bias towards the K-Pg. The addition of site-specific lithological covariates provides information on how geological context influences detection capacity. We also highlight the importance of recording absence information in future palaeontological studies.

Diverse dentitions in the earliest chondrichthyans

***Richard P. Dearden**¹, **Matt Colfer**² and **Sam Giles**³

¹Muséum national d'Histoire naturelle, Paris, France

²University of Oxford, UK

³University of Birmingham, UK

The teeth of most living chondrichthyans (cartilaginous fishes) are a series of parallel, ever-replacing files, very unlike the site-specific, shedding dentition of osteichthyans (bony fishes). Reconciling these morphologies, and understanding their implications for the early evolution of teeth, relies on uncovering dental anatomy in the earliest jawed vertebrates.



The Palaeozoic ‘acanthodians’, the earliest-known articulated stem-chondrichthyans, exhibit neither morphology, instead bearing a profusion of morphologically and terminologically diverse bones, splints and whorls. Here we use tomographic methods to investigate the mandibular structures of several acanthodian-grade stem-chondrichthyans. We characterize the dentigerous jaw bones of ischnacanthids as growing bones, similar in structure to the gnathal bones of stem-gnathostomes but with unidirectional growth. *Acanthodopsis*, which has a morphology otherwise identical to the toothless acanthodids, has dermal teeth, although unlike those of any other known stem-chondrichthyan. We demonstrate ‘mandibular splints’ to be dermal bones which may be limited to acanthodid taxa. In the context of current understanding of early chondrichthyan relationships, we argue that the growth of dental elements by the unidirectional addition of cusps may be a chondrichthyan character and that similarities between ischnacanthid jawbones and placoderm gnathal plates may be gnathostome symplesiomorphies, underlining that a shedding dentition evolved twice in gnathostomes.

The impact of the Pliensbachian-Toarcian crisis on belemnite biogeography and evolution

Kenneth De Baets¹, Patricia Rita^{1,2}, Luís Vítor Duarte^{2,3}, Pascal Neige⁶, Laura Piñuela⁴, José Carlos García-Ramos⁴ and Robert Weis⁵

¹University of Erlangen–Nuremberg, Germany

²MARE Marine and Environmental Sciences Centre, Portugal

³University of Coimbra, Portugal

⁴Museo del Jurásico de Asturias, Spain

⁵Luxembourg National Museum of Natural History, Luxembourg

⁶Université de Bourgogne, France

The Pliensbachian–Toarcian transition has been considered a major bottleneck in the early evolution of belemnites, probably related to major palaeoenvironmental changes during the Early Toarcian. Previous research has focused on the study of belemnites from higher, temperate latitudes, while high-resolution studies on diversity and size of subtropical belemnite assemblages in the northwest Tethys are comparatively rare. The lack of high-resolution (ammonoid subzone) data on diversity and size distributions of belemnite assemblages does not allow separating changes during the Pliensbachian–Toarcian boundary event from those during the Toarcian anoxic event. Rarefied diversity analyses on new data from Iberian sections suggest the Pliensbachian–Toarcian corresponds to a slight decrease in diversity and an adult size decrease within particular lineages. Cluster and non-metric multidimensional scaling analyses, however, suggest that the largest changes in diversity and palaeogeographic distribution of belemnite assemblages occurred during the Toarcian oceanic anoxic event (TOAE) rather than the Pliensbachian–Toarcian boundary. In southern basins like the Lusitanian Basin and Riff Mountains, belemnites even disappear entirely during the TOAE. The lack of widespread anoxia in southern basins of the northwest Tethys indicates that direct impact of warming or increased $p\text{CO}_2$ triggered by volcanism as well as indirect effects on nutrient availability and productivity might have played an important role during both crises.



Penya Rubí: a new Middle Triassic coastal ichnoassemblage from the Catalan Basin (Catalunya, Iberian Peninsula)

***Francho Chabier de Jaime Soguero¹, Eudald Mujal^{1,2} and Josep Fortuny¹**

¹*Institut Català de Paleontologia Miquel Crusafont, Spain*

²*Museum für Naturkunde Stuttgart, Germany*

The recent discovery of the Middle Triassic ichnosite of Penya Rubí (Vallirana, Barcelona) in the Catalan Basin (northeast Iberian Peninsula) provides new interesting information about the study of coastal and near-coastal environments in the Western Tethys palaeoregion. Tetrapod footprints were recovered from middle Muschelkalk detrital facies (late Anisian–middle Ladinian), in reddish sandstones and mudstones and greyish dolomites. The outcrop incorporates a sample of a moderate biodiversity in an intertidal ecosystem to the ichnological fossil record. Footprints belong to widely-known Middle Triassic tetrapod ichnogenes including *Rhynchosauroides* (the most abundant), *Procolophonichnium*, *Rotodactylus* and *Chirotherium*. Also, a repichnia trackway of a marine limulid, tentatively assigned to the ichnogenus *Koupichnium*, has been discovered. Several photogrammetric 3D models of selected footprints were performed, being useful for morphological description and depth analyses as indicators of the trackmaker's pressure-weight distribution and the locomotion–substrate interaction. Based on the 3D models and the excellent preservation of the ichnites, together with the sedimentological analyses, it has been possible to obtain ichnotaxonomical and palaeoecological results. This new ichnoassemblage offers a window on to the biodiversity and palaeoecology of intertidal ecosystems in southwest Europe during the Middle Triassic, with further implications for the Western Tethys ichnorecord.

Dinosaurs, fossils and heritage

Lara de la Cita García¹, Mercedes Llandrés² and Ángela Delgado Buscalioni¹

¹*Universidad Autónoma de Madrid, Spain*

²*Museo de Paleontología de Castilla-La Mancha (MUPA), Spain*

Palaeontological heritage has become a resource used by governments to encourage a region's economic growth by creating educational and exhibition spaces. We aim to explore how these actions, in conjunction with education, mass media and outreach efforts, have promoted the scientific culture of Cuenca's citizens in central Spain. Because of its relevant palaeontological heritage and dinosaur discoveries, two exhibition spaces were successively created (first MCCM and then MUPA). We performed two surveys spaced apart in time. In 2010 there was a significant difference in the respondents' answers according to their age: youngsters absorbed more scientific information and performed better in answering questions. Educational system efforts were responsible for these results. However, in 2019 the trend changed, showing that people born in Cuenca are more aware of their heritage than non-natives, but older people answered better than youngsters. Despite efforts in the ten-year period we observed oversimplified and imprecise answers (taxonomy, biodiversity) and a lack of answers linking related topics. Nowadays, outreach activities and mass media news may be playing an important role in broadcasting the relevance of palaeontological discoveries. Even though dinosaur fossils are the main attraction of MUPA's exhibitions, this cannot shadow and impoverish scientific knowledge.



Reconstructing the braincase and inner skull cavities of *Parabenodus atancensis*, a henodontid placodont from the Upper Triassic of Spain

Carlos de Miguel Chaves, Alejandro Serrano-Martínez, Francesco Gascó, Francisco Ortega and Adán Pérez-García

Universidad Nacional de Educacion a Distancia, Spain

Parabenodus atancensis is a recently described cyamodontoid placodont from the Carnian–Norian interval (Upper Triassic) of El Atance fossil site (Guadalajara Province, Spain). It was identified as the sister taxon of the highly specialized German *Henodus chelyops*, both taxa composing the clade Henodontidae. The holotype and only known specimen of *Parabenodus atancensis*, a partial but well-preserved skull, was CT-scanned, allowing us to significantly increase our knowledge of its cranial anatomy. In addition, the internal cavities were digitally reconstructed, including the partial brain, nerves, blood vessels and part of the bony labyrinth. The CT-scanning of the holotype of *Parabenodus atancensis* allows the characterization of several bones and structures previously unknown for this taxon, as well as the identification of several synapomorphies of the braincase of Cyamodontoidea, so far unknown in Henodontidae. The study of the brain and neurosensory structures of *Parabenodus atancensis* suggests a relatively lower reliance on vision, the pineal system and the pituitary than in other Triassic sauropterygians. The morphology of the labyrinth supports a lifestyle associated with shallow marine waters. These results provide a new reconstruction of the animal, based on the skeletal remains and the inferred neuroanatomy.

3D limb biomechanics of the stem-archosaur *Euparkeria capensis*

***Oliver E. Demuth¹, Emily J. Rayfield¹ and John R. Hutchinson²**

¹*University of Bristol, UK*

²*Royal Veterinary College, UK*

Triassic archosaurs and stem-archosaurs show remarkable disparity in their ankle and pelvis morphologies leading to functional diversity. However, the implications of these different morphologies for locomotion have never been quantitatively assessed. Here we present a novel quantitative analysis of the locomotory abilities of a stem-archosaur, applying 3D modelling techniques. Micro-CT scans of multiple specimens of *Euparkeria capensis* enabled the reconstruction and three-dimensional articulation of the ankle, pelvis and pectoral girdle in unprecedented detail and the discovery of previously unknown morphological features in this taxon. The maximal joint mobility of the hind- and forelimb were quantified in 3D to address previous qualitative hypotheses regarding posture, gait and stance of *Euparkeria*. The range of motion analysis supports an erect posture indicated by the hip morphology, as the femur and humerus could be fully adducted to position the feet beneath the body. However, more sprawling poses could not be excluded and hip abduction remained feasible. The oblique mesotarsal ankle joint in *Euparkeria* implies a more abducted hindlimb and reveals seemingly contradicting morphological characters. The posture of archosaurs appears to have evolved in a complex mosaic-like fashion and cannot be determined by relying solely on morphological characters.



Palaeoecology of deep-water Silurian corals

***Alavya Dhungana¹ and Emily G. Mitchell²**

¹Durham University, UK

²University of Cambridge, UK

Corals have been an important part of Earth's benthic ecosystems since the Cambrian period as major ecological engineers and have the ability to alter the environment, changing resource distributions, altering water flow and creating new environments. A diverse *in situ* deep-water fauna dominated by corals, preserved under volcanoclastic sediments in the Silurian midland valley of Ireland, allows us to investigate the spatial palaeoecology of this mass mortality assemblage. Spatial point pattern analysis (SPPA) is a set of powerful techniques to analyse the ecology of sessile organisms, whose positions are described as spatial points in an observational window. SPPA can be used to resolve organism dispersal/reproduction, competition for resources, differential mortality and physical environmental effects. This technique has been used on extant coral assemblages; however, no SPPA has been conducted on coral-dominated assemblages in the fossil record. Here we use photogrammetry and LiDAR to map the fossiliferous assemblages of the Irish Silurian. Our analyses enable us to compare the spatial ecology of extinct (tabulate and rugose) corals in the Silurian and assess their behaviour relative to extant forms, shedding light on how the ecology of corals has changed through deep time.

Taphonomy of modern vertebrate remains from Doñana National Park (Spain)

M. Soledad Domingo¹, David M. Martín-Perea^{1,2}, Catherine Badgley³ and Juan José Negro⁴

¹Universidad Complutense de Madrid, Spain

²Museo Nacional de Ciencias Naturales – CSIC, Spain

³University of Michigan, USA

⁴Doñana Biological Station-CSIC, Spain

Doñana National Park (southwestern Spain) is an outstanding natural laboratory for actualistic studies of vertebrate taphonomy for several reasons. 1) The vertebrate fauna, especially mammals and birds, is abundant. 2) Carcasses remain in their natural setting after animals die. 3) Human disturbance of carcasses is minor. 4) The Doñana ecosystem has multiple distinct habitats, including shifting dunes, shrubland, pine woods, marshes, lake and river margins, and ecotone boundary between dunes and marshes. Across this landscape, several depositional settings with counterparts in the fossil record occur. We present results of taphonomic monitoring of modern vertebrate carcasses and skeletal remains from this coastal Mediterranean ecosystem. Bones generally show good preservation with little damage, which is partly the consequence of low levels of predation. The wild boar is a frequent scavenger of vertebrate remains, and the abundance of boar in the different habitats is positively correlated with the frequency of chewed, fractured and scattered bones. The lake margins have the highest potential to produce fossil assemblages, since vertebrate remains are abundant and become rapidly buried, especially from trampling in the soft, wet substrate.



New insights into the colonization process of small mammals in southwestern Europe during the Holocene

***Ángel Carmelo Domínguez García**¹, **César Laplana**², **Paloma Sevilla**¹,
Norberto Palomares Zumajo³ and **Luis Benítez de Lugo Enrich**^{4,5}

¹Universidad Complutense de Madrid, Spain

²Museo Arqueológico de la Comunidad de Madrid, Spain

³Anthropos S.L., Spain

⁴Universidad Autónoma de Madrid, Spain

⁵Universidad Nacional de Educación a Distancia, Spain

In the Mediterranean realm, the interchange of small mammal species was relevant during the Holocene favoured by anthropic translocations. Thus, it is generally accepted that several species colonized southwestern Europe from Africa and the Levant. However, many details of this process remain unclear still, particularly concerning the precise age of first arrivals or of how the dispersal events occurred. In such a context, Castillejo del Bonete site (southeastern Spain) provides valuable information thanks to its rich and diverse small mammal assemblage, dated by radiocarbon to 3,796–3,615 cal. BP. The presence and relative abundance (12.45 % of MNI) of the western Mediterranean mouse (*Mus spretus*) in the assemblage is particularly interesting, since this species has few reliable records of this age in Iberia. An updated critical review of small mammal occurrences was performed, suggesting that *M. spretus* did not colonize southwest Europe earlier than the Late Northgrippian. On the other hand, the absence of the black rat (*Rattus rattus*) and the Etruscan shrew (*Suncus etruscus*) in this rich and diverse assemblage supports the pre-existing idea of a later arrival of these two species in the Iberian Peninsula, an idea that fits with their geographical and chronological records.

Biogeographic selectivity and latitudinal range shifts across a Mesozoic hyperthermal mass extinction

Alexander M. Dunhill¹, **Erin E. Saupe**² and **Graeme T. Lloyd**¹

¹University of Leeds, UK

²University of Oxford, UK

Geographic range size is regarded as one of the most important and consistent predictors of extinction risk. We tested how well geographic range size predicts extinction over the mid Triassic to mid Jurassic, an interval inclusive of the Late Triassic mass extinction event. The Late Triassic mass extinction coincided with a period of extreme warming that caused preferential extinction of tropical taxa. We therefore also tested whether surviving marine taxa shifted their geographic ranges poleward. Geographic range size was estimated using great circle distance and latitudinal range. A generalized linear mixed modelling framework was employed to predict odds of extinction based on range size across intervals of background and mass extinction. Latitudinal range shifts across interval boundaries were calculated whilst accounting for changes in temporal and spatial sampling regimes. Large geographic and latitudinal ranges increased the odds of survival during intervals typical of 'background' extinction, but this effect was severely diminished across the Late Triassic mass extinction event. A large latitudinal range offered greater insurance against extinction than a broad geographic range, both during periods of mass and background extinction. Taxa that survived the Late Triassic mass extinction seemed to have shifted their latitudinal ranges away from the equator.



Developmental biology of *Charnia masoni* and the affinity of Rangeomorpha

***Frances S. Dunn¹**, **Philip. R Wilby²**, **Dmitriy V. Grazhdankin^{3,4}**, **Alexander G. Liu⁵** and **Philip C. J. Donoghue⁶**

¹University of Oxford, UK

²British Geological Survey, UK

³Trofimuk Institute of Petroleum Geology and Geophysics, Russia

⁴Novosibirsk State University, Russia

⁵University of Cambridge, UK

⁶University of Bristol, UK

Molecular clock analyses estimate that divergences between the basal metazoan phyla took place tens of millions of years before the earliest unequivocal fossil records of crown group phyla. Opposing interpretations rationalize this mismatch as a consequence of systematic biases in the rock record versus the inaccuracy of molecular clock methods. Fossils of the Ediacaran macrobiota have the potential to bridge these perspectives, but their unusual bodyplans have made direct comparison to living groups difficult. Rangeomorpha are amongst the oldest and are the most palaeogeographically widespread of the Ediacaran macrofossils, but their precise phylogenetic position is uncertain. Here we show, through developmental and phylogenetic analysis of the rangeomorph *Charnia masoni*, that rangeomorphs were non-bilaterian eumetazoans. The complex programme of development exhibited by *C. masoni*, involving sympodial growth and developmental shifts, provides a new milieu in which to resolve homology of frondose architecture across Rangeomorpha. Bayesian phylogenetic analysis unequivocally supports a stem-eumetazoan affinity for *C. masoni*, indicating that macroscopic total group eumetazoans were present by at least 571 Ma.

The role of climate in the ecological rise of dinosaurs

***Emma Dunne¹**, **Alex Farnsworth²**, **Sarah E. Greene¹**, **Roger B. J. Benson³**, **Pedro Loreno Godoy⁴**, **Daniel J. Lunt²** and **Richard J. Butler¹**

¹University of Birmingham, UK

²University of Bristol, UK

³University of Oxford, UK

⁴Stony Brook University, USA

During the dinosaurs' rise to ecological dominance, their spatiotemporal patterns of diversity are hypothesized to have been intrinsically linked to environmental conditions. However, these hypotheses remain largely untested, in part due to the absence of palaeoclimate reconstructions with sufficient temporal and spatial coverage. We explored the palaeoclimatic niche space of early dinosaur species during the Late Triassic and Early Jurassic using occurrence data from the Paleobiology Database alongside a general circulation palaeoclimate model, and statistical and macroevolutionary modelling approaches. Our results provide the first quantitative assessment of early dinosaur palaeoclimatic niche space. We found that sauropodomorph dinosaurs were comparatively more restricted in their palaeoclimatic niche space during the Late Triassic. While their palaeoclimatic niche space expanded into the Early Jurassic to match that of other tetrapods, there is no evidence to suggest that they, or other dinosaurs, were constrained by climatic conditions. Instead, these expansions in palaeoclimatic niche space and global distribution were likely due to morphological changes and variation in spatial and temporal



sampling. Our results also demonstrate that early dinosaurs shared palaeoclimatic niche space with other large tetrapods (e.g. pseudosuchians), which is in contrast to the notions of general dinosaur superiority that have long pervaded the literature.

Who's boneheaded? How cranial microanatomy reflects fossoriality in lepidosaurs

Roy Ebel, Johannes Müller and Eli Amson

Museum für Naturkunde, Berlin, Germany

The acquisition of a fossorial lifestyle in squamates provides an excellent framework to study convergent evolution. In that context, the gross morphology of the skull in these head-first-burrowers has been the subject of several studies. However, to our knowledge, the inner structure of the cranial bones has never been quantified. We here test whether the convergent acquisition of fossoriality is associated with skull roof structural features. Using micro-CT-scans and the image analysis software ImageJ, we generated a comprehensive dataset that comprises most extant fossorial non-Serpentes lepidosaurs and their respective sister-clades (68 species), along with five extinct lacertibaenians. Thickness and compactness of the main skull roof bones were measured and plotted along an anteroposterior cranial profile. The latter differed consistently according to fossoriality, especially in the anterior region of the skull. For example, the fully fossorial amphisbaenians (worm lizards) showed a greater thickness and compactness than their surface-terrestrial sister-taxa, the lacertids (true lizards). The convergent evolution of cranial bone structure across lepidosaurs is shown by mapping the measured traits on a timetree. Extinct lacertibaenians, such as the Eocene *Cryptolacerta*, feature thick and compact skull roof bone, which suggests that bone microanatomical adaptations were present in these early forms.

Mass death by anoxia – or an exceptional preservation interval? The Middle Triassic bivalve beds of eastern Svalbard

Victoria Engelschiøn¹, Sofie Bernhardsen², Fredrik Wesenlund³, Øyvind Hammer¹, Jørn Hurum¹, Aubrey J. Roberts¹, Lene L. Delsett¹, Hans Arne Nakrem¹ and Atle Mørk²

¹Natural History Museum, University of Oslo, Norway

²Norwegian University of Science and Technology, Norway

³UiT The Arctic University of Norway, Norway

The Middle Triassic deposits of Svalbard consist of organic-rich, black shales deposited distally in an ocean bay of northern Pangea. The succession is known as the Botneheia Formation and the characteristic cliff-forming, phosphorous shales of the upper part are well-known for fossils. In particular, bivalves are found in rock-forming quantities, forming repeated layers. The bivalve beds, along with numerous ichthyosaur specimens, have previously been interpreted as the result of mass mortality events. The Middle Triassic had high biological productivity in the upper water column and episodic algal blooms. The combination of reduced oxygenation levels at depth and sulphurous bottom-waters is thought to have caused mass die-offs of both benthic and pelagic life. However, among the mass mortality bivalve beds are also layers of *Thalassinoides* burrows, an ichnotaxon associated with oxygenated environments. If the bivalve beds were caused by lethal anoxia, the bioturbated layers must represent temporally limited episodes of oxygenated bottom-



waters. This study investigates possible processes for the oxygenation events and the alternation between bivalve beds and *Thalassinoides* beds. Here we present results from the correlation of sedimentology and taphonomy to provide a better understanding of the depositional environment and whether the bivalve beds represent true mass mortality events.

The first articulated cyclocystoid (Echinodermata) from the Silurian of North America and a review of Silurian cyclocystoid distribution

Timothy A. M. Ewin¹, Mike Reich², Mark R. Graham¹ and Mario E. Cournoyer³

¹Natural History Museum, London, UK

²SNSB—Bavarian State Collection of Palaeontology and Geology, Germany

³Musée de paléontologie et de l'évolution, Canada

Cyclocystoids are a poorly known, rare, extinct class of bi-facially flattened, disc-shaped echinoderms, ranging from the Middle Ordovician to the Early Carboniferous. Articulated cyclocystoids are relatively common in the Ordovician but rarer in younger strata. We describe *Perforocycloides nathaliae*, a new genus and species, from the early Silurian of Anticosti Island, Québec, Canada, the first articulated cyclocystoid from the Silurian of North America. This taxon is primarily distinguished by the unique presence of pores and canals that penetrate the sutures between marginal plates. However, their function remains speculative. *Perforocycloides* most closely resembles the Ordovician–Silurian genus *Zygocycloides*, suggesting that this genus may have diversified more widely during the Silurian than previously reported. A review of global Silurian cyclocystoid distribution suggests taxa were geographically confined and that greatest diversity appears to have been located within Baltica. However, it also demonstrates our current limited knowledge and no specimens have been recorded from Gondwana (e.g. Africa, Australia, South America), Siberia, and North and South China, nor are any specimens known confidently anywhere from Pridoli strata.

The basal sauropodomorph *Anchisaurus polyzelus* enlightens sauropod skull evolution

***Matteo Fabbri¹, Guillermo Navalon², Nicolas Mongiardino Koch¹, Michael Hanson¹, Holger Petermann¹ and Bhart-Anjan S. Bhullar¹**

¹Yale University, USA

²University of Bristol, UK

The evolution of the skull in sauropods is believed to have been mainly driven by pedomorphosis and biomechanical optimization for feeding specialization. However, the dearth of quantitative studies and the rarity of sauropodomorph skulls make these observations largely qualitative. Here we studied the skull material of juvenile and adult individuals attributed to the Early Jurassic basal sauropodomorph *Anchisaurus*, traditionally considered closely related to Sauropoda. Micro-CT scan data allows us to infer an interesting mosaic of basal and derived characters in this taxon. During ontogeny, the braincase rotates ventro-distally, shifting the lower temporal fenestra below the orbit, as in sauropods. On the other hand, the snout is elongated, a condition similar to other basal sauropodomorphs. We performed geometric morphometrics on a dataset of 60 archosaur taxa and their ontogeny, when different developmental stages were available. Our results suggest that an increased craniofacial growth acceleration was a driving variable for



shaping the skull morphology of sauropods. We also found a complete developmental shift for the ontogenetic series of sauropods. We conclude that a combination of neomorphogenesis and peramorphism were key variables in the evolution of the largest land-dwelling animals that ever roamed the planet.

Skeletal taphonomy of anurans from the Eocene Geiseltal Konservat-Lagerstätte (Germany)

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

¹*University College Cork, Ireland*

²*Central Repository of Natural Science Collections (ZNS), Germany*

The middle Eocene Geiseltal biota is a lacustrine-hosted Konservat-Lagerstätte from Saxony-Anhalt in central Germany that includes diverse vertebrates, invertebrates (especially insects), plants and trace fossils. The soft tissue and skeletal taphonomy of the Geiseltal vertebrates are poorly understood. We analysed the skeletal taphonomy of 47 anurans from Geiseltal, and scored each specimen for orientation, completeness and articulation. Most specimens are orientated ventrally and a minority, dorsally. Most slabs show (near-) complete skeletons; the remainder show a spectrum of preservational states, including isolated skeletal elements, partly articulated body units (*e.g.* limbs or the vertebral column) and clusters of skeletal elements. Larger and more proximal skeletal elements (cranium, limbs, spine, pelvis) are typically better articulated and more complete than more distal and smaller elements (tarsals, carpals, phalanges). Completeness is highest for the ilia and vertebral column and lowest for the forelimb and hindlimb phalanges, metacarpals, metatarsals, carpals and tarsals. Few forelimb and hindlimb phalanges are articulated; this contrasts sharply with the metacarpals and metatarsals, most of which are articulated. These patterns of disarticulation and completeness differ to those in fossil amphibians from the Miocene Libros biota, suggesting different transport and/or depositional mechanisms.

Untangling the tree of life: can novel partitioning strategies improve phylogenetic inference?

***Stella M. Felsinger and Martin R. Smith**

Durham University, UK

Morphological characters are known to evolve at remarkably different rates, which complicates the inference of phylogeny. Grouping together characters expected to evolve at similar rates accommodates this rate heterogeneity. Partitioning by codon position is commonplace in molecular phylogenetics; for morphological data, no such general rule exists. Rosa, Melo and Barbeitos (2019) advocate partitioning characters according to their homoplasy index on a maximum parsimony tree. This method relies on a tree to infer a tree – but what if that first tree is unreliable? We tested homoplasy partitioning on strongly-supported and weakly-supported initial topologies and found little effect on inferred trees. Secondly, a homoplasy-based model is directly derived from the data. It seems intuitive that the data will show better fit to such a model than to a more naïve model. We compared these two approaches and found that no partitioning strategy was consistently superior: the optimal model, whether partitioned or not, depended on the quality and characteristics of the dataset. Our results suggest that rate heterogeneity can rarely be explained by a single evolutionary pattern. Though partitioning has the capacity to significantly increase model fit, in many cases an unpartitioned model may show better fit to the data.



Spatiotemporal fluctuations of decapod crustacean diversity from the Eocene of the south-central Pyrenees (Spain)

Fernando Ari Ferratges¹, Samuel Zamora², Emilio L. Pueyo² and Marcos Aurell¹

¹*University of Zaragoza, Spain*

²*IGME, Instituto Geológico y Minero de España, Spain*

Understanding how diversity changes in a single systematic group across the same formation is not always possible, especially when formations are very homogeneous, outcrops are limited or the group has little potential of fossilization. Here we present an exceptional example of decapod crustacean distribution from the middle-upper Eocene (Bartonian–Priabonian) Arguis-Pamplona marls (Jaca Basin, South-central Pyrenees) in a mixed carbonate–siliciclastic system that spans *c.* 1,000 km² of well-exposed outcrops in the Huesca province (Spain). This formation also represents a wide range of environments ranging from shallow marine reef complexes to prodelta/outer platform deeper conditions as a result of a progradation of facies to the west due to synsedimentary folds. More than 500 specimens of decapod crustaceans have been collected from different lithofacies. Preliminary results show that major peaks in diversity are correlated with very specific taphonomic conditions in the proximal prodelta environments. Decapod assemblages also show an unequal distribution in different environments. All this, together with the outstanding magnetostratigraphic frame in the Jaca Basin (more than 25 km of studied sections), provide a unique opportunity to study the spatiotemporal distribution of a single invertebrate group in a relatively small area in order to understand the control factors for such distribution.

Deterioration causes an identification of pathologies at La Virgen del Campo palaeoichnological site

***Mireia Ferrer Ventura, Angélica Torices, Raúl San Juan Palacios and Pablo Navarro Lorbés**
Universidad de La Rioja, Spain

La Virgen del Campo is one of the best-known palaeontological sites found in the Enciso locality (La Rioja, Spain). La Rioja has one of the best palaeoichnological fossil records in the world, with almost 10,000 dinosaur footprints and around 1,000 trackways. This site, which has an important function in the economic development of the region, is exposed to many natural or/and artificial ageing and deteriorating agents. We analysed the site visually, photographically, and collected some samples. In addition, we began monitoring the temperature and humidity at the site. With all this information, we could start the identification of different deterioration causes. These causes are related to chemical, physical or/and biological processes. After identifying them, we can determine which pathologies are causing the damage and map these pathologies for future interventions. With the analysis and the ICOMOS-ISCS illustrated glossary on stone deterioration patterns, we can compare and determine the degradation issues that are harmful for the site. The recognized pathologies are cracks and deformation, detachment, features induced by material loss, discolouration, and deposit and biological colonization. Combining all this information, we designed laboratory tests for the restoration materials that will be used during the next field season.



Dental anatomy and palaeoecological implications of Miocene Rhinocerotids (Neogene) from the little-known Leon province's (Duero basin, Spain) record

***Darío Fidalgo-Casares¹, Ismael Coronado^{1,2} and Esperanza Fernández-Martínez¹**

¹Universidad de León, Spain

²Institute of Paleobiology (PAN), Poland

Miocene mammals of the Duero basin represent one of the lesser-studied fossil records of Spain. This situation is especially marked in provinces such as Leon, where this work is based. Taking as a starting point the previous thorough review of all the specimens and fossil sites of this area (e.g. Laguna de Negrillos, Santalla del Bierzo and Urdiales del Páramo), we now face the challenge of understanding the palaeobiological peculiarities of its Miocene mammal fauna. Dental anatomy of one of the best-represented taxonomic groups of this record, the family Rhinocerotidae, has been assessed via the application of CT-scanning in several specimens of Neogene age and their extant relatives, making it possible to analyse aspects linked to their palaeobiology, palaeoecology and functional anatomy. Among the studied specimens are a hemimandible fragment documented for the first time and a previously-published partial skull of *Diaceratherium* sp. The study of processes like dental wear patterns and differences in tooth structure tell us about food preferences, vegetation and evolutionary pressures related to the latter. Furthermore, the dental eruption characteristics and the development of these pieces should lead us to a better understanding of this mammal's ontogeny, revaluing a little-known fossil record.

New data from the Late Triassic 'Elgin Reptile' fauna revealed by micro-CT scanning techniques

Davide Foffa¹, Richard J. Butler², Stig Walsh^{1,3}, Paul M. Barrett⁴, Stephen L. Brusatte³ and Nicholas C. Fraser^{1,3}

¹National Museums Scotland, UK

²University of Birmingham, UK

³University of Edinburgh, UK

⁴Natural History Museum, London, UK

The Late Triassic herpetofauna of the Lossiemouth Sandstone Formation of Elgin (Moray, Scotland), the 'Elgin Reptiles', includes some enigmatic close relatives of dinosaurs, pterosaurs, crocodylians and lepidosaurs. These specimens are thus pivotal to the understanding of the early evolution of such groups. However, even after 150 years of study, the potential of these fossils is still underexploited because their unusual preservation (voids or crumbled bones within hard sandstone) hinders conventional study of the skeletons. The aim of this project was to investigate the 'Elgin Reptiles' specimens using micro-CT-scanning techniques, allowing full investigation of their anatomy in a non-destructive way. To date, some of the most promising results come from understudied specimens. One of these revealed an assemblage of over 100 bones, representing multiple skeletons. Specifically, we identified the remains of a procolophonid parareptile *Leptopleuron lacertinum*, preserved alongside a small pseudosuchian archosaur. The latter, historically referred to the pseudosuchian *Ornithosuchus woodwardi*, instead exhibits similarities with another pseudosuchian, *Erpetosuchus granti*. However, distinct cranial and postcranial characters hint at a unique combination of features that might distinguish this specimen from any other known taxon. Ultimately, the results from this study suggest that the richness of the Elgin deposits might have been seriously underestimated.



Trophic community structure of the Late Jurassic Kimmeridge Clay Formation

Isobel Fortune, Bethany J. Allen and Alexander M. Dunhill

University of Leeds, UK

Food webs, the networks of feeding links between taxa, provide a tractable representation of biodiversity and species interactions which are central to our understanding of community structure and ecosystem function. Feeding interactions have been largely ignored in palaeobiology due to the uncertainty surrounding the life histories of extinct organisms. Here we present a trophic community reconstruction of the Late Jurassic marine ecosystem of the Kimmeridge Clay in order to determine whether Mesozoic marine ecosystems possessed a similar structure to modern marine ecosystems. Food webs were built from occurrence data derived from literature searches and museum collections. Interactions between species were defined by palaeoecological evidence and summarized within an inferential model framework. Community structural metrics were calculated and were compared to well-defined modern marine communities. The Kimmeridge Clay ecosystem is largely comparable to modern marine ecosystems supporting a pre-Late Jurassic timing for the establishment of modern ecological structure in the oceans via an early culmination of the Mesozoic Marine Revolution. However, the Kimmeridge Clay food webs are more densely connected than modern marine webs as fossil reconstructions using inferential methods are more likely to reproduce fundamental trophic niches rather than the realized trophic niches which are observable in modern marine ecosystems.

Planktic foraminifer test size during the Neogene: palaeoenvironmental response in the Atlantic Ocean

Andrew J. Fraass¹, Phoebe O'Brien¹, Barnaby Roberts¹, Chloe Todd^{1,2} and Daniela N. Schmidt¹

¹*University of Bristol, UK*

²*University of Southampton, UK*

Pelagic carbonate is an important part of the Earth's climate processes; it acts as a large but reactive reservoir of carbon dioxide. Planktic foraminifera make up a significant part of the open ocean's contribution. To that end, we have generated new records of planktic foraminiferal test size and accumulation over the past ~7 million years at several scientific ocean drilling sites from the Atlantic Ocean. Samples were imaged using automated microscope systems and analysed using Olympus Stream Viewer software to identify foraminifer tests and detect their sizes. Two sites, Ocean Drilling Program (ODP) Site 925 and Integrated Ocean Drilling Program (IODP) Site U1313, were analysed at ~3-kyr resolution to examine orbital forcing, while two others were paired with existing data (ODP Site 659: dust and siliciclastic input; IODP Site U1396: volcanic input) to determine their response to external nutrient sources as potential productivity drivers. Orbital forcing intriguingly appears to be reflecting a non-climate signal. At Site 659 test size was compared to an existing record of terrestrial material at that site and there appears to be a concomitant size increase with increased terrestrial input, likely owing to increased local productivity.



An investigation into the shallow water biodiversity of the London-Brabant Massif in the Late Cretaceous period

***Maximilian Fursman**

Natural History Museum, London, UK

The Cretaceous Period was characterized by rising sea levels, which created many new shallow sea environments, including around the London-Brabant Massif, in what today would be areas of Southern England. This investigation looked at sites to the north and the south of the Massif, Clophill Quarry, Bedfordshire and Patteson Court Quarry, Surrey, with the aim of identifying tooth fossil remains. Significant fossil remains were uncovered from each locality, mainly consisting of teeth. Identification of fossils using a microscope was carried out over a two-month period of the summer, with almost all teeth being 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 new shallow water Aptian Echinoderm-Lagerstätte from Spain

***Álvaro García¹, James Saulsbury², Marcos Aurell¹ and Samuel Zamora³**

¹University of Zaragoza, Spain

²University of Michigan, USA

³IGME, Instituto Geológico y Minero de España, Spain

Aptian (Lower Cretaceous) Echinoderm-Lagerstätte are extremely rare worldwide. Faunas from the southern hemisphere (Antartica) have been recently documented, but our view from Tethyan communities comes largely from isolated material that is extensive only in the case of echinoids. Other groups like asterozoans or crinoids remain poorly known. The Aptian record of the Maestrazgo basin (eastern Spain) is well developed and comprises carbonate platforms and marly hemipelagic deposits which record the succession of several invertebrate communities including echinoderms. The Oliete Formation (Oliete Sub-basin) represents a shallow carbonate platform dated as upper Aptian by means of ammonite biostratigraphy. It constitutes a single depositional sequence, with a lower transgressive interval (Cabezo Negro limestones and Dehesa marls members) followed by an upper regressive interval (Los Estancos limestone member), showing an upwards increase in siliciclastic input. The Estancos member contains tabular bioclastic limestone horizons with marly interbeds which are rife with complete crinoids, goniasterid asterozoans and regular echinoids preserving spines. These beds are found between oyster horizons evidencing an inner ramp depositional environment, and grade laterally to encrinites containing disarticulated crinoid material and complete irregular echinoids. This site represents a unique snapshot to the Aptian echinoderm communities from shallow marine environments in the Tethyan region.



New evidence of large-sized ornithopod dinosaurs from the upper Barremian Morella Formation in the western Maestrazgo basin (Spain)

José Manuel Gasca¹, Ignacio Díaz-Martínez², Beatriz Bádenas¹ and Marcos Aurell¹

¹University of Zaragoza, Spain

²Instituto de Investigación en Paleobiología y Geología (CONICET-UNRN), Argentina

Large-sized ornithopod dinosaurs closely related to *Iguanodon* (i.e. Styracosterna) were regular members of vertebrate communities during the Early Cretaceous on the European land masses. Their fossils are widespread and recorded in different palaeogeographical domains, including Iberia. However, it is still uncertain to what extent populations would be connected or not and what the geographic distribution of a given species might be. We present new fossils of large-sized ornithopods from the upper Barremian Morella Formation, discovered near the village of Miravete de la Sierra, Galve sub-basin (western Maestrazgo basin, Spain). They broaden the dinosaur record from the Morella Formation (well known in the neighbouring Morella sub-basin but unreported in the Galve sub-basin). In the Miravete area, the Morella Formation is formed of an 80 m-thick succession of mudstones with interbedded sandstones that represent deposition in coastal-alluvial setting. The ornithopod record consists of: 1) isolated postcranial bone remains from four different horizons, which accumulated in floodplains and brackish lagoons; and 2) abundant tracks preserved as natural casts, some of them being clearly trydactyl and wider than long, with one pad impression in each digit and in the heel. The dinosaur casts were produced in relation with avulsion deposits.

Species or stage – resolving ontogeny in derived representatives of Chasmosaurinae using elliptic Fourier analysis

*Joshua Gauweiler and Joachim T. Haug

Ludwig-Maximilians University of Munich, Germany

Whether certain morphotypes represent distinct dinosaur species, or actually ontogenetic stages of already described species, has been a heavily discussed topic among palaeontologists over the last decade. A prominent example of this is the debate about the validity of *Torosaurus latus*, as it might actually represent a late ontogenetic stage of *Triceratops horridus*. Both are considered to be highly derived representatives of Chasmosaurinae. In this study we used elliptic Fourier analysis in an attempt to resolve skull shape, since it contains the most differences between species. We focused on the two recognized species of *Triceratops* and *Torosaurus* respectively, while taking the basal ontogenetic trajectory of Chasmosaurinae into consideration. The basal pattern in Chasmosaurinae shows a strong influence of the length of the frill and the size of the horncores during ontogeny. While a combined analysis of *Triceratops horridus* and *Torosaurus latus* shows a similar trend, an analysis of *Triceratops prorsus* shows a more neotenous ontogenetic development. Due to the two *Triceratops* species being well separated through time, we propose that *Torosaurus latus* is not a valid species and that some of the more enigmatic morphological trends within derived representatives of Chasmosaurinae can be explained by an increasingly neotenous development.



Exceptionally preserved palynomorphs from the British Zechstein Sea suggest a wetter Late Permian climate

Martha Gibson and Charles H. Wellman

University of Sheffield, UK

The Zechstein Sea was a semi-isolated inland sea that occupied the Southern Permian Basin during the Late Permian (~258 Ma). Classic Zechstein reconstructions show an equatorial sea that endured for five million years and underwent five cycles of evaporation (EZ1-5), resulting in cyclic regressions and evaporative down draw, leading to extensive hypersaline conditions and barren hinterlands by EZ3. Here we show how palynological investigation of borehole material from northeast England has led to the recovery of unexpectedly abundant palynomorph assemblages dominated by taeniate and striate bisaccate pollen taxa, as well as monosaccates and trisaccates forms. Assemblages recovered from the Carnallitic Marl Formation (EZ4) and the Boulby Halite and Brotherton formations (EZ3) are identified as identical in composition to those recovered from earlier cycles when the vegetation was most extensive (EZ1-2). These assemblages provide an updated environmental reconstruction for the latest British Permian, including a transient gymnosperm-dominated vegetation, composed of conifers, ginkgophytes, rare cycads, pteridosperms and pteridophytes, persisting up to the P-T boundary. It is suggested that there was sufficient precipitation to support vegetation despite the global aridization trends at the P-T boundary, providing further support for the regionalized and varying severity of extinctions in the terrestrial flora at this time.

Palaeoenvironmental evolution of the Pliocene series of Baza (Baza Basin, southeast Spain) as deduced from the study of ostracod assemblages

***Alejandro Granados¹, Antonio Guerra Merchan¹, Maria Patrocinio Espigares¹, José Manuel García Aguilar¹, Sergio Ros Montoya¹, Bienvenido Martínez Navarro^{2,3,4} and Paul Palmqvist Barrena¹**

¹*Universidad de Málaga, Spain*

²*IPHES, Institut català de Paleocologia Humana i Evolució Social, Spain*

³*Universitat Rovira i Virgili (URV), Spain*

⁴*ICREA, Institució Catalana de Recerca i Estudis Avançats, Spain*

The Baza Basin (Betic Cordillera) preserves one of the best sedimentary and palaeontological records of the European Plio-Pleistocene. Here we show the results obtained in the study of the ostracod assemblages from Baza-1, a 60 m-thick Pliocene series that outcrops 1 km away from the city of Baza, in a southwest position, where one of the main palaeontological sites of the basin with vertebrate remains of Ruscinian age (4.5–4.0 Ma) was found. This series is characterized by a succession of somerization cycles that show marls or calcilitites to the base and marly-limestones or limestones to the top. The ostracod assemblages allow us to differentiate between three intervals in the series. The lower one (the first 23 m) shows a predominance of *Cyprideis torosa* shells with smooth surfaces, indicating the presence of a high-salinity lacustrine environment. The intermediate interval (23–35 m) is characterized by an alternation of levels with smooth-shaped *C. torosa* shells and levels with nodose-shaped *C. torosa* shells, which indicates a period of changing salinity. The upper interval (35–55 m) shows a clear predominance of *C. torosa* shells of nodose surface, which points to a period of lower salinity.



New information on the Middle Jurassic lepidosauromorph *Marmoretta oxoniensis* from synchrotron tomography

***Elizabeth Griffiths¹, Roger B. J. Benson¹, David Ford¹, Susan E. Evans² and Vincent Fernandez³**

¹University of Oxford, UK

²University College London, UK

³Natural History Museum, London, UK

The anatomy and ecology of stem-group lepidosaurs is poorly known, obscuring the context of early lepidosaur evolution. Stem-group lepidosaurs are currently represented by a few taxa, primarily early-late Triassic in age. *Marmoretta oxoniensis* is a fossil lepidosaur from the Bathonian of the UK and Portugal. The most complete specimen, NMS G1992.47.1a–b, from the Kilmaluag Formation of Skye, was first described by Waldman and Evans in 1994. Only a few bones projecting from the surface of its slab were visible, providing a relatively incomplete account of its morphology. Synchrotron tomography with phase contrast allows description of the complete specimen in 3D, providing new data on the skull and postcranium within the matrix. *Marmoretta oxoniensis* possesses an unusually large squamosal, large midline parietal crest, and an ecologically-specialized manus morphology including long, dorsoventrally curved penultimate phalanges and tall, narrow unguals. This is comparable to extant arboreal lizards such as *Gekko gekko* and *Basiliscus basiliscus*, and to the Early Cretaceous lizard *Scandensia ciervensis*, among others. These observations contradict previous suggestions that *Marmoretta* was aquatic, based on its abundance in water-lain sediments. Sedimentological data for the Kilmaluag Formation indicates that *Marmoretta* inhabited a marginal marine environment, an estuarine environment analogous to extant mangrove forests.

Redox controls on the preservation of organic fossils through the Neoproterozoic and the Cambrian

Romain Guilbaud¹, Ben J. Slater², Thomas H.P. Harvey³ and Nicholas J. Butterfield⁴

¹CNRS Géosciences Environnement Toulouse, France

²Uppsala University, Sweden

³University of Leicester, UK

⁴University of Cambridge, UK

Small carbonaceous fossils (SCFs) offer a substantial alternative to the records from shelly fossils and rare ‘exceptionally preserved’ biotas in reconstructing the Cambrian radiation. Because of their organic nature, SCFs may fossilize where the preservation of mineralized forms is otherwise compromised and, because of their small size, they are less prone to alteration than larger structures (*e.g.* Burgess Shale macrofossils). However, the taphonomic pathways which control their preservation are poorly understood. Here, we studied C, Fe and P systematics throughout eight cored SCF-bearing sections from early- to middle-Cambrian strata of the Baltic Basin. We evaluate the role of major geochemical processes usually associated with ‘exceptional preservation’ of organic remains, including phosphatization, pyritization and the involvement of highly reactive iron minerals. We found that water column redox chemistry exerts major controls on SCF preservation, patterned by anoxic and iron-rich conditions. We draw comparisons with geochemical patterns exhibited for the preservation of macroscopic organic compressions in equivalent sediments, and for early to mid-Neoproterozoic acritarchs. We find a remarkable similarity in the taphonomic behaviour of SCFs and ornamented Neoproterozoic acritarchs,



suggesting that a ferruginous water column may be a prerequisite for the preservation of delicate organic fossil structures.

Changes in the morphological features of ostracods along the facies gradient in the Late Ordovician shelf basin

***Stefi Guitor and Tõnu Meidla**

University of Tartu, Estonia

Several studies address the relationships between the systematic composition of ostracods and palaeoenvironmental conditions in the early Palaeozoic seas but relationships between the distribution of morphological features and changing palaeoenvironmental conditions have never been analysed quantitatively. The highly diverse and abundant Ordovician ostracod fauna in Baltoscandia shows excellent preservation and has a great potential of revealing principal trends of changes along the facies gradient. The published distribution data of the Late Ordovician ostracods in Estonia, complemented with previously unpublished quantitative data (specimen counts), served for analysing the main trends of changes in roundness, shape, convexity and spinosity of ostracod carapaces, dimorphism, data on sculpture and ornamentation of the valve surface and morphology of the median sulcus (S2) in palaeocopes. The changes in dominant morphology were analysed in several stratigraphic intervals (regional stages) in core sections forming profiles that were nearly parallel to the facies gradient. The generally accepted view on diversity decrease in relation to increasing depth was supported but the observed trends in carapace morphology did not fully support previous views, *e.g.* on relationships between the granulometric composition of the sediment and roundness of the carapace and on distribution of ornamented and unornamented taxa and carapaces.

New records of rostroconch molluscs from the Ordovician of Gondwana

Juan Carlos Gutierrez-Marco¹ and Artur A. Sá²

¹*Instituto de Geociencias (CSIC-UCM), Spain*

²*UTAD - University of Trás-os-Montes and Alto Douro, Portugal*

Rostroconch molluscs are relatively rare fossils from Ordovician clastic sediments deposited at high to intermediate palaeolatitudes in Gondwana (present day circum-Mediterranean Europe and North Africa, and the Central Andean Basin of South America). In the present work we added new records of ribeirioid rostroconchs from Argentina, Bolivia, Morocco, Peru and Spain that expand the geographic distribution of some genera and species. We also include here new taxa with potential interest for the supra-generic classification. The main taxonomic novelties from South America are the identification of *Ribeiria* cf. *compressa* in the Tremadocian of the Cordillera Oriental of Argentina, and of a new species of *Ribeiria* from Floian strata of the Cordillera Oriental of Peru. In North Africa, ribeirioid rostroconchs (*Ribeiria*, *Tolmachovia*, *Technophorus*) are documented in diverse Ordovician formations from the Moroccan Anti-Atlas, with *Ribeiria apusoides* confidently recognized for the first time outside Bohemia. Finally, in the Middle Ordovician of Spain we have recorded several representatives of *Ribeiria*, *Tolmachovia*, *Technophorus* and ?*Anisotechnophorus*, and possibly some new taxa whose study will require additional material.



Eckicrinidae – a new lineage of Triassic crinoids

Hans Hagdorn

Muschelkalkmuseum Ingelfingen, Germany

The Middle Triassic *Eckicrinus radiatus* is only known from stalk fragments but is well characterized by low cylindrical columnals, long bifurcating crenulation, and cirrus sockets that are usually small but may be extremely enlarged in dististele extending to adjacent internodals. Their multiradiate articulations question the original assignment to Holocrinidae which have synarthrial articulations. New finds suggest establishing the new family Eckicrinidae: 1) a distal pluricolumnal consisting almost exclusively of cirrinodals with inflexible multiradiate radicular cirri represents an attachment mode not observed before among Triassic crinoids; 2) undescribed Early Triassic Eckicrinidae from Timor comprising specimens with holdfasts and such with large multiradiate radicular cirri. These are explained by secondary growth after column break enabling the crinoids to re-attach. As early as in Olenekian times, three modes of substrate attachment occur: 1) by incrusting holdfasts (Eckicrinidae, later typical for Encrinida); 2) by motile cirri with synarthrial articulations allowing re-attachment (Holocrinidae, early Isocrinidae); 3) by prop-like immotile multiradiate radicular cirri (secondarily among Eckicrinidae). Post-Palaeozoic crinoids are regarded as offshoots of advanced Cladida. Their putative common ancestor had a stalk with both a holdfast and cirri. Synarthrial cirrus articulation is an Early Triassic synapomorphy of the holocrinid lineage which became the most successful post-Palaeozoic crinoid clade.

Smithian and Spathian (Olenekian, Early Triassic) palaeoecology of central Spitsbergen, Svalbard

***Bitten B. Hansen¹, Øyvind Hammer¹, Jørn H. Hurum¹, Morgan T. Jones²,
Elke Schneebeli-Hermann³ and Hugo Bucher³**

¹Natural History Museum, University of Oslo, Norway

²University of Oslo, Norway

³University of Zurich, Switzerland

The Early Triassic recovery was initially considered a slow process that did not lead to diverse ecosystems until the Anisian. Recent discoveries of Olenekian diverse ecosystems have shifted the views on how recovery rates differ significantly between regions and ecological communities. Also, more details are being gathered on the global crisis around the Smithian–Spathian boundary (SSB). In an ongoing project, the Olenekian marine deposits of Svalbard, Arctic Norway, are being reassessed to construct a detailed regional palaeoecology. Of special interest is the existence of a rich fossil deposit from the Spathian displaying a diverse nekton. Both fossil and geochemical interpretations are integrated with the palaeoecological reconstruction. Emphasis is put on the placement of the SSB in order to recognize local events associated with the boundary. Current results from the project confirm an Hg/TOC anomaly in the Olenekian but place it in the middle Smithian and question any causal link with the SBB crisis. The nektonic Spathian fossil deposit has been excavated and identifications are in progress. The morphological evolution of the Smithian ammonoid *Arctoceras blomstrandii* is being quantified. Further research in the Olenekian invertebrate faunas is under way to gain a comprehensive understanding of the palaeoecological development in the Boreal region.



Ion beams versus fossil cells; novel imaging technology reveals structure of osteocyte networks in early vertebrates

Yara Haridy¹, Markus Osenberg², André Hilger², Ingo Manke² and Florian Witzmann¹

¹Museum für Naturkunde, Berlin, Germany

²Helmholtz Centre for Materials and Energy, Germany

The first true vertebrate bone in the fossil record is that of heterostracans and is anosteocytic (lacks bone cells), followed by osteocytic bone, an innovation of the jawless osteostracans, sister-group to all jawed vertebrates. Osteocytes are bone cells imbedded in mineral matrix, their lacunae and canaliculi spaces are preserved in fossilized bone and serve as an established proxy for these cells. Virtually nothing is known about what physiological pressures would have initially favoured osteocytic bone over anosteocytic bone. This gap in knowledge is largely due to previous studies being limited to histological sections or high-resolution synchrotron tomography. In this study focused ion beam-SEM tomography (FIB) is used for the first time to image fossil material, providing novel high-resolution 3D images of the first observable cell spaces in the fossil record. Osteostracan and ‘placoderm’ bone was sampled using FIB, revealing the intricate lacuna-canalicular network in stunning detail. This allows for morphological description of early osteocytes, and the first cell connectivity analyses to be performed on the oldest bone. We anticipate this new application of FIB will provide resolution comparable to modern cell biology for future palaeontological research, allowing for further testing into the origins of mineralized tissues.

Marine biodiversity and environmental change during the Permian–Triassic mass extinction and recovery in western Utah, USA

***Elise M. Harris^{1,2} and Richard J. Twitchett²**

¹Imperial College London, UK

²Natural History Museum, London, UK

The Late Permian mass extinction most notably affected benthic marine organisms in shallow shelf settings due to climate warming and anoxic conditions. This study used quantitative palaeoecological analyses to assess how functional and taxonomic diversity of shallow marine ecosystems changed in response to this event in the Confusion Range of western Utah, USA. A total of 28 horizons spanning the uppermost Gerster and lowermost Thaynes formations yielded 36,586 identifiable fossil bioclasts, representing a minimum of 19,131 individual animals from 45 species, including bivalves, gastropods, brachiopods, bryozoans, echinoderms, ostracods and microconchids. The Permian subtidal limestones of the Gerster Formation contain high taxonomic and functional diversity assemblages (Simpson’s index = 0.85, Shannon’s index = 2.28), whereas the Lower Triassic Thaynes Formation limestones have low diversity and complexity (Simpson’s index = 0.47, Shannon’s index = 1.25). Sedimentary facies indicate stressful environments, including hypersaline lagoons with microbialites, after the extinction, which affected taxonomic and functional composition and impacted local recovery rates. Taxonomic and functional diversity correlate with bulk $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from the same horizons, highlighting the role that environmental changes such as productivity, temperature and salinity had in shaping benthic ecosystems during this important interval in Earth history.



Convergent evolution in neuropteran insect larvae: a tale of chimeras and other weird creatures

Carolin Haug and Joachim T. Haug

Ludwig-Maximilians University of Munich, Germany

Similarities between different organisms are either the result of inheritance from the same ancestor, or they evolved independently. The latter is termed convergence, although there are very different views how this term should be applied. Therefore, convergence (or convergent evolution) is often used rather qualitatively, although some quantitative approaches have been proposed in recent years. If morphological convergence is the focus of a study, measurements of different body parts are especially crucial to quantify the degree of similarity of different organisms. Here we present examples of apparently convergent evolution in larvae of different neuropteran insects (lacewings). Neuropteran larvae of different ingroups share some morphological characters, such as the mouthparts formed as stylets for catching prey, as well known from the most prominent representatives, ant lions. Yet, certain morphological details of neuropteran larvae are very characteristic for their corresponding ingroup. We investigated a large number of extant as well as fossil neuropteran larvae, the latter mainly from Burmese amber (Cretaceous, *c.* 100 Ma), and performed measurements of different morphological structures. Convergent evolution of larval characters appears to have occurred several times in Neuroptera, between different ingroups and on different body parts, sometimes resulting in larvae appearing like composite creatures or chimeras.

Geographic, taxonomic and environmental bias in the ray-finned fish fossil record

***Struan A. C. Henderson and Sam Giles**

University of Birmingham, UK

As one of the largest vertebrate groups, with around 32,000 known extant species, the Actinopterygii (ray-finned fishes) are key to understanding vertebrate evolution. How they attained this staggering current diversity is uncertain, and there has been little research to date addressing diversity trends of actinopterygians in their evolutionary history. Palaeozoic taxa in particular have received limited attention despite their substantial fossil-record and importance to early ray-finned fish evolution. Previous work on all fish groups has suggested major faunal turnover from the Devonian–Carboniferous, with actinopterygians becoming a more dominant faunal component. Diversity trends within ray-finned fish specifically, however, and importantly the impact of biases on the record of the group, have not been closely examined. Here we show with a novel occurrence dataset that the diversity of the actinopterygian fossil record is tightly linked with localities and formations and fluctuates through time by environment, indicating sources of sampling and environmental bias. Occurrences are highly concentrated in regions that industrialized early and have established academic institutions, showing geographic and collector biases, though this changes in recent years. Furthermore, comparison of species- and genus-level diversity shows that peaks in species counts are largely due to high species diversity within poorly-defined ‘waste-basket’ genera.



Glendonite occurrences in the Tremadocian of Baltica: first early Palaeozoic evidence of massive ikaite precipitation at temperate latitudes

Lars Holmer^{1,8}, Leonid Popov², J. Javier Álvaro³, Mansoureh Ghobadi Pour⁴, Andrei Dronov⁵, Oliver Lehnert⁶, Olle Hints⁷ and Zhifei Zhang⁸

¹Uppsala University, Sweden

²Amgueddfa Cymru – National Museum Wales, UK

³Instituto de Geociencias (CSIC-UCM), Spain

⁴Golestan University, Iran

⁵Geological Institute, Russian

⁶GeoZentrum Nordbayern, Germany

⁷Institute of Geology, Estonia

⁸Northwest University, China

The Tremadocian is currently considered a time span of greenhouse conditions. In the high-latitude Baltoscandian Basin, these data are in contrast with the discovery of glendonite, a pseudomorph of ikaite ($\text{CaCO}_3 \cdot 6\text{H}_2\text{O}$) and valuable indicator of near-freezing bottom-water conditions. Previous records of glendonites display an apparent gap from Neoproterozoic to Permian times. However, similar calcareous nodular aggregates embedded in Tremadocian black shales of the East Baltica have been known for more than 150 years. During Tremadocian times, the basinal depocentre recorded black shale deposition episodically punctuated by wave and storm-induced processes. In contrast, nearshore environments comprised uncemented, well-washed, cross-laminated quartzose sands, which included high concentrations of allochthonous obolid coquinas that were continuously reworked along the shorelines. The most surprising aspect of this new record is that the precipitation of glendonite is contemporaneous with the record of conodonts displaying low $\delta^{18}\text{O}$ values, which would suggest high temperatures ($>40^\circ\text{C}$) in the water column. Therefore, the early Tremadocian sediments of Baltoscandia contain both 'greenhouse' pelagic signals and near-freezing substrate indicators. This apparent paradox may suggest both the influence of isotopically depleted freshwater yielded by fluvial systems, and the onset of sharp thermal stratification patterns in a semi-closed basin.

New material of *Tetraclaenodon* (Mammalia, 'Condylarthra'), from the San Juan Basin, New Mexico, USA, reveals insights into its evolution and palaeoenvironment

***Sofia Holpin¹, Thomas E. Williamson², Sarah L. Shelley³ and Stephen L. Brusatte¹**

¹University of Edinburgh, UK

²New Mexico Museum of Natural History and Science, USA

³Carnegie Museum of Natural History, USA

During the early Cenozoic, mammals rapidly diversified and dispersed, rising to taxonomic and ecological dominance beyond their Mesozoic norms. Among the initial groups that ushered in the Age of Mammals, early Palaeogene 'condylarths' are thought to include the ancestors of extant odd-toed ungulates. Within the 'condylarth' group Phenacodontidae, *Tetraclaenodon* is the oldest genus and was a medium sized, lightly built (average body mass ~10 kg) terrestrial mammal. We assessed 124 teeth of *Tetraclaenodon* using statistical and multivariate analyses in order to explore dental and body mass variations throughout its evolutionary history. Molar measurements were subject to principal component analysis



to test for trends over time. Body mass estimates were obtained via a regression equation of the area of m1. The specimens were ordered by their biostratigraphical reference into six time bins, from Tj1 (~63.8 Ma) through Tj6 (~62.4 Ma). Our results suggest that Torrejonian populations of *Tetraclaenodon* were relatively constant in body size throughout Tj1-3, but between Tj3 and Tj4 underwent an increase in body mass and a shift in dental proportions that subsequently stabilized. A similar trend is seen in contemporary populations of the periptychid 'condylarth' *Periptychus*, suggesting that there were selective environmental pressures acting on these species.

A sessile Early Cambrian lobopodian

Richard J. Howard^{1,2,3}, Xianguang Hou³, Gregory D. Edgecombe^{2,3}, Tobias Salge⁴, Xiaomei Shi³ and Xiaoya Ma^{1,2,3}

¹University of Exeter, UK

²Natural History Museum, London, UK

³Yunnan University, China

Facivermis yunnanicus is a worm-like animal from the early Cambrian Chengjiang biota of south-western China. It represents a bilaterian with five pairs of spiny anterior arms, an elongated body, and a swollen posterior. This unusual morphology has prompted diverse interpretations. Initially compared to annelids, authors later considered *Facivermis* more similar to lobopodians – the fossil grade modern panarthropods (arthropods, onychophorans and tardigrades) derive from. However, some continued to support an annelid affinity for *Facivermis*, and radically different affinities have also been proposed (e.g. Lophophorata, Pentastomida). As such, the evolutionary significance of *Facivermis* is not well characterized, and previous description as a burrowing predator is poorly supported. We re-examine *Facivermis* from new material as well as its holotype in order to assess its systematic position and ecomorphology. Phylogenetic analyses under parsimony, Bayesian inference and maximum likelihood all support a luolishaniid lobopodian affinity for *Facivermis* within the onychophoran stem group, revealing a series of secondary losses to accommodate a sessile, tube-dwelling lifestyle – uniquely among lobopodians. Our study reveals that the superficially worm-like *Facivermis* was not intermediate between cycloneuralian and panarthropod body-plans (i.e. representing an endobenthic – epibenthic panarthropod transition as previously suggested) and therefore the phylogenetic origin of paired appendages remains obscure.

An investigation into the effect of phylogeny on the inferred biogeography of Ornithopoda (Dinosauria: Ornithischia)

***Katy Hudson and Susannah C. R. Maidment**

Natural History Museum, London, UK

Ornithopoda were an extremely successful group of herbivorous ornithischian dinosaurs, achieving a global distribution as the clade diversified across most of the Mesozoic from the Middle Jurassic to Late Cretaceous, a temporal scale which encompasses a huge amount of palaeogeographic change: the breakup of the supercontinent Pangea. This vast spatiotemporal distribution makes ornithopods a particularly interesting subject for biogeographical analysis. In addition, the systematic position and interrelationships of ornithopods remain uncertain, and hypotheses have continued to change with the discovery



of new fossils, taxonomic revisions, and continued development of phylogenetic methods. Here we use a comparative, historical approach to investigate the effect of increased taxonomic sampling and changing phylogenetic hypotheses on the estimated ancestral area of ornithopods. Using selected phylogenies from the literature, we test the robustness and stability of results of biogeographical testing across changing phylogenies from the last twenty years. Biogeographical analyses of each phylogeny with BioGeoBEARS estimate different areas of origin for both the ancestral node of Ornithopoda and clades within the group, indicating that biogeographic inferences are sensitive to changes in phylogeny, taxonomic sampling, and in some cases, changes in palaeogeographic scenario.

A new bivalved arthropod from the Burgess Shale with a unique posterior shield: a case of convergence?

***Alejandro Izquierdo Lopez¹ and Jean-Bernard Caron^{1,2}**

¹*University of Toronto, Canada*

²*Royal Ontario Museum, Canada*

The body of Cambrian ‘bivalved arthropods’ is typically composed of a cephalo-thorax and a telson bearing caudal rami. Here we present a new bivalved arthropod from the Burgess Shale Marble Canyon locality in Kootenay National Park, British Columbia, Canada which is instead equipped with a large posterior shield. About 1–2.5 cm in length, this species has an ovoid cephalo-thoracic carapace that covers two thirds of its length. A single antero-ventrally curved spiny process separates two pedunculated eyes, and the carapace also possesses two small processes on the antero-ventral margins. The cephalic appendages are poorly differentiated, although a pair of frontally oriented limbs may represent antennae. The thorax is elongated, with *c.* 35 homonomous segments bearing undifferentiated, possibly uniramous limbs, subdivided into *c.* 24 or more podomeres that taper in length frontally and posteriorly. Most remarkably, the last 12 thoracic segments of the body extend ventro-laterally and posteriorly into a single posterior shield with spiny margins. This structure is reminiscent of a pygidium, a plate-like structure that covers multiple hind-limbs commonly found in artiopods and basal chelicerates; a close connection to these groups is contradicted by other aspects of the body plan, suggesting instead an unusual case of convergence.

A Mid-Cretaceous amber lizard preserves evidence of male anatomy

Kelsey M. Jenkins¹, Emily Stelling² and Juan D. Daza²

¹*Yale University, USA*

²*Sam Houston State University, USA*

Mid-Cretaceous Burmese amber is well-known for preserving a plethora of organisms spanning plants, fungi, arthropods, and micro-vertebrates. Vertebrates are commonly represented by only partial elements, like a tail, single wing or foot, but some miniaturized vertebrates are preserved in full. The diversity of squamates recovered from burmite includes gekkonomorphs, anguimorphs, iguanians, lacertoideans and possibly snakes. Here we present a squamate from those deposits that preserves skin, enclosing a void space that only contains appendicular elements. The scales are preserved in fine detail, conserving keels, and includes well-defined scales in the cloacal region. Bulging near the cloaca at the base of the tail (interpreted as the hemipenal bulge) indicates that the specimen is male, and



possibly represents the oldest definitive male squamate. While more diagnostic elements like the skull are not preserved, preventing diagnosis to lower taxonomic levels, the scales and overall body form ally this specimen with either gekkonids or scincomorphans. Other amber lizards and anurans from the same deposit, as well as other amber deposits, record similar preservation, indicating a peculiar but perhaps common taphonomic effect associated with internal decomposition after being embedded in amber.

Taphonomic control on trace fossil distribution in the late Ediacaran Cijara Formation, Spain

Sören Jensen¹, J. Javier Álvaro² and Teodoro Palacios¹

¹Universidad de Extremadura, Spain

²Instituto de Geociencias (CSIC-UCM), Spain

The Cijara Formation is an upper Ediacaran sandstone-dominated unit, widely developed in the Central Iberian Zone of Spain, which records the effects of the active denudation of a Cadomian Arc on a retro-arc basin. The upper part comprises sandstone/shale alternations that reflect wave and storm activity associated with slope-related deposition. Trace fossils are dominated by simple horizontal forms typical of late Ediacaran successions worldwide, such as *Gordia* and *Helminthooidichnites*. Their preservation is typically related to event beds that exhumed tunnels encased in a muddy substrate, subsequently infilled with sand. Trace fossils are absent on bed soles with evidence of surficial sediment erosion, such as flute casts and tool marks, attesting to the relatively surficial and shallow nature of these trace fossils. Irregular accumulations of small sandstone fragments on bed soles are interpreted as ichnoclasts, that is, reworked sand-filled trace fossil fragments. The best preserved trace fossils are found on scattered fine-grained sandy/silty layers, where *Gordia*-type trace fossils are several decimetres long. A morphologically distinct trace fossil in these beds shows a series of tightly coiled bedding parallel traces. These observations attest to strong preservation factors controlling the trace fossil distribution in the Cijara Formation.

Famennian thylacocephalans from Morocco and their role in Late Devonian food webs

***Melina E. M. Jobbins¹, Carolin Haug² and Christian Klug¹**

¹University of Zurich, Switzerland

²Ludwig-Maximilians University of Munich, Germany

Thylacocephalans are pelagic arthropods with an erratic fossil record stretching from the Silurian, possibly Cambrian, to the Cretaceous. In the few localities where they occur, they are quite abundant. This holds true for the Thylacocephalan Layer in the Maider region (eastern Anti-Atlas, Morocco). This epicontinental basin hosts some strata with taphonomic properties of a Konservat-Lagerstätte, yielding exceptionally-preserved gnathostomes and invertebrates. A thin argillaceous interval in the earliest middle Famennian carries thylacocephalans in such great numbers that they became eponyms of this unit. Therein, we discovered two new species of thylacocephalans, *Concavicaris submarinus* sp. nov. and *Madenecaris iugumata* gen. et sp. nov., representing the first records of Thylacocephala from Africa. In the CT imagery, the holotype of *Concavicaris submarinus* sp. nov. revealed anatomical details including its eyes, appendages, and some muscles. Facies and faunal composition of the Thylacocephalan Layer suggest that these



animals populated the water column above the low-oxygen seafloors. The Thylacocephalan Layer is rich in remains of chondrichthyans and placoderms. Accordingly, these putative eucrustaceans likely represented an important component of their diet. The abundance of thylacocephalans in other Konservat-Lagerstätten such as the Cleveland Shale (USA) and the Gogo Formation (Australia) underline their key role in Late Devonian pelagic food webs.

Uneven spatial sampling in Phanerozoic palaeoclimate curves

***Lewis A. Jones¹, Kilian Eichenseer² and Claire Veillard³**

¹Imperial College London, UK

²University of Plymouth, UK

³Equinor ASA Oslo, Norway

Reconstructions of global palaeoclimate are widely used to test evolutionary hypotheses and to act as a baseline against projected global warming, but their accuracy is hampered by uneven spatial sampling. Whilst the palaeontological community has accounted for biases through estimates of sample-standardized diversity, less attention has been given to similar biases in palaeoclimatic reconstructions, such as the global Phanerozoic temperature curve. The spatial distribution of palaeoclimatic data remains influenced by variable stratigraphic completeness and by preferential geographic sampling, despite a continuous increase in the amount of data. Thus, global mean temperatures stem from samples that are often concentrated in relatively few geographic regions, or climate zones. Here we assess the impact of spatial biases by rarefying present-day temperatures to sampling levels representative of palaeotemperature records. We use these results to yield a fairer representation of the evolution of global Phanerozoic temperatures, and open the discussion of how to best standardize climate proxy records.

Pterosaur predation on coleoids in the Late Jurassic and implications for their palaeoecology

Christian Klug¹, Dirk Fuchs² and René Hoffmann³

¹University of Zurich, Switzerland

²SNSB–Bavarian State Collection of Palaeontology and Geology, Germany

³Ruhr-Universität Bochum, Germany

Late Jurassic conservation deposits of southern Germany yield abundant coleoids, commonly preserved with soft tissues. Particularly, mantle remains and the ink sac are present in many cases. Additionally, there is a broad range of differently-sized species ranging from over 1 m long *Leptoteuthis* to the minute muensterellid *Tyrionella*, which probably did not grow much larger than 20 mm. Here we present some newly discovered species and new cases of predator-prey-relationships. The most spectacular example is a complete specimen of *Plesioteuthis*, which preserves all soft-parts, and which displays a tooth of the pterosaur *Rhamphorhynchus* in its mantle. Since the tooth is surrounded by phosphatized soft tissue, we conclude that this represents evidence of a failed predation attempt by the pterosaur on this coleoid. In light of the new findings, we discuss the behaviour of predator and prey as well as the positions of coleoids in Late Jurassic foodwebs of the Solnhofen Archipelago.



The ethological nature of full-body impressions

***Richard Knecht¹, Jacob Benner² and Javier Ortega-Hernández¹**

¹*Harvard University, USA*

²*University of Tennessee, USA*

Ethological categories (as parataxonomies) for trace fossils were first suggested by Seilacher in 1953. The original proposal consisted of five categories: cubichnia (resting), domichnia (dwelling), fodichnia (feeding), pascichnia (grazing) and repichnia (locomotion). Since then, ethological classification has been modified and expanded with the present number of categories at fourteen and several additional subcategories. The category cubichnia has remained relatively unchanged since its inception and is commonly referred to as ‘resting traces’, or more aptly put, a temporary cessation of locomotion. However, these two criteria of cubichnia, resting (as an ethological interpretation) and temporary immobility (as a temporal interpretation), are neither definable nor quantifiable in the trace fossils themselves and therefore invalidate cubichnia as an ethological category. Using apterygote and pterygote full-body impressions from the Late Carboniferous Wamsutta Formation of Massachusetts, USA, we explore the limitations of cubichnia as an ethological category. The nature of these full-body impressions blurs the distinction between the systematics of traces and trace makers, thus adding to the debate surrounding ichnotaxonomy for traces with well-associated trace makers.

Peteinoid acritarchs from the Ordovician of Öland, Sweden: many ecophenotypes of one single organism?

***David M. Kroeck¹, Mats E. Eriksson², Anders Lindskog², Axel Munnecke³ and Thomas Servais¹**

¹*CNRS UMR 8198, Université de Lille, France*

²*Lund University, Sweden*

³*University of Erlangen–Nuremberg, Germany*

The classification of acritarchs remains a major problem for studies of this heterogeneous fossil group. It can be assumed that a large number of the taxa described are not real biological entities but rather represent different (eco-)phenotypes. Thus, whereas morphological changes have been interpreted mostly as the result of evolution, in many cases they rather seem to reflect changing environmental conditions. Previous investigations have also shown a large intraspecific morphological variability among many acritarchs. Here we present a new study on populations of peteinoid acritarchs from Ordovician sections on Öland, Sweden, including statistical analyses based on morphometric measurements. Whereas the peteinoid acritarchs from these localities have been described as species rich, the results of a principal component analysis indicate that many of the taxa recorded only represent morphotypes from a wider cluster of morphologies, and cannot be considered distinct species. Several extant dinoflagellates are known to develop variable cyst morphologies depending on environmental factors, *e.g.* temperature and salinity. Considering that many acritarchs are probably resting cysts of dinoflagellate-like organisms, the different peteinoid acritarch morphologies observed likely represent a response to changing environmental conditions.



Morphological traits and macroevolution of Cenozoic planktonic foraminifera

***Grace Lamyman¹**, **Barry G. Fordham²**, **Paul N. Pearson³**, **Bridget S. Wade⁴**, **Jeremy R. Young⁴**
and **Tracy Aze¹**

¹*University of Leeds, UK*

²*Australian National University, Australia*

³*Cardiff University, UK*

⁴*University College London, UK*

Planktonic foraminifera have one of the most complete fossil records of the Cenozoic Era; as such they are widely employed for micro and macroevolutionary analyses. Much of this research effort is focused on analyses of measurable morphological traits. At present, there is a disparate literature describing which of these measurable traits have been observed to be related to a biological function and, in turn, impact fitness. This research presents an integrated approach to synthesizing updated phylogeny of the planktonic foraminifera, including microperforate and macroperforate species, detailing both morphospecies and evolutionary lineage relationships throughout the last 66 million years. To supplement the phylogenies we have collated the data of the functional roles of all commonly-measured planktonic foraminifera morphological traits and arranged the features in order of certainty of function and importance to the organisms' fitness and ecosystem functioning. A trait function hierarchy has been established, for traits with 1) known, 2) possible and 3) unknown functional affinity. Traits will be mapped onto an updated phylogeny allowing the assessment of rates of trait evolution throughout the last 66 million years, with particular focus on the relationship between the recovery of diversity and disparity of this clade after the end-Cretaceous mass extinction.

Reconstructing the Pleistocene (Calabrian) habitats of hominins in continental East Asia: a new multi-proxy approach

***Catherine Langford¹**, **Steffen Mischke¹**, **Hialong Zhao²** and **Chengjun Zhang³**

¹*University of Iceland, Iceland*

²*Hebei Normal University, China*

³*Lanzhou University, China*

Several important hominin sites composed of fluvio-lacustrine deposits occur in the Nihewan Basin (Pleistocene, Calabrian, *c.* 1.6 – 0.8 Ma), northern China. Many sites have a magnetostratigraphic chronology alongside lithological and sedimentological data. However, for sites lacking magnetostratigraphy, their integration into a broader picture of early hominin habitats in this region remains problematic. This study aims to rectify this by using ostracods, regionally recognized synchronous sedimentary patterns, grain size analysis and isotope analysis to provide additional tools for correlation. Eight sites in the Nihewan Basin have been analysed with this new multi-proxy approach. Here we demonstrate a correlation between the previously documented Majuangou and Banshan sites with a new site at Shigou. An ostracod assemblage of 13 different cold stenothermic, non-marine fluvio-lacustrine species supports this correlation. A repetitive disappearance and reappearance of the ostracod species *Ilyocypris* suggests a similar but fluctuating aqueous environment. Dramatic changes in ostracod concentration, alongside erosional boundaries and sudden changes in sedimentology, provide new evidence for flooding events in the basin. The occurrence of a river at Shigou has also been inferred from similar analyses. These analyses have resulted in high-resolution stratigraphy, suggesting that the fluvio-lacustrine environment of the Nihewan Basin fluctuated constantly within the Calabrian.



Widespread functional diversity in morphologically convergent sabre-tooth vertebrates

Stephan Lautenschlager¹, Borja Figueirido², Thomas Stubbs³ and Eva-Maria Bendel^{4,5}

¹University of Birmingham, UK

²Universidad de Málaga, Spain

³University of Bristol, UK

⁴Museum für Naturkunde, Berlin, Germany

⁵Humboldt-Universität zu Berlin, Germany

The acquisition of elongated, sabre-like canines in at least six different vertebrate clades during the last 265 million years represents a remarkable example for convergent evolution. Sabre-tooth morphologies have evolved independently in Permian mammal-like gorgonopsians, in the marsupial *Thylacosmilus* and in five different groups of carnivorous mammals. Due to the striking similarities in the cranial skeleton, the same/similar skull and jaw functions have been inferred and interpreted as adaptation to the hunting and killing of large-bodied prey. Although sabre-tooth felids have been divided into separate ecomorphologies – dirk-toothed and scimitar-toothed taxa – the functional diversity within and between groups and the evolutionary trajectories leading to these specializations is unknown. Using digital visualization, biomechanical analyses and evolutionary modelling, functional performance measures (absolute/effective jaw gape, bite force, mandibular stability) were compared across seven groups of sabre-toothed vertebrates. The results demonstrate that these performance measures varied considerably between different groups and between different species. Functional diversity was widespread among sabre-toothed species, and cranial function and prey-killing strategies progressed along a continuum but are largely obscured by superficial morphological similarity. Opposing biomechanical trends in sabre-tooth felids further suggest that this functional diversity was at least partially driven by niche-partitioning to avoid intra- and inter-clade competition.

New thylacocephalans from Mazon Creek: a new insight into thylacocephalan lifestyle

Thomas Laville^{1,2}, Joachim T. Haug² and Carolin Haug²

¹Muséum national d'Histoire naturelle, Paris, France

²Ludwig-Maximilians University of Munich, Germany

Thylacocephala is an enigmatic ingroup of Euarthropoda known from at least Silurian (~435 Ma) up to the late Cretaceous (~85 Ma). Anatomy, mode of life and phylogenetic affinities of Thylacocephala still remain largely unknown. They are characterized by a prominent bivalved shield enveloping most of the body, large compound eyes, three pairs of large, presumably raptorial appendages and a trunk with eight to 22 stout segments bearing swimming appendages. This study is focused on thylacocephalans from the Mazon Creek Lagerstätte, USA (~307 Ma, Middle Pennsylvanian, Carboniferous). A new species is described from siderite nodules of Mazon Creek: *Eodollocaris keihtflinti* gen. et sp. nov. The new species displays a particular combination of characters typical for Palaeozoic species on the one hand and Mesozoic species on the other hand. Additionally, new details of the trunk and of the appendages are also provided for already known species from the same formation, namely *Concavicaris georgeorum* Schram, 1990 and *Convexicaris mazonensis* Schram, 1990. The new information is helpful to our understanding of the possible lifestyle of these representatives of Thylacocephala. Functional interpretation of



Concavicularis remipes Schram, 1990 also indicates a possible alternation between benthic and nektonic modes of life.

Super-traits of Ediacaran organisms from Newfoundland, Canada: establishing the key biological traits for ecosystem dynamics

***Erin Leahy, Alexander G. Liu and Emily G. Mitchell**

University of Cambridge, UK

The Ediacaran sedimentary successions of Newfoundland, Canada, record some of the oldest known palaeocommunities of large, complex organisms. Much of the biology and behaviour of these organisms remain unclear. However, as fossil positions on bedding planes can be interpreted to reflect the original biological and ecological processes affecting these sessile organisms during their lives, *in situ* preservation enables resolution of their traits. Precisely which biological traits are key to determining taxon interactions remains unknown, since specimen height and population height distributions have not been found to govern community dynamics, contrary to prior hypotheses. This study investigates whether any biological 'super-traits' (single traits that explain multiple different behaviours) exist to correlate these organisms with their community structure, allowing determination of the dominant biological controls on species distributions on Ediacaran bedding planes. 3D laser-scanning of fossil communities in the field permitted measurement of bioAreas and bioVolumes to calculate whether traits such as total branch area, unit area, or total specimen area, indicate super-traits. We then used multivariate regression analyses to determine whether any of the identified traits correlate with community metrics such as species diversity, richness, or species interactions.

Preliminary study of structural modularity in archosaurs using anatomical network analysis

***Hui Wai Lee^{1,2}, Arkhat Abzhanov^{1,2} and Borja Esteve-Altava³**

¹Imperial College London, UK

²Natural History Museum, London, UK

³Universitat Pompeu Fabra, Spain

Members of archosaur lineages are morphologically diverse from snout and serrated teeth in crocodiles to large orbits and kinetic beaks in birds. Yet, the phenotypic growth of their skulls was constrained by organizational modularity, which had not been extensively studied in avemetatarsalians. In this study, we investigated their clade-dependent topological similarities and how skull organization could act as a developmental constraint in archosaur skulls. Modules defined by bone-bone relationship were analysed using anatomical network analysis. We showed topological complexity and number of bones could discriminate avians, non-avian dinosaurs and crurotarsans by their morphospace, and corroborated with Williston's law and previous work done by Esteve-Altava *et al.* (2013). Fusion of bones was also observed with evolutionary transition as support for anisomerism (*i.e.* specialization of bones). We expanded this analysis by adding juvenile-adult pairs of extant birds and alligators, and showed 1) adult and juvenile *Alligator mississippiensis* were topologically similar; 2) juvenile birds were topologically closer to non-avian dinosaurs than adult birds, showing clade and ontogenetic difference in skull organization were due to the postnatal fusion of bones; 3) juvenile birds were also significantly different from non-avian dinosaurs and crurotarsans by the number of bones and sutures.



A possible case of neoteny in new anomalocystitid mitrates (Echinodermata, Stylophora) from the upper Emsian (Lower Devonian) of Navarra (Spain)

Bertrand Lefebvre¹, Jorge Esteve² and Samuel Zamora³

¹Université Claude Bernard Lyon 1, France

²Universidad de los Andes, Colombia

³IGME, Instituto Geológico y Minero de España, Spain

In the western Pyrenees (Navarra, northern Spain), the Arizacun Limestone located in the Basque domain of the Baztan valley has yielded a diverse, well-preserved, fully marine, Early Devonian assemblage (lower part of the upper Emsian), dominated by brachiopods, tentaculitids and trilobites. Although a minor component of this fauna, echinoderms are represented by crinoids and locally abundant remains of fully articulated mitrate stylophorans. Stylophorans are an extinct class of unattached, benthic echinoderms, consisting of a flattened body (theca) and a single feeding arm (aulacophore). The mitrates from Navarra represent not only the first record of stylophorans in the Devonian of Spain, but also their youngest occurrence in the Iberian Peninsula. They consist of a monospecific assemblage of small-sized anomalocystitids, morphologically identical (*i.e.* reduced extension of cuesta-shaped thecal ornamentation, large placocystid plate) to similarly-sized juvenile individuals of *Placocystites forbesianus* from the Wenlock of Britain. The absence of larger specimens in Navarra questions a possible ecological partitioning of juvenile versus more mature individuals, or more likely, a possible case of heterochrony (neoteny).

Middle Devonian Global Events: examples from the Iberian Peninsula (Spain)

Jau-Chyn Liao¹, José I. Valenzuela-Ríos¹ and Peter Carls²

¹University of Valencia, Spain

²University of Braunschweig, Germany

Recent study of Upper Eifelian to basal Frasnian (Middle-Upper Devonian) deposits from the Iberian Range (IR) and Central Pyrenees (CP), has revealed new, more detailed information of both the conodont sequence and global Middle Devonian bioevents. Five selected sections in the IR (Camino de Molino) and CP (Renanué, La Guàrdia d'Ares, Compte and Villech) were analysed. They document four global Devonian events of different magnitude and facies: the Kačák Event, the Pumilio Event, Taghanic Event, and Frasnian Event. The position of the two levels of the Kačák Event is tentatively traced in three sections: Camino de Molino, Renanué and La Guàrdia d'Ares. The record of the Pumilio Event is close to Bed 44 in the Renanué section. A thin black multilayer of the Villech section corresponds to a regressive pulse of the Taghanic Event. The Frasnian Event is recognized in three Pyrenean sections: Villech, La Guàrdia d'Ares and Compte. Using the conodont biostratigraphic high-resolution method, the Middle Devonian global events seem to be multiphase at least for the Kačák and Taghanic. The analysed stratigraphic framework allows recognition, characterization and timing of these four global bioevents in different settings of the Iberian Peninsula.



Picky eaters: the chemosensory capabilities of early Cambrian microborers

***Emma J. Long¹, Xi-Guang Zhang², Kate J. Dobson¹ and Martin R. Smith¹**

¹Durham University, UK

²Yunnan University, China

A subset of phosphatized microfossils from the early Cambrian Yu'anshan and Shuijingtuo formations (China) contain microborings, which represent evidence of early euendolithic activity. Examples are known from the surfaces of *Microdictyon* plates, lingulid valves, euarthropod carapaces, and tommotiid sclerites, but microborings have not been reported in contemporary trilobites or palaeoscolecid worms, indicating a degree of substrate specificity. This study uses synchrotron X-ray computed tomography to reconstruct microboring traces in three dimensions, from within a phosphatized lobopodian from China's Yu'anshan Formation. The borings comprise hundreds of blind-ended tubular structures within the fossil, in contrast to the solely superficial borings that have previously been reported. Most microborings belong to a population with a modal diameter of 13 µm. The presence of a further microboring morphology, with a notably larger diameter of 30 µm and stunted distal bifurcations, indicates an assemblage of two microborer species. The microborer's paths deflect away from body cavities, without intersecting them. This suggests chemosensory capabilities that enabled the borers to avoid open cavities, and thus remain in the phosphatized soft tissue of the animal.

The onychophoran protocerebrum was ancestrally bipartite: developmental evidence from a phosphatized early Cambrian lobopodian

***Emma J. Long¹, Xi-Guang Zhang², Jie Yang², Kate J. Dobson¹ and Martin R. Smith¹**

¹Durham University, UK

²Yunnan University, China

The arthropod head is an evolutionarily and morphologically plastic region comprising modified appendage-bearing segments. Despite almost 45 years of genetic and palaeontological research, the homologies of these segments remain disputed. The last common ancestor of bilaterians possessed an asegmental labral *optix* domain, which lacked the *engrailed* (*en*) segment boundary indicator gene, and a segmental *orthodenticle* (*otd*) domain, which expressed both eyes and *en*. These regions fused into a single 'head segment' on at least two occasions, once in the arthropods and once in the distantly-related annelids. But how this fusion occurred, and whether these elements were once truly distinct, remains unknown. Until now, this hypothesis has been based principally on modern development, supplemented with adult arthropod macrofossils. Here we provide the first palaeodevelopmental data, from a phosphatized Cambrian (stage 3) stem-group onychophoran embryo from China's Yu'anshan Formation. This specimen possesses a bipartite protocerebrum. An apical asegmental domain contains a dorsal brain, which innervates antenniform frontal appendages. A subsequent domain, homologous with the ocular *otd* element, contains ventrolateral eyes. The unfused nature of these components indicates that the head regions fused independently in onychophorans and euarthropods, suggesting that the fused head evolved multiple times within Panarthropoda.



The actinopterygian fauna of Nusplingen (Upper Jurassic; Germany)

Adriana Lopez-Arbarello¹, Erin E. Maxwell² and Günter Schweigert²

¹Ludwig-Maximilians University of Munich, Germany

²Staatliches Museum für Naturkunde Stuttgart, Germany

The Nusplingen Lithographic Limestone has been excavated occasionally since the nineteenth century and the Stuttgart State Museum of Natural History has been carrying out scientific excavations uninterrupted since 1993. Since then, c. 350 species of excellently preserved fossil plants, animals and ichnofossils have been recorded. The entire section of the Nusplingen Lithographic Limestone is Late Kimmeridgian in age as indicated by its ammonite fauna. Nusplingen is not part of the Solnhofen Archipelago complex and the preservation of the ichthyofauna differs from the type generally observed at Solnhofen: soft tissues are not preserved, and the fishes tend to show a higher degree of disarticulation. So far, 27 actinopterygian species have been identified in Nusplingen, but none of them were studied thoroughly until recently. The fauna encompasses halecomorphs (40 %), teleosts (56 %) and one pycondont. Among the halecomorphs, we described a new genus and species with very interesting unique anatomical features. This new halecomorph is probably related to several *Furo*-like species, which are extraordinarily abundant in Nusplingen. Among the teleosts, four specimens of pachycormiforms represent at least two different taxa: *Hypsocormus macrodon* and a new genus and species. The three taxa are extremely rare and were likely occasional visitors to the lagoon.

Aimia armata and the crucial role of non-amiiform halecomorphs to understand the history of neopterygians

Adriana Lopez-Arbarello

Ludwig-Maximilians University of Munich, Germany

Within the Late Jurassic Lagerstätte complex of the Solnhofen Archipelago in Southern Germany, the oldest (Late Kimmeridgian) locality of Brunn has yielded an excellently preserved vertebrate fauna, including selachians, several groups of actinopterygian osteichthyans, and some clades of tetrapods. The halecomorphs of Brunn include potentially endemic species as well as more widely distributed Kimmeridgian taxa, which are absent in the Tithonian. Among them, an exceptionally well-preserved and complete specimen of *Aimia armata* triggered a new study of this taxon, which is easily distinguished by its peculiar pattern of squamation limited to numerous reversed rows of tiny ganoid scales covering the dorsum and ventrum of the caudal peduncle. The phylogenetic relationships of *Aimia* are explored through the cladistic analysis of a large data set, including 345 morphological characters scored for 106 taxa (32 halecomorph species, 38 ginglymodians, three dapediiforms, 29 teleosts and four more distant outgroups). Published hypotheses of halecomorph phylogenetic relationships are incompatible, and my results so far are controversial, raising questions about the monophyly of several clades and emphasizing the important role of the early Mesozoic non-amiiform halecomorph taxa to elucidate the evolutionary history of crown neopterygians. The latter topic is the main emphasis of this presentation.



Taphonomic processes leading to the exceptional preservation of trilobites from the Walcott-Rust Quarry, New York (Upper Ordovician)

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

Harvard University, USA

Trilobites are a dominant group of euarthropods from the Palaeozoic but despite their impressive diversity with over 20,000 described species, the appendicular anatomy is only known from 31 taxa. Enrolled specimens of *Ceraurus pleurexanthmus* and *Flexycalymene senaria* from the Rust Formation in Herkimer County, New York show preservation of soft tissues in a unique mode. During transportation within a turbidite, sediment infiltrated the partially enrolled trilobite, surrounding the ventral anatomy and lithifying before decay of soft tissue. Calcite precipitated in the void space left after decay in at least two phases: an isopachous rim of fibrous crystals pointing inwards and infill of large sparry crystals. Calcite is also located outside the enrolled specimen, either in pockets adjacent to the specimen or in veins through the matrix. Pyrite framboids and polyhedra co-precipitated with the calcite but are also found throughout the matrix. Sulfate-reducing bacteria appear to have moderated the chemistry within the specimen to facilitate the precipitation of calcite, but it is unclear if this was unique in enrolled individuals. Examination of hundreds of prepared thin sections with petrographic microscopy, scanning electron microscopy and cathodoluminescence further our understanding of the taphonomic processes leading to this unique mode of exceptional preservation.

A new Euchelicerate from the early Ordovician Fezouata Biota

***Lorenzo Lustri, Pierre Gueriau and Allison C. Daley**

University of Lausanne, Switzerland

The Fezouata Formation in southeastern Morocco is an Early Ordovician Lagerstätte that preserves a wide variety of non-biomineralized taxa. Two different undescribed euchelicerates are particularly abundant, a modern-looking horseshoe crab, and a taxon ascribed to the closely related ‘synziphosurines’. Specimens of the new synziphosurine taxon were examined using microscopy then photographed, and a limited number of specimens were selected for 3D surface rendering and synchrotron radiation X-ray tomographic microscopy. This taxon is characterized by the presence of biramous prosomal appendages similar to those of the Herefordshire synziphosurines, but also has characters of the prosomapoda euchelicerates, such as the ophthalmic ridge. We undertook a phylogenetic analysis to clarify the phylogenetic position of the group. The new taxon was coded into two different character matrices, which were analysed using both Parsimony and Bayesian methods. Our taxon resolves as a stem-euchelicerate with Prosomapoda affinities. Linking our new findings on euchelicerate diversity during the Great Ordovician Biodiversification Event to the earliest origin of the phylum, as recorded in the Cambrian Burgess Shale-type biotas, provides a more complete picture of euarthropod evolution during these major events.



Diverse feeding mechanics of oviraptorosaurian dinosaur jaws revealed by finite element analysis

***Wai Sum Ma¹, Stephan Lautenschlager¹, Michael Pittman² and Richard J. Butler¹**

¹University of Birmingham, UK

²The University of Hong Kong, Hong Kong

Oviraptorosaurs are a group of feathered dinosaurs that have anatomical features that deviate from those of other theropods, which include the possession of a relatively deep, pneumatized skull and a beak. Basal oviraptorosaurs have undergone partial tooth reduction while the more advanced ones – caenagnathids and oviraptorids – are completely edentulous. Investigating the mandibular function of oviraptorosaurs by qualitative comparison is challenging because their toothless jaws lack obvious adaptations to a certain kind of diet. Here we conduct the first comprehensive investigation into the functional morphology of oviraptorosaur jaws using finite element analysis (FEA). Sixteen 2D FEA models of basal oviraptorosaurs, caenagnathids and oviraptorids were constructed. Three-dimensional FEA models of *Gigantoraptor* and *Nemegtomaia* were developed using photogrammetry and digital restoration. Comparison between 2D and 3D FEA models confirms 2D models are good representations of the jaw biomechanics. In general, the jaws of oviraptorids are more resistant to dorsoventral bending and feeding-induced stress, and have higher bite efficiency compared to those of caenagnathids. Substantial differences in jaw biomechanics are observed in the three major clades of oviraptorosaurs, suggesting the presence of feeding specialists. Our results reveal a diverse functional capacity among oviraptorosaur jaws, which potentially indicates a wide inter- and intra-clade dietary range.

Spatial and temporal shifts to Southwestern Atlantic oceanography during the Late Quaternary, using Uruguayan margin planktonic foraminiferal records

***Andrew Mair, Ruza F. Ivanovic, Robert J. Newton, Jason Harvey and Tracy Aze**

University of Leeds, UK

The Brazilian-Malvinas Confluence (BMC) is sited off the Uruguayan margin and represents an important oceanographic heat exchange between the warm Brazilian Current and cool Malvinas Current, thermally regulating the South Atlantic Ocean. A primary control on planktonic foraminiferal species occurrence is the water temperature in which the species dwell; the contrasting water mass temperatures within the BMC therefore influence proportions of subtropical versus subpolar species in foraminiferal assemblages. Mixing of these two thermally-contrasting water masses leads to rapid shifts in the proportion of planktonic foraminiferal species present margin-wide. This project utilizes a dense collection of core tops to map in high resolution the transition between warm and cold foraminiferal assemblages based on known species ecologies. This forms a ‘modern’ baseline against which to assess temporal variation of fossil assemblages, and in turn determine north/south BMC migration. Down core assemblage studies and isotopic analysis seek to assess changes from the oceanographic status quo using the most northern core of the collection, UPC 028, to determine shifts from the present warm-subtropical status. Initial findings of down core assemblages and isotopic data suggests temporal variation in the water masses bathing UPC 028, impacting the foraminiferal communities present and implying BMC migration.



Amphibians and reptiles from Upper Unit V from El Salt (Alcoi, Spain): palaeoenvironmental and palaeoclimatic implications

***Rafael Marquina Blasco**^{1,2}, **Ana Fagoaga Moreno**^{1,2}, **Vicente Daniel Crespo Roues**^{2,3,4},
Francisco J. Ruiz-Sánchez^{2,5}, **Salvador Bailon**⁶, **Carolina Mallol**⁷, **Cristo M. Hernández Gómez**⁷
and Bertila Galván Santos⁷

¹University of Valencia, Spain

²Museu Valencià d'Història Natural, Spain

³Museo Paleontológico de Alpuente, Spain

⁴Museo de La Plata (UNLP), Argentina

⁵Universidad Estatal Península de Santa Elena, Ecuador

⁶CNRS UMR 7194, Muséum National d'Histoire Naturelle and Sorbonne Universités, France

⁷Universidad de La Laguna, Spain

El Salt (Alcoi, Spain) has provided valuable data regarding the context of Neanderthal extinction in the region. In fact, one of the last records in south-eastern Spain has been recovered from the base of Unit V. Most parts of this unit are archaeologically sterile; however, in its uppermost part, dated at 44.7 ± 3.2 kyr (MIS 3), some remains of human activity have been recovered, but without the possibility of ensuring its precise cultural attribution. The herpetofaunal assemblage described is composed of four anurans (*Anura* indet., *Pelodytes* sp., *Alytes obstetricans* and *Epidalea calamita*), three lizards (*Lacertilia* indet., *Lacertidae* indet. and *Chalcides bedriagai*) and nine snakes (*Serpentes* indet., *Colubridae* indet., *Colubridae* indet. 2, *Coronella* sp., *Coronella* sp./*Zamenis* sp., *Natrix maura*, *Malpolon monspessulanus*, *Viperidae* indet. and *Vipera latastei*). In order to reconstruct the climate at the time of formation of the unit, we studied the current distribution of the species described by using Mutual Ecogeographic Range (MER) method. Preliminary results suggest a mean annual temperature of 11.37 ± 4.32 °C and a mean annual precipitation of $1,665.00 \pm 213.13$ mm. These results show a colder and slightly wetter climate than those recorded in Alcoi at the present day. The surrounding area of El Salt would be dominated by open dry areas, alternating with rocky areas and scrub and forest patches.

Sinotubulites: growth and close phylogenetic relationship with *Cloudina*

Monica Marti Mus¹, **Sören Jensen**¹, **Ivan Cortijo**² and **Teodoro Palacios**¹

¹Universidad de Extremadura, Spain

²Villuercas-Ibores-Jara UNESCO Global Geopark, Spain

The first biomineralizing metazoans inhabited late Ediacaran carbonate settings and represent a relatively diverse assemblage, including the genera *Cloudina* and *Sinotubulites*. While similarities between them have been noted, their phylogenetic relationship is unclear, as are many aspects of their biology, including their detailed mode of growth, only partly known for *Cloudina*. Material from central Spain sheds light on the mode of growth of *Sinotubulites*, and its close phylogenetic relationship with *Cloudina*. *Sinotubulites* grew in a similar way to *Cloudina*, by progressively adding funnel-shaped growth units terminally. However, in the case of *Sinotubulites* each 'funnel' is folded over itself, forming two concentric cylinders. This construction implies that the soft parts of *Sinotubulites* extended well beyond the aperture and embraced the tube from the outside. It has been assumed that both *Cloudina* and *Sinotubulites* represent external skeletons, once inhabited by a worm- or polyp-like small metazoan. However, the data presented herein show that the soft parts of



Simotubulites must have been relatively large, perhaps unable to withdraw entirely inside the tube. This in turn suggests that the function of the skeleton was not protection but rather substrate colonization and stability in a carbonate setting.

Ecological dynamics of the predatory ichthyofagous fishes at Las Hoyas palaeowetland

Hugo Martín-Abad

Universidad Autónoma de Madrid, Spain

Fishes constitute one of the two main hubs in the trophic network of the Early Cretaceous (Barremian) palaeowetland of Las Hoyas (Cuenca, Spain). Among the high diversity of fishes at this locality, predatory ichthyofagous fishes are represented by four different species (three amiiforms and a coelacanth). Studies on the age distribution of their populations suggests that they occupied different niches. Going a step further, the analysis of the occurrence of the individuals of these species in different layers of the locality suggests that their presence at the ecosystem varies throughout the temporal record of the site: one species seems to be much more common and have a more extensive temporal presence, whereas the other three are less common and restricted to certain layers (moments). Moreover, the distribution of isolated scales, small-sized articulated individuals and large individuals is not homogeneous throughout time either. These data agree with the record observed in other taxa, such as plants and tetrapods, supporting the interpretation of the exceptional fossil assemblage of Las Hoyas as a dynamic ecosystem rather than as a static picture. Understanding the ecological dynamics of fishes is fundamental to complete this holistic interpretation of the palaeowetland.

Taphonomic study of the carnivoran-dominated assemblage of Batallones-3 (Late Miocene, Madrid basin, Spain)

David M. Martín-Perea^{1,2,3}, M. Soledad Domingo² and Jorge Morales¹

¹*Museo Nacional de Ciencias Naturales – CSIC, Spain*

²*Universidad Complutense de Madrid, Spain*

³*The Institute of Evolution in Africa (IDEA), Spain*

The Batallones butte (Madrid Basin, central Spain) is home to nine late Miocene mammalian sites. Two of these sites, Batallones-1 and Batallones-3, contain an unusually large concentration of carnivoran remains: 98.39 % in Batallones-1 and 99.58 % in Batallones-3. In Batallones-3, a total of 19,187 large-mammal remains have been retrieved, belonging to at least 15 different species. The most abundant taxa are the sabre-toothed cats *Machairodus aphanistus* (35.92 %) and *Promegantereon ogygia* (28.81 %) and the ursid *Indarctos arctoides* (19.64 %), with less abundant species such as the hyaenid *Protictitherium crassum*, the amphicyonids *Magericyon anceps* and *Thaumastocyon* sp., the mustelids *Eomellivora piveteaui*, aff. *Adroverictis ginsburgi* and aff. *Circamustela decheseauxi* and the mephitid *Promephitis* nov. sp.. Remains are found in marl deposited inside a dome-shaped pseudokarstic cave, with an upper opening in the centre inferred due to the presence of fallen block and a centre-outward preferential orientation of the bones. However, remains appear to have suffered little to no transport, as for each species the number of density clusters correlates to the MNI. Remains are commonly complete, unweathered, diagenetically fractured and rootmarked, with a high percentage of the remains showing marks that could correspond to trampling.



Integration and modularity in the maniraptoran limbs: from a common pattern to diversification

***Sergio Martínez Nebreda**¹, **Manuel Hernández Fernández**² and **Jesús Marugán Lobón**¹

¹Universidad Autónoma de Madrid, Spain

²Universidad Complutense de Madrid, Spain

Limb evolution and their morphological relationships are intriguing aspects of vertebrates' history that gain special interest in the dinosaur–bird transition. For the first time in this macroevolutionary context, we used one-dimensional Procrustes analysis (OPA) to assess the morphological evolution (variation patterns) and the integration (covariation patterns) of forelimbs and hindlimbs in a large sample encompassing 150 extinct and extant maniraptoran dinosaurs. Apart from neatly mapping the transformation of the anterior and posterior limbs across the dinosaur–bird transition, our results reveal high levels of integration between forelimb and hindlimb variation underlying such patterns, mostly affecting the transformation of the autopod (manus and pes). We interpret that such inertial evolutionary coupling possibly indicates constraints associated with a lineage's evolutive history, hence a plesiomorphic development programme. However, modularity is higher within each maniraptoran lineage, marked by differences in limb disparity between stem and crown groups. Whereas forelimbs tend to evolve more disparately in non-avian maniraptorans and basal avians, hindlimbs show most of the variation in crown birds. Such relatively independent trends could be the result of different selective pressures associated with in-group specialized locomotion.

Tetrapod tracks from the Permian of Mallorca (western Mediterranean): preliminary data, biostratigraphic and biogeographic inferences

Rafel Matamales-Andreu^{1,2}, **Josep Fortuny**¹, **Eudald Mujal**^{1,3} and **Àngel Galobart**^{1,4}

¹Institut Català de Paleontologia Miquel Crusafont, Spain

²Museu Balear de Ciències Naturals, Spain

³Staatliches Museum für Naturkunde Stuttgart, Germany

⁴Museu de la Conca Dellà, Spain

Mallorca is the largest of the Balearic Islands, an archipelago of Alpine origin located in the western Mediterranean. There, Permian outcrops were first described in the 1980s, together with the discovery of beds with tetrapod ichnites, which were scarcely studied. The present work revisits those localities and provides new ichnotaxonomic data, integrated with stratigraphic and sedimentologic considerations. The beds with abundance of (normally isolated) tetrapod footprints occur in the lower lithostratigraphic unit of the Permian sequence. Hitherto, we have identified the ichnogenera *Amphisauropus*, cf. *Ichniotherium*, *Hylodichnus*, *Varanopus*, *Dromopus* and *Dimetropus*. By comparing the stratigraphic ranges of all these ichnotaxa it can be concluded that the ichnoassemblage belongs to the early-middle Permian. The lack of temnospondyl amphibian tracks and the relative abundance of *Hylodichnus* and *Varanopus*, similar to some North American and European deposits, further constrains the age to the latest Artinskian–earliest Kungurian. Based on track–trackmaker correlations, the following tetrapod groups were present in the Permian of Mallorca: seymouriamorph reptiliomorphs, diadectomorph reptiliomorphs, captorhinomorph eureptiles, araeoscelid diapsids and sphenacodontid 'pelycosaur'. Biogeographically, the Mallorcan ichnoassemblage is notably similar to those occurring in the Artinskian–Kungurian of southern North America and the Italian Praelps.



Microstructural and crystallographic characterization of *Gigantoproductus* shells: environmental and/or biological influence in the columnar crystal size

***J. Ricardo Mateos-Carralafuente¹, Ismael Coronado^{2,3} and Sergio Rodríguez¹**

¹Universidad Complutense de Madrid, Spain

²Institute of Paleobiology (PAN), Poland

³Universidad de León, Spain

Crystal size changes in brachiopod shells may be in relation to environmental factors and/or ontogeny, and could be crucial in geochemical sampling. Three *Gigantoproductus* shells (early Serpukhovian, Mississippian), two from the Guadiato area (Spain) and one from Montagne Noire (France), have been selected and sectioned parallel and perpendicular to the shell growth. The samples have been analysed using SEM and CIP (computer-integrated polarization) microscopy in order to evaluate microstructural (crystal size) and crystallographic changes during shell growth. *Gigantoproductus* shells have a concavo-convex morphology with a dorsal valve with a laminar appearance and three layers with different microstructure in the case of the ventral valve. The primary layer is absent in all samples, the secondary layer has a laminar appearance formed by lath crystals, and the tertiary layer has a columnar appearance formed by large crystals with sandwiched growth lines with a laminar appearance. Columnar crystals show size changes due to: 1) abrupt growth interruption related to growth line formation triggered by stressing environmental conditions; 2) biocrystallization processes during the ontogeny, which follow a marked inverse U-shape trend with an increase in crystal size from younger to adult stages and decreasing crystal size from adult to gerontic stages.

Calymenid trilobites from the uppermost Katian (Upper Ordovician) Slade and Redhill Mudstone Formation, South West Wales

Lucy M. E. McCobb¹, Patrick D. McDermott² and Alan W. Owen³

¹Amgueddfa Cymru – National Museum Wales, UK

²Independent

³University of Glasgow, UK

Recent sampling of the previously largely-neglected uppermost Katian (Rawtheyan) Slade and Redhill Mudstone Formation in the Llanddowror area of Carmarthenshire, South West Wales has yielded a trilobite fauna comprising some 25 genera. Whilst isolated sclerites are most common, a number of complete or partially articulated trilobites were also recovered. Calymenids were collected from eight out of 20 trilobite-bearing localities. Complete specimens are extremely rare, but calymenid sclerites constitute a significant proportion of the trilobite remains at several localities. A new species of *Gravicalymene* is the numerically most numerous calymenid in the formation, while *Diacalymene* cf. *D. marginata* Shirley, 1936 occurs at the largest number of localities. A highly unusual flexicalymenine with a narrow-based anterior projection occurs at a single locality, which also yielded other taxa that are rare in the formation, namely the asaphid *Birmanites* and the large cheirurid *Hadromeros*, suggesting an atypical environment represented by the fauna at that site.



Assessing diversity and disparity amongst unifoliate rangeomorphs from Newfoundland, Canada

***Anna McGairy, Charlotte G. Kenchington and Alexander G. Liu**

University of Cambridge, UK

Late Ediacaran siliciclastic successions from Newfoundland, Canada record the oldest deep-marine palaeocommunities of complex macro-organisms, and include early large, complex animals. These palaeocommunities were dominated by rangeomorphs – a diverse group of frondose organisms characterized by a self-similar branching architecture. While aspects of the palaeoecology of these enigmatic organisms are starting to be resolved, the power of ecological analyses is limited by the fact that several common taxa have not yet been formally described. We focus here on a newly discovered rangeomorph, informally called the “banana frond”, from the Bonavista Peninsula, Newfoundland. Our method combines multivariate statistical analyses, hierarchical cluster analyses, and the study of ontogenetic growth series to identify the diagnostic morphological and ontogenetic characters in populations of the “banana fronds”. Our method incorporates factorial analysis of continuous and categorical variables in tandem to avoid bias of analyses, and thus of taxonomic classification, towards any one set of characters. We compare the “banana fronds” to other unifoliate taxa, including *Charnia*, *Trepassia*, *Beothukis* and *Vinlandia*, to constrain the diversity and disparity of unifoliate fronds in Newfoundland, and to determine whether the “banana frond” is a novel taxon.

Reconstruction and functional morphology of the Oviraptorosaur cranium

***Luke E. Meade, Richard J. Butler and Stephan Lautenschlager**

University of Birmingham, UK

Oviraptorosaurs were a group of theropod dinosaurs from the Cretaceous of North America and Asia that evolved robust toothless beaks and highly modified skulls, leaving their skull function, diet and ecosystem position uncertain. Biomechanical analyses on digital 3D models of skulls representing species throughout Oviraptorosauria may inform how the shape of these dinosaurs’ skulls affected their function, what they may have eaten, and how they evolved. In order to conduct biomechanical analyses, digital 3D models generated from CT scans of oviraptorosaur skulls have been retrodeformed to an in-life condition to remove the effects of taphonomic damage – digitally repairing cracks and breaks, replacing missing elements and reversing any plastic deformation. 3D models of skulls derived from CT-scanned specimens of key taxa such as *Citipati* and *Incisivosaurus* have been restored in the specialist software packages Avizo and Landmark. These 3D models will form the basis for reconstructions of their cranial musculature and analyses of their biomechanical function including finite element analysis. Ultimately, this may reveal a picture of how complex functional and dietary diversity patterns were throughout Oviraptorosauria over millions of years. Insight from this may be applied to interpret trends in other important extinct and extant taxa and ecosystems.



The influence of environmental setting on the community ecology of Ediacaran organisms

Emily G. Mitchell¹, Nikolai Bobkov^{2,3}, Natalia Bykova^{2,4}, Alavya Dhunghana⁵, Nikita Sozonov^{2,3}, Anton Kolesnikov^{2,6,7}, Tom Mustill¹, Alexander G. Liu¹, Shuhai Xiao⁴ and Dmitriy V. Grazhdankin^{2,3}

¹University of Cambridge, UK

²Trofimuk Institute of Petroleum Geology and Geophysics, Russia

³Novosibirsk State University, Russia

⁴Virginia Polytechnic Institute and State University, USA

⁵Durham University, UK

⁶Geological Institute (RAS), Russia

⁷Moscow Pedagogical State University, Russia

The role that the global environment plays in early animal evolution is much debated; it is still unknown how broad-scale environments influence organisms at small spatial scales or where key evolutionary mechanisms operate. To investigate how regional-scale environment influences community ecology we used spatial point process analyses to examine the community structure of seven palaeocommunities across a range of environmental settings. The palaeocommunities showed a marked difference in how they interacted with sub-metre-scale habitat heterogeneities. The shallow-water palaeocommunities were heavily influenced by local habitat variations, while the deep-water palaeocommunities showed no significant environmental interactions or associations. Our results suggest that the increase in species richness between deep-water and shallow-water Ediacaran assemblages may have been driven by this environmental patchiness, because such habitat heterogeneities are known to lead to diversification in modern marine environments. Furthermore, the presence of grazers and detritivores in the shallow-water communities could have led to further local patchiness, starting a chain of increasing heterogeneity of benthic communities from the shallows to the deep sea. Our results support the hypothesis that early animal diversification during the Ediacaran was driven by patchiness in the local environment, so was a benthic rather than pelagic event.

Titanosaurs from Lo Hueco (Campanian-Maastrichtian) reveal new information about the evolutionary history of European titanosaurs

Pedro Mocho^{1,2}, Adrián Páramo², Fernando Escaso², Fátima Marcos-Fernández^{2,3}, Daniel Vidal² and Francisco Ortega²

¹Universidade de Lisboa, Portugal

²Universidad Nacional de Educacion a Distancia, Spain

³Universidad Complutense de Madrid, Spain

Lo Hueco (Cuenca, Spain) represents a Campanian–Maastrichtian multitaxic bonebed, with several partial titanosaurian skeletons, mostly articulated or with low dispersion. Their analysis is key to understanding the phylogeny of European and North African titanosaurs. Two taxa were identified in Lo Hueco, but recent works on axial remains are suggesting a higher diversity. *Lobuecotitan pandafilandi* (holotype HUE-EC-01) is the first established taxon, and its detailed description is revealing the presence of shared features, in the caudal series, with *Paludititan*. HUE-EC-02-to-05, HUE-EC-11 and HUE-EC-13 are six new specimens preserving articulated and well-preserved sections of the axial skeleton (almost



complete in HUE-EC-02). They provide detailed information regarding morphological changes throughout the series (e.g. laminae patterns and pneumaticity), important for the codification of new characters. Furthermore, some specimens from Lo Hueco (e.g. HUE-EC-04) exhibit features traditionally considered as aeolosaurine synapomorphies, never reported previously in the Cretaceous of Europe. Our preliminary phylogenetic analyses recovered *Lohuecotitan*, HUE-EC-02 and *Paludititan* as possible members of Lirainosaurinae together with *Lirainosaurus* and *Ampelosaurus*. Lirainosaurinae is recovered as an early branching member of Saltasauridae and, in some analyses, as sister taxa of a clade including members of Colossosauria.

A total-evidence and time-calibrated phylogeny of Echinoidea

***Nicolas Mongiardino Koch¹** and **Jeffrey R. Thompson²**

¹*Yale University, USA*

²*University College London, UK*

Echinoids, one of the five living groups of echinoderms, constitutes one of the most iconic clades of marine animals. A little over 1,000 species of echinoids live today in the oceans, including species commonly known as sea urchins, heart urchins and sand dollars. The combination of a rich extant diversity, an extraordinary fossil record, and a wealth of information on their developmental biology makes echinoids a unique clade with which to address evolutionary questions across deep time. Nonetheless, research on echinoid macroevolution has been halted by the phylogenetic uncertainty and conflict arising from molecular and morphological datasets. Here we combine genomic, morphological and stratigraphic data to obtain a total-evidence, tip-dated phylogeny of echinoids. We show that a significant fraction of the supposed conflict between morphological and molecular datasets is alleviated by employing a Bayesian inference approach, especially once a morphological clock is enforced. Our analyses also suggest that multiple lineages of early crown echinoids might in fact fall along the clade's stem. Our study constitutes the most comprehensive analysis of crown echinoid relationships and divergence times, and represents a significant step forward towards the development of echinoids as a model clade for macroevolutionary research.

Synchrotron imagery of phosphatized eggs in *Waptia* cf. *fieldensis* from Utah

***Justin Moon¹** and **Jean-Bernard Caron^{1,2}**

¹*University of Toronto, Canada*

²*Royal Ontario Museum, Canada*

Isolated Ediacaran and Cambrian phosphatized eggs provide important palaeoembryological data, even preserving cellular-level details, but biological and evolutionary interpretations are limited by the uncertainty over the egg-producing organisms. In contrast, *in situ* eggs preserved as carbonaceous compressions alongside adult Cambrian arthropods, including of the Burgess Shale mandibulate *Waptia fieldensis* Walcott, 1912, provide insight into brood care strategy, but embryos are poorly or not preserved. Here we report 3D phosphatized eggs preserved *in situ* within the compressed carbonaceous remains of *Waptia* cf. *fieldensis* from the middle Cambrian Spence Shale of Utah. The individual possesses 11 eggs, the largest measuring approximately 1 mm in diameter. Nine of the best-preserved eggs, including one in isolation, were studied at the European Synchrotron Radiation Facility (Beamline ID 19) in Grenoble, France, using



synchrotron X-ray tomography techniques. Some eggs preserve a stalk-like structure, not recognized in any Burgess Shale material, which may have attached them to the adult carapace. The eggs do not contain discernible internal embryological structures, suggesting that they were either not fertilized or that early embryological structures were not preserved. Our results demonstrate the viability of this method for studying similarly preserved fossils, potentially illuminating the developmental and reproductive biology of early metazoans.

3D reconstruction of small vertebrates from isolated fossil remains; an example with soricids (Eulipotyphla, Mammalia)

***Raquel Moya Costa, Gloria Cuenca-Bescós and Blanca Bauluz**

University of Zaragoza, Spain

We have designed a protocol for reconstructing virtual skulls of small vertebrates. It enables the 3D reconstruction of skulls from fragmentary and concreted fossils from different individuals; therefore, the protocol is of interest when there is a lack of complete skulls. The protocol requires the use of micro-CT, free software for 3D reconstructions (SPIERS), image analysis (FIJI) and 3D design and printing (Meshmixer, Meshlab), and a commercial computer of mid-range; this allows making the process of reconstruction possible to a wide audience, including researchers not focused on this type of technique. Specifically, we have reconstructed the skulls of two early Pleistocene shrews from Burgos (Spain): *Beremendia fissidens* and *Dolinasorex glyphodon*. In addition, we have reconstructed four species of extant shrews to compare them and to reconstruct the parts lacking in the fossil record. The resulting skulls allow us to take measurements only possible with 3D models, test the movement of the mandibles, and analyse the interior of the skulls (nasal cavities, roots, pulpar cavities of the teeth *etc.*). The final models can also be used for different purposes such as in research (anatomy, biomechanics, simulations, replicas *etc.*) or in activities for the dissemination of scientific knowledge (museums, videos *etc.*).

The body of *Stanleycaris* and the origin of hurdiid radiodonts

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

¹*University of Toronto, Canada*

²*Royal Ontario Museum, Canada*

Radiodonts are extinct organisms which occupy a key position in the euarthropod stem group. Isolated radiodont frontal appendages hint at considerable diversity, but articulated body remains are rare, leaving large gaps in the understanding of their evolution. We describe new fossils assignable to *Stanleycaris*, including whole-body specimens, from Burgess Shale localities in the ‘Thick’ Stephen Formation. This taxon was previously known with certainty only from appendages and oral structures from the ‘Thin’ Stephen Formation. Intact individuals tend to be less than 50 mm long, making *Stanleycaris* among the smallest known radiodonts. While the appendages are of hurdiid type, the body – with anterior eyes, small rounded head sclerites, a constricted neck, and an elongate trunk with sixteen flap-bearing segments – is surprisingly more comparable to non-hurdiid radiodonts like *Anomalocaris*. Our phylogenetic analysis finds *Stanleycaris* as the most basally diverging hurdiid, supporting the recent hypothesis that the greatly enlarged head and reduced trunk region characteristic of most hurdiids (*e.g. Cambroraster*) represents a derived morphology. The high quality of preservation of the new material also sheds new



light on radiodont trunk segmentation and internal organ morphology, and demonstrates that frontal appendage structure may be somewhat decoupled from other aspects of the body plan.

Impact of diagenetic and metamorphic overprint on our view of Cambrian Lagerstätten: a case study from North Greenland

***Morten Lunde Nielsen¹, Mirinae Lee², Philip R. Wilby^{3,4}, Hong Chin Ng¹, Katharine R. Hendry¹, Arne T. Nielsen⁵, Tae-Yoon Park² and Jakob Vinther¹**

¹University of Bristol, UK

²Korea Polar Research Institute, South Korea

³British Geological Survey, UK

⁴University of Leicester, UK

⁵University of Copenhagen, Denmark

Understanding the preservational pathways and subsequent alteration of Cambrian Lagerstätten is crucial for identifying any biases in the record that they generate. The Sirius Passet Lagerstätte, North Greenland provides one of the earliest windows on modern-style ecosystems. Body fossils are preserved as reflective films in the classic Burgess style but, uniquely, labile soft tissues (*e.g.* muscles) are silicified. This has led to the hypothesis that silicification was an important taphonomic pathway leading to exceptional preservation during the Cambrian. A combination of textural, geochemical and isotopic evidence contradicts this view and indicates that silicification was secondary after early diagenetic phosphatization. This was one of a series of mineral transformations that occurred during regional greenschist-grade metamorphism, terminating with the late-stage mineralization of many bedding-plane surfaces during unloading. These surfaces generally show lower fossil abundances and diversities than comparable non-mineralized bedding-planes and offer a distinctly different view of the biota – one biased towards taxa with large or robust bodies. Recognition of the impact of metamorphic overprint reduces the number of perceived pathways to exceptional preservation in the Cambrian, and highlights the potential for there being significant, previously unrecognized, taphonomic biases present in collections.

Proclivity of nervous system preservation in Cambrian Burgess Shale-type deposits

Javier Ortega-Hernández, Rudy Lerosey-Aubril and Stephen Pates

Harvard University, USA

Recent investigations on neurological tissues preserved in Cambrian fossils have clarified the phylogenetic affinities and head segmentation in pivotal members of stem-group Euarthropoda. However, palaeoneuroanatomical data are often fragmentary or described from single exceptional specimens, raising concerns about the morphological interpretation of fossilized neurological structures and their significance for early euarthropod evolution. Here we describe the central nervous system (CNS) of the short great-appendage euarthropod *Alalcomenaeus* based on material from two Cambrian Burgess Shale-type deposits of the American Great Basin, the Pioche Formation (Stage 4) and the Marjum Formation (Drumian). The specimens reveal complementary ventral and lateral views of the CNS, preserved as a dark carbonaceous compression throughout the body. The Great Basin fossils strengthen the original description – and broader evolutionary implications



– of the CNS in *Alalcomenaeus* from the Cambrian Stage 3 Chengjiang deposit of South China. The spatiotemporal recurrence of fossilized neural tissues in Cambrian Konservat-Lagerstätten across North America and South China indicates that their preservation is congruent with the diagenetic mechanism of Burgess Shale-type deposits, without the need to invoke alternative taphonomic pathways or the presence of microbial biofilms.

Counting the years – measuring evolutionary change, recovery and radiation in real time in the Early Jurassic

Kevin Page

University of Exeter, UK

Ammonoids are exemplary stratigraphic guide fossils, their rapid morphological evolution making them ideal for high-resolution correlations of sedimentary sequences. But just how good are they? Recent work on Milankovitch-driven cyclostratigraphy of Early Jurassic successions in southwest Britain indicates that units at the level of ‘biohorizon’ can have a duration of less than 50,000 years. In addition, as even passively-planktonic organisms could theoretically circum-navigate the globe equatorially in only 2.56 years, only very brief events, such as extra-terrestrial impacts, can offer any higher resolution. However, once calibrated against orbital-cycles, an ammonite stratigraphy of zones and ‘horizons’ can be used to provide a timescale against which to assess all manner of changes, including biological. Such a timescale is now established for the Hettangian and work in progress will soon produce one for the Pliensbachian and Toarcian stages, and subsequently the Sinemurian. These calibrations can be used to define timescales for extinctions and radiations, oceanic perturbations and biogeographical ‘events’ and rates of morphological evolution. Crucially, as the Hettangian saw the recovery and radiation of Ammonoidea after the devastating effects of the end-Triassic extinction phase, the rate of recovery can now be measured in years.

The ammonite family Perisphinctidae and the development of biogeographical polarization across Europe during the Oxfordian (Upper Jurassic)

Kevin Page¹, Julia Bello² and Guillermo Melendez³

¹*University of Exeter, UK*

²*IES Miguel Servet, Zaragoza, Spain*

³*University of Zaragoza, Spain*

The end Callovian–Early Oxfordian saw one of the phases of greatest overlap between Boreal and Tethyan ammonoid faunas in the entire Jurassic, when an absence of north–south barriers allowed Sub-Boreal Province Cardioceratidae to mix with Mediterranean Province Phyloceratina in southern France. Through the Lower Oxfordian and into the Middle Oxfordian, however, increasing restrictions on faunal interchange led to the beginnings of a strong faunal provincialism, which lasted until the Early Cretaceous. This provincialism is first recognizable at the level of species, later genera and subfamily, and ultimately family level, with at least eight separate provinces being recognizable globally by the end of the Jurassic. This process of separation, however, began in the Middle Oxfordian and can be recognized in the development of endemic species and genera, and ultimately subfamilies, within the Perisphinctina across Europe and beyond, including the separation of Sub-Boreal *Perisphinctes* s.s. from Sub-Mediterranean *Martelliceras* and



the origins of Mediterranean Passendorferinae (as particularly well demonstrated in the Iberian Cordillera, eastern Spain). Independent changes as faunal polarization developed also occurred in Sub-Boreal regions of southern Britain and these will be incorporated to demonstrate how, and why, Jurassic environments between southern and northern Europe became increasingly separated.

Dental microwear or dental morphology for trophic inferences on extinct elasmobranchs?

Maria Victoria Paredes-Aliaga¹, Humberto G. Ferrón², Carlos Martínez-Pérez^{1,2}, Alejandro Romero³ and Héctor Botella¹

¹*University of Valencia, Spain*

²*University of Bristol, UK*

³*University of Alicante, Spain*

In the absence of other data, dental morphology is typically used to predict trophic ecology and the role of a species in the ecosystem. Contrarily, other studies state that dental morphology provides limited support in this sense. In contrast, quantitative techniques, like microwear analysis, have shown their utility for predicting trophic ecology. This technique has been applied to several taxonomic groups but has never been applied to elasmobranchs. In this context we have developed a comparative framework based on actual elasmobranch species to infer the trophic ecology of hybodontid sharks and related taxa from the Middle Triassic of the Iberian Range (Spain). Our results show a palaeocommunity composed of durophagous and generalist elasmobranchs in an environment with a high ecological diversity. Moreover, the results suggest that dental morphology provides information about food processing while dental microwear is more useful for making trophic inferences. Therefore, we conclude that to study trophic inferences in fossil elasmobranchs it is important to apply quantitative analysis of microwear and morphofunctional inferences.

A molecular palaeobiological approach to understand velvet worm terrestrialization

Luke A. Parry¹, Richard J. Howard², David A. Legg³, Davide Pisani⁴ and Jesus Lozano-Fernandez^{4,5}

¹*Yale University, USA*

²*University of Exeter, UK*

³*The University of Manchester, UK*

⁴*University of Bristol, UK*

⁵*Institute of Evolutionary Biology (CSIC-UPF), Spain*

Onychophora, the velvet worms, is the only animal phylum that is terrestrial throughout the entire life cycle. This small invertebrate lineage of multi-legged animals has a restricted distribution, mostly inhabiting the soils of tropical forests. Their present biogeographic distribution differs considerably from the rich diversity of onychophoran-like organisms (lobopodians) found in marine Cambrian Lagerstätte. The most recent terrestrial fossil extends to the Carboniferous, while the oldest unambiguous crown-group taxon is found in Burmese amber (100 Ma). Both of these fossil occurrences suggest a relatively late origin and terrestrialization for the group compared to the Palaeozoic origins of other major



terrestrial arthropod groups. Here we approach the question of Onychophora origin using a total evidence approach, integrating the molecular information of living taxa together with the morphology of both living and fossil taxa. We have compiled a morphological matrix of key Palaeozoic lobopodians together with putative stem and crown group onychophoran fossils in order to assess the phylogenetic affinities of fossil taxa relative to the extant group. The results of analysing this dataset will shed light on the sequence of character evolution along the onychophoran stem and on the divergence dates for the crown Onychophora to establish a minimum age for this group's colonization of land.

Understanding morphological variability of the cephalic region in hurdiid radiodonts: insights from a new species of *Cambroraster*

***Stephen Pates, Rudy Lerosey-Aubril and Javier Ortega-Hernández**

Harvard University, USA

Radiodonts were once solely depicted as the apex predators of the early Palaeozoic seas, but recent studies have revealed a much greater ecological diversity. Most exceptionally-preserved biotas include several of these stem-euarthropods, which differ in size, lifestyle and feeding habit. For example, hurdiids – radiodonts with well-developed tripartite cephalic carapaces – include nektobenthic to epibenthic, microphagous to macrophagous sediment sifters, along with small to gigantic nektonic suspension-feeders. Here we report the discovery of the epibenthic *Cambroraster* in the Drumian Marjum Formation of Utah, USA which provides an opportunity to explore the relationships between cephalic morphology and ecology in hurdiids. This new species is characterized by a triangular dorsal carapace element with marginal spines, rounded optical notches and a short nuchal region. Using geometric morphometry, we show that the morphological variability of hurdiid central carapace element is largely explained by its antero-posterior elongation. This trait is tightly connected to lifestyle: elongate morphologies are observed in nektonic taxa, whereas benthic forms typically exhibit wide, but short dorsal element. The development of an acuminate anterior margin or conversely, a nuchal region is another important component, apparently related to ecology and ontogeny. We conclude that head morphology is a good indicator of lifestyle in hurdiid radiodonts.

Ordovician metazoan reef development in the Mingan Islands, Quebec

Amelia Penny¹, Björn Kröger¹ and André Desrochers²

¹Finnish Museum of Natural History, University of Helsinki, Finland

²University of Ottawa, Canada

The first coral and bryozoan reefs appeared during the Ordovician Period, 485–444 million years ago. During this time, the dominant style of reef formation changed globally, from microbial- to skeletal-dominated. Encrusting sheet-like metazoans (SLMs), including corals, bryozoans and stromatoporoids, formed reef-building consortia with pre-existing microbial communities and invaded soft-substrate marine settings worldwide; an example of the global impact of metazoan ecosystem engineering. The well-exposed reef-bearing carbonate rocks of the Mingan Archipelago National Park Reserve, Quebec, present an excellent opportunity to investigate the controls on SLM reef development in a Middle Ordovician (Darrivilian) carbonate platform. The reefs are matrix-rich, metre-scale mounds, sometimes forming larger complexes, and contain abundant diverse skeletal fossils. We used point counts to measure reef composition, and mapped reef distributions



with the aim of reconstructing the determinants of reef composition and growth. We also collected sedimentological and stratigraphic data to supplement previous studies and provide additional context. We find considerable taxonomic and compositional heterogeneity in the reefs of the Mingan Formation, and also gradients in reef composition over small spatial scales. Ultimately, we expect this work to yield insights into the relationship between ecosystem engineers and abiotic environmental conditions in determining the character of early Palaeozoic reefs.

Morphology and evolution of basal Cheirurina (Trilobita) from the Fezouata Biota (Lower Ordovician, Morocco)

***Francesc Perez-Peris¹, Lukáš Laibl¹, Muriel Vidal² and Allison C. Daley¹**

¹University of Lausanne, Switzerland

²University of Brest, France

Pilekiinae is a group of phacopid trilobites considered to be the basal-most members of the suborder Cheirurina, and therefore they are crucial for understanding the early evolution and morphological diversification of the group. In the Fezouata Shale (Lower Ordovician, southeast Morocco), numerous species of pilekiids have been described. Owing to taphonomical and morphological variability, it is possible that the group has been split into too many species. In this contribution, numerous specimens have been studied in order to clarify the taxonomy and to re-describe the morphology of cheirurids from the Lower Ordovician of Morocco. Morphological and biostratigraphical data suggest that most of the described species are co-specific and belong to the genus *Anacheirurus*. In addition, a few specimens preserve the post-antennal appendages. The limb morphology of *Anacheirurus* shows a combination of characters that is typical for both Cambrian and Ordovician trilobites. The appendage morphology of *Anacheirurus* is important because this species comes from stratigraphic levels that are associated with the Great Ordovician Biodiversification Event and reveals the faunal transition from Cambrian to post-Cambrian ecosystems. Indeed, the unusual combination of ancestral and derived characters in the *Anacheirurus* appendages may be attributed to more specific adaptations of trilobites in the post-Cambrian world.

New lacewings bearing assemblable proboscides from the Cretaceous amber of Spain

Ricardo Perez-de la Fuente¹, Alba Sánchez-García², Enrique Peñalver³, Michael S. Engel⁴ and Xavier Delclòs⁵

¹Oxford University Museum of Natural History, UK

²University of Valencia, Spain

³IGME, Instituto Geológico y Minero de España, Spain

⁴University of Kansas, USA

⁵Universitat de Barcelona, Spain

The fossil record often reveals how extant lineages are sometimes traces of their former glory. Among insects, this is the case of the Neuroptera, encompassing lacewings, antlions, and their relatives. Whereas no extant neuropterans bear fluid-feeding proboscides, different neuropteran lineages showed this trait during the Mesozoic. One such group, the Paradoxosyrinae, was recently described based on a single specimen from 99-million-



year-old Burmese amber; four additional coeval taxa were subsequently described. Five paradoxosyrine specimens, currently under study, have been found in Cretaceous amber from Spain, Albian in age (~105 Ma): three complete specimens representing new morphotypes, two from the Peñacerrada I locality (Burgos, northern Spain) and one from the San Just locality (Teruel, northeast Spain), plus two fragmentary specimens from the Peñacerrada I and El Soplao localities (Cantabria, northern Spain). The new morphotypes bear assemblable, relatively short proboscides composed of paired laciniae and galeae that formed a siphoning tube when conjoined, and an unpaired cylindrical mouthpart labial in origin, likely a ligula. Due to their inferred fluid-feeding habits, paradoxosyrines were potential plant pollinators and, as such, are important in elucidating the role that insects played in the explosive diversification of flowering plants (angiosperms) during the mid Cretaceous.

The microvertebrate succession from the late early Pleistocene sequence of Quibas-Sima (Murcia, Spain)

Pedro Piñero^{1,2}, Jordi Agustí^{1,3}, Hugues-Alexandre Blain^{1,8}, Marc Furió^{4,5}, César Laplana⁶, Oriol Oms⁵ and Paloma Sevilla⁷

¹IPHES, Institut català de Paleoeecologia Humana i Evolució Social, Spain

²CONICET, Universidad Nacional de La Plata, Argentina

³ICREA, Institució Catalana de Recerca i Estudis Avançats, Spain

⁴Institut Català de Paleontologia Miquel Crusafont, Spain

⁵Universitat Autònoma de Barcelona, Spain

⁶Museo Arqueológico Regional de la Comunidad de Madrid, Spain

⁷Universidad Complutense de Madrid, Spain

⁸Universitat Rovira i Virgili, Spain

The microvertebrate succession from Quibas-Sima, one of the two main karstic structures of the Quibas site (Murcia, Spain), is here presented. The section includes seven stratigraphic levels. Five of them have yielded vertebrate fossils (QS-1 to QS-4, QS-7). A continuous small vertebrate succession has been recovered, including representatives of the families Bufonidae, Pelodytidae, Testudinidae, Gekkonidae, Blanidae, Lacertidae, Colubridae, Viperidae, Soricidae, Erinaceidae, Rhinolophidae, Vespertilionidae, Muridae, Gliridae, Sciuridae, Leporidae and Ochotonidae. The ecological affinities of the taxa point towards a progressive reduction in forest cover and spreading of shrublands or grasslands from QS-1 to QS-4. The age of Quibas-Sima can be roughly constrained between 1.2 and 0.9 Ma on the basis of its correlation with other late early Pleistocene sites from Spain, such as Fuente Nueva-3 (Guadix-Baza Basin) and Cueva Victoria (southeast Spain). The presence of *Allophaiomys* sp. and *Neomys* sp. in QS-1 suggests a somewhat younger age than Fuente Nueva-3 (~1.2 Ma), whereas the replacement of *Allophaiomys* sp. by a more advanced arvicolid (*Allophaiomys chalinei*) in Cueva Victoria (~0.9 Ma) indicates that Quibas-Sima is somewhat older. The study of this sequence thus contributes to expand our knowledge of the biotic and climatic events that took place in the southern Iberian Peninsula at the beginning of the Early-Middle Pleistocene transition.



Tortonian Conidae of Crete; mystic colour patterns revealed under UV light

Christos Psarras¹, Efterpi Koskeridou¹ and Didier Merle²

¹National and Kapodistrian University of Athens, Greece

²Muséum national d'Histoire naturelle, Paris, France

Conidae, a very diverse family of gastropods with over 900 extant species, present beautiful colour patterns. These patterns are useful to biologists for the systematic approach of this taxon. In absence of colour patterns in fossil samples, Conidae were difficult to distinguish to species level, resulting in an ambiguous knowledge of this clade's fossil record. Here we present the first part of a PhD project that intends to clarify the diversity of the Conidae through the Late Miocene in central and eastern Crete, Greece. Using ultraviolet light, the colour pattern of fossil Conidae is revealed, so far showing amazing results. From the genus *Conilithes* Swainson, 1840 and *Conus (Kalloconus)* da Motta, 1991 we have found 11 species in Tortonian deposits in Crete, five of them being new to the scientific community. This study will greatly enrich the fossil record of this clade in the Mediterranean, and will be compared with similar Middle Miocene Paratethyan faunas, other Tortonian faunas in the Mediterranean, as well as Early Pliocene Mediterranean faunas mainly from Italy. This work will be part of the first systematic approach of Conidae in the Late Miocene of Greece.

Anatomy and affinity of *Lasanius*, an enigmatic vertebrate from the Silurian of Scotland

***Jane Reeves, Roy A. Wogelius, Robert S. Sansom and Joseph N. Keating**

The University of Manchester, UK

The evolution of vertebrates is a major evolutionary event and a diverse assemblage of fossils provides our only direct evidence of this time. Establishing a well-supported phylogeny is essential to understand this. Yet, conflicting interpretations of anatomy in several soft-bodied fossils have resulted in poor resolution of relationships. Chief amongst the problematic taxa is *Lasanius*: a small, primarily soft-bodied genus that unusually exhibits areas of localized mineralization. This curious mix suggests *Lasanius* is a transitional form between biomineralized and non-biomineralized taxa. However, knowledge of its anatomy is poor, subject to conflicting interpretations and ambiguous taphonomy. By using an array of modern techniques, the anatomy of *Lasanius* has been reassessed. A new reconstruction demonstrates preserved features that include paired sensory organs, a notochord and digestive tract, while no strong evidence for a proposed anal fin is found. EDS-XRF analysis suggests a bone-like composition of mineralized parts but fails to find support for mineralized dermal armour. Phylogenetic analysis recovers *Lasanius* as an early stem-cyclostome, supporting previous work, and suggesting biomineralization in vertebrates includes multiple occurrences of secondary loss and evolution events.



The Early Triassic 'Grippia' bone bed of Spitsbergen and its implications for the understanding of ecosystem recovery after the P-T

Aubrey J. Roberts¹, Victoria Engelschiön¹, Lene Delsett¹, Øyvind Hammer¹, Bitten B. Hansen¹, Benjamin Kear² and Jørn Hurum¹

¹Natural History Museum, University of Oslo, Norway

²Museum of Evolution of Uppsala University, Sweden

Four expeditions to Flower Dalen in central Spitsbergen, Arctic Norway have resulted in the discovery and excavation of several tonnes of material from the Early to Middle Spathian (Lower Triassic) bonebed on Marmiefjellet. This material has been sorted and contains bones in multiple size classes from large bone elements and fin spines (<10 cm) to microscopic bones, teeth, scales and conodonts. This material includes elements from ichthyopterygians, amphibians, chondrichthyans, sarcopterygians, actinopterygians and possibly sauropterygians. These fossils were deposited in the Early Triassic Boral Ocean, part of the Panthalassa Ocean, on the northern rim of the supercontinent Pangea at approximately 45° palaeolatitude. The 'Grippia' bone bed, in association with the three other Early and Middle Triassic bone beds in central Spitsbergen are the only large high-latitude localities for Early Triassic marine reptiles in the world, as the majority of fossiliferous locations are deposits from the Tethys Sea. Here we present the preliminary taxonomical identifications of the material and their implications for understanding the evolution and biogeography of Early Triassic marine reptiles. This material provides a significant amount of data regarding the understanding of recovery and diversification after the Permian–Triassic mass extinction.

Ultrastructure of three-dimensionally preserved fossil anuran skin from the Quercy (Eocene, France)

Ninon Robin¹, Patrick J. Orr², Fleur Noailles¹ and Maria E. McNamara¹

¹University College Cork, Ireland

²University College Dublin, Ireland

In vertebrates, the skin fulfils various key roles related to physiology and ecology, including camouflage, chemical communication, venom secretion, respiration and, critically, protection of internal systems from dehydration. Attempts to study the evolution of skin using fossils are hampered by difficulties in interpreting fossilized skin structures and relating these to modern equivalents, requiring a more comprehensive understanding of skin taphonomy. Here we use high-resolution synchrotron tomography and SEM to investigate the three-dimensionally preserved skin of *c.* 40 Ma lissamphibians and snakes from the Late Eocene of the Quercy (France). All studied samples reveal multiple phosphate phases defined by layered, botryoidal and granular textures. Despite this evidence for diagenetic overprint of original tissue structure, the skin of one anuran specimen reveals globular structures that are strikingly similar to dermal glands in extant lissamphibians in terms of size, location, internal contents, and connection to the skin surface via a canal. Variations in the morphology/distribution of these features are compared to those in modern representatives using 3D-reconstruction, SEM and histology. The absence of other preserved tissues in the Eocene anurans suggests that different ultrastructural components of the skin follow different taphonomic pathways relating to the relative extent of decay and/or timing of phosphatization.



Experimental taphonomy of melanosomes: impact on trace element chemistry

***Valentina Rossi¹, Samuel Webb² and Maria E. McNamara¹**

¹University College Cork, Ireland

²Stanford Synchrotron Radiation Lightsource (SSRL), USA

Fossil melanosomes are a major focus of palaeobiological research as they can inform on the biology of ancient animals. Our recent study of the inorganic chemistry of extant and fossil vertebrate melanosomes revealed a pervasive tissue-specific chemical signal, strongest in amphibians. In extant amphibians, liver melanosomes are associated with Cu and Fe, and those from the skin are associated with Ca. Melanosomes in some fossil amphibians, however, are associated with elevated concentrations of Cu in all soft tissues. This suggests diagenetic overprinting of original chemistry, but this hypothesis has not been tested. We resolve this issue using controlled laboratory experiments on melanosomes from extant amphibians. We matured melanin extracts from the skin and liver of the African clawed frog (*Xenopus laevis*) in distilled water or in a Cu-rich solution at 200°C, 130 bar for 24 h and analysed the residues using synchrotron X-ray fluorescence (XRF) and X-ray absorption near edge structure spectroscopy (XANES). Our experiments reveal that after maturation all melanosomes are depleted in Fe and/or Ca and converge towards a common inorganic composition, losing the tissue-specific signal present *in vivo*. These results provide the first experimental basis for assessments of the extent of diagenetic alteration of fossil melanosome chemistry.

Bite marks and predation of fossil jawless fish during the rise of jawed vertebrates

Robert S. Sansom¹ and Emma Randle^{1,2}

¹The University of Manchester, UK

²University of Birmingham, UK

Although modern vertebrate diversity is dominated by jawed vertebrates, early vertebrate assemblages were predominantly comprised of jawless fishes. Theories for this faunal shift and the Devonian decline of jawless vertebrates include predation and competitive replacement. The nature and prevalence of ecological interactions between jawed and jawless vertebrates are highly relevant to both hypotheses, but direct evidence is limited. Here we use the occurrence and distribution of trace fossil bite marks in jawless armoured heterostracans to infer predation interactions. A total of 41 predated specimens are recorded; their prevalence increases through time, reaching a maximum toward the end of the Devonian. The bite mark type traces significantly co-occur with jawed vertebrates and their distribution through time is correlated with jawed vertebrate diversity patterns, particularly placoderms and sarcopterygians. Environmental and ecological turnover in the Devonian, especially relating to the nektonic revolution, have been inferred as causes of the faunal shift from jawless to jawed vertebrates. Here we provide direct evidence of predation from jawed vertebrates as a contributing factor to the demise and extinction of ostracoderms.



Dental mesowear analysis of the Middle Miocene *Tethytragus* (Bovidae) assemblage from the Somosaguas site (Spain)

***Noelia Sánchez Fontela**^{1,2}, **Manuel Hernández Fernández**^{3,4}, **Laura Domingo**^{3,5} and **Soledad M. Domingo**³

¹University of Burgos, Spain

²University of Oviedo, Spain

³Universidad Complutense de Madrid, Spain

⁴Instituto de Geociencias (CSIC-UCM), Spain

⁵University of California Santa Cruz, USA

Somosaguas is a Middle Miocene (Middle Aragonian, MN5) vertebrate locality based in the Madrid Basin (Spain) and constitutes one of the oldest assemblages in the world with remains of the bovid *Tethytragus*. In this preliminary study, we examine the diet of *Tethytragus* from this 14 Ma locality and evaluate dietary changes undergone by this genus during the Middle Miocene. Palaeodietary assessment of the Somosaguas bovid material was undertaken applying three dental mesowear analysis methods (Mesowear I, Mesowear II and Mesowear III) and using a comparative database of 61 extant species of browsing, grazing and mixed feeding ruminants. Mesowear analysis indicates an abrasion-dominated signal, consistent with a mixed diet. *Tethytragus* teeth from Somosaguas show a mesowear pattern similar to that observed in extant African antelopes with mixed habits, such as *Ourebia ourebi*, *Gacella dorcas*, *Gazella leptoceros*, *Nanger soemmerringi* and *Nanger granti*. Our mesowear dietary results for the Somosaguas *Tethytragus* assemblage agree with previous ecological reconstruction studies of this fossil site. We do not find changes in the diet of this genus when we compare our results with other studies of younger Middle Miocene *Tethytragus* populations, and therefore we consider it as a generalist ruminant.

New postcranial remains of an ornithopod from the Upper Jurassic of Alpuente (Valencia, Eastern Iberia)

***Sergio Sanchez Fenollosa**^{1,2}, **Maitte Suñer**², **Francisco J. Verdú**³, **Arturo Gamonal**² and **Carlos Santisteban**¹

¹University of Valencia, Spain

²Museo Paleontológico de Alpuente, Spain

³Fundación Conjunto Paleontológico de Teruel-Dinópolis, Spain

The ornithopod fossil record from the Upper Jurassic of the Iberian Peninsula is scarce and fragmentary. In the present work we provide information regarding finds of axial and appendicular remains of an ornithopod dinosaur from the Villar del Arzobispo Formation at the locality of Alpuente (Valencia, Spain), with a preliminary Tithonian age. The new locality, named “Fuentecillas”, could be considered one of the most important ornithopodian records of this lithostratigraphic unit. The remains comprise four sacral vertebrae, eight caudal centrums, the distal half of a left humerus and a possible phalanx. The proportions of the amphicoelus caudal vertebrae and the humerus (slender, with moderately developed condyles), are similar to those of basal ankylopollexians such as *Draconyx loureiroi*, *Camptosaurus dispar* and *Cumnoria* (= *Camptosaurus*) *prestwichii* from the Upper Jurassic of Europe and North America. More specifically, the humerus is very similar to that of *Cumnoria* due to the presence of a characteristic lateral concavity at the radial condyle. Despite this resemblance, the remains will be provisionally assigned to *Ankylopollexia* indet.



Isotopic geochemistry of the Turolian site (Upper Miocene) of Corral de Lobato (Molina de Aragón, Spain)

***Dánae Sanz**¹, **Manuel Hernández Fernández**^{1,2}, **María Belén Muñoz-García**¹, **Patricia Pérez-Dios**³, **Jorge Morales**⁴ and **Laura Domingo**^{1,5}

¹Universidad Complutense de Madrid, Spain

²Instituto de Geociencias (CSIC, UCM), Spain

³Ministerio de Política Territorial y Función Pública, Spain

⁴Museo Nacional de Ciencias Naturales-CSIC, Spain

⁵University of California Santa Cruz, USA

This work encompasses a multidisciplinary study in order to reconstruct palaeoenvironmental, palaeoecological and palaeoclimatic conditions of the karstic fossil site of Corral de Lobato (MN13, Late Miocene), situated near the village of Molina de Aragón (Guadalajara, Spain). The study combines 1) the characterization of Miocene geological materials found in the surroundings and within the fossil site, and 2) tooth enamel carbon ($\delta^{13}\text{C}_{\text{CO}_3}$) and oxygen ($\delta^{18}\text{O}_{\text{CO}_3}$) stable isotope analyses on medium- to large-sized mammals recovered at Corral de Lobato. Two lithological Miocene units have been differentiated in the area: a widespread siliclastic unit and a local carbonate unit, genetically related with the palaeontological site. Based on the characterization of the different facies associations of the latter unit, a fluvio-lacustrine environment has been interpreted for the Late Miocene. Tooth enamel stable isotope results point to intermediate conditions from woodland-mesic C3 grassland to open woodland-xeric C3 grassland. From the standpoint of predator-prey interactions, statistical post-hoc tests and a Bayesian mixing model based on $\delta^{13}\text{C}$ values support some extent of resource and habitat partitioning between the hyaenids *Thalassictis hipparionum* and *Adcrocuta eximia*.

From a systematic waste basket to the fossil record of giant isopods

Mario Schädel¹, **Matúš Hyžný**² and **Joachim T. Haug**¹

¹Ludwig-Maximilians University of Munich, Germany

²Comenius University in Bratislava, Slovakia

Where fossils do not show phylogenetically important characters, taxonomy as it is currently practised quickly reaches its limits. In such situations misconceptions of diagnoses often (slowly) lead to form-genera (a form of parataxonomy). ‘*Palaega*’, a group of fossil crustaceans, an ingroup of Isopoda (woodlice and their relatives) is a very good example of such a situation. For many of the fossils interpreted as representatives of ‘*Palaega*’, in fact only a very coarse systematic interpretation is possible. Interestingly, many of the ‘*Palaega*’ species, including the type species of *Palaega*, *Palaega carteri* Woodward, 1870, can instead be interpreted as fossil representatives of *Bathynomus*. *Bathynomus* is a group of Isopoda that is well known for comprising the largest representatives of the group, with modern-day individuals in the deep sea reaching almost half a metre in size. Most of the evolutionary history of *Bathynomus* may hide in fossils labelled as ‘*Palaega*’. Based on measurements on extant specimens of *Bathynomus* and using machine learning, the original body size can be estimated even for very incomplete fossil specimens, allowing insights into the evolution of gigantism in this lineage of Isopoda.



What makes the difference between schizochroal phacopid and other trilobite eyes?

Brigitte Schoenemann¹ and Euan N.K Clarkson²

¹*University of Cologne, Germany*

²*University of Edinburgh, UK*

Trilobites show two main principles of compound eyes. Often, numerous lenses lie densely packed in hexagonal arrays – the so-called holochroal eyes. The schizochroal eye is restricted to the subfamily Phacopinina; here the lenses lie separated from each other and are much larger. Recently, a trilobite was analysed from the base of the lower Cambrian which is probably among the oldest systems possible. In phosphatized preservation its holochroal eyes excellently show concepts of modern apposition eyes. Wolfgang Stürmer was a pioneer of X-ray analyses in fossils. He was scorned by his comrades when he found traces of white lines in a phacopid eye, which he interpreted as light guiding structures. Reconsideration of his material has revealed that these lines indeed were an integrated part of the eye. On top of them, one can clearly recognize sets of individual ommatidia with spherical lenses, sharing the large aperture of their covering big lens. This finding unmasks the enigmatic phacopid system as consisting of small compound eyes below each of the lenses. The now small ommatidia may have invaded from the sides, explaining the big interspaces between the lenses. This 400-million-year-old eye is revealed as a highly sophisticated system.

The influence of predation on early vertebrate evolution – biomechanics of the earliest vertebrate skeletons

Caitlin M. Sclater, *Oliver E. Demuth, Emily J. Rayfield and Philip C. J. Donoghue

University of Bristol, UK

The mineralized skeleton represents one of the most important innovations in vertebrate evolutionary history. It is first manifest in the extinct jawless ‘ostracoderms’, which were encased in a comparatively thick mineralized skeletal layer, conventionally interpreted as performing a protective armour function, adept in resisting predatory loads – the hypothesis we sought to test. Specifically, we examined whether increased complexity in dermal architecture improves resistance to loading. We created 2D finite element models representing 1) a stylised homogenous, 2) regular heterogeneous (cancellous), and 3) a complex heterogeneous structure of the dermal bone of heterostracans, the earliest of the ostracoderms. The models were informed by CT analysis of representative species and used to test the comparative resistance of the different structures to predatory load at 1) local microscopic and 2) whole-body macroscopic scales. The cancellous architectures efficiently resisted loading, suggesting resistance to predatory loads. Calculations of the maximum loading the heterostracan exoskeletons could withstand before failure showed an additional link between size increase and survival potential. All results corroborate the prior hypothesis that the dermal skeleton of ostracoderms was adapted to resist loads applied by predators and, thus, predation served as a selective driver in the early evolution of the vertebrate mineralized skeleton.



Virtual ammonite pavement: time-series photogrammetry documents rapid changes in Lyme Regis' famous Early Jurassic formation

Amy Scott-Murray, Zoë E. Hughes and Richard J. Twitchett

Natural History Museum, London, UK

The 'ammonite pavement' is a unique Early Jurassic bed within the Blue Lias Formation, exposed only on the English coast near Lyme Regis. It is a focus for research and is part of a key succession of rocks that document recovery from the Late Triassic mass extinction. Storm damage has caused structural weakness, leading to significant undercutting and the development of further cracks. Several metre-sized blocks have become detached and the holes within the bed have increased in size. It is inevitable that breakup will continue, and likely accelerate. We made regular visits to the site over the past two years and continue to do so each quarter. We conducted photogrammetric surveys on each occasion. The 3D models generated after each visit are directly comparable to one another, meaning that the progress of the pavement's disintegration can now be visualized and quantified in great detail. Additionally, the work provided excellent opportunities both to refine our techniques for field photogrammetry and to automate the reconstruction process as far as possible. Here we present the results of our survey, some insights into the process which have been gained so far, and some possibilities for how the models may be put to use.

The endangered fossil sites from the Plio-Pleistocene Lower Segura Basin (Spain)

***Joaquín R. Sendra Sáez**

University of Valencia, Spain

The Lower Segura Basin is located at the eastern end of the Betic Cordillera in southern Spain. During the Pliocene, this large area formed a shallow marine platform where calcarenites, sands and silts were deposited, and where a large number of invertebrate, vertebrate (including marine and continental mammals, micro-, macro- and megafossils) and plant remains can be found. Although most of the recovered remains are hosted at the Guardamar del Segura and Rojales local palaeontological museums, the requirements of new areas for urban expansion and the fossil hunting of fossiliferous beds have destroyed a large amount of the outcrops; *e.g.* the Lower Pleistocene unit known as the 'Segura Conglomerates' which contains abundant continental mammals. In this work we discuss this situation and present new outcrops of conglomerates with an important fossil vertebrate assemblage, outcrops that deserve special treatment in order to study and/or preserve them.

The Balaenidae of southeast Spain: fossil assemblages, ichnology and taphonomy

***Joaquín R. Sendra Sáez¹ and Matias Reolid²**

¹*University of Valencia, Spain*

²*Universidad de Jaén, Spain*

The marine fossil assemblages of the Pliocene of southeast Spain constitute the record of the marine fauna that colonized the western Mediterranean after the Messinian Salinity Crisis. This work focuses on the analysis of marine mammals, especially cetaceans from the Vera Basin (southeast Spain). The sedimentary sequences of the northern region of the Vera Basin display stratigraphical, sedimentological and palaeontological features that correspond to the evolution from a shallow marine shelf (early-mid Pliocene Cuevas



Formation) to a Gilbert-type fan delta (mid-late Pliocene Espiritu Santo Formation). The progradation of the fan-delta lobes in this narrow basin resulted in the partitioning of the basin and formed a small sub-basin with restricted stagnant conditions. The high input of siliciclastics due to the uplift context of the margins of the basin favoured a high sedimentation rate and the fast burial of vertebrate remains. Cetaceans occur from shallow shelf deposits to bottomset, and lower part of the clinoforms in the foreset. Sirenians are only recorded in coarse sand facies deposited in shallow waters near the shoreline. The presence of cetaceans in this narrow and relatively protected basin is interpreted as an area of reproduction and a nursery for juveniles.

Endocranial anatomy of the allodaposuchid *Agaresuchus fontisensis* (Crocodyliformes, Eusuchia) from the Late Cretaceous of Spain

***Alejandro Serrano Martínez¹, Fabien Knoll^{2,3}, Iván Narváez¹, Stephan Lautenschlager⁴ and Francisco Ortega¹**

¹Universidad Nacional de Educación a Distancia, Spain

²Fundación Conjunto Paleontológico de Teruel-Dinópolis, Spain

³The University of Manchester, UK

⁴University of Birmingham, UK

Agaresuchus fontisensis is an allodaposuchid crocodyliform known only from the Upper Cretaceous (Campanian–Maastrichtian) site of Lo Hueco (Cuenca, Spain). Allodaposuchidae is a clade of European basal eusuchians, considered in recent analysis as a close outgroup to Crocodylia or within this crown-group. The holotype and paratype skulls of *Agaresuchus fontisensis* were CT-scanned and their internal cavities, including those of the brain, nerves and blood vessels as well as the paratympanic and paranasal sinus systems, were digitally reconstructed. The cranial endocast and pneumatic sinuses were then compared with those of other mesoecrocodylians. The neuroanatomy of *Agaresuchus fontisensis* is reminiscent of that of primitive mesoecrocodylians, but already shows the morphological traits present in extant crocodylians. The endocast of *Agaresuchus fontisensis* has a cylindrical shape. In lateral view, the hindbrain region medial to the prootics extends dorsally almost as far as the forebrain. In their morphology and orientation, the cranial nerves show the same pattern as in other eusuchians. The pneumatic sinuses form a voluminous complex surrounding the mid-hindbrain region. The neurosensorial and cognitive capabilities inferred for *Agaresuchus fontisensis* are similar to those of other eusuchians. The olfactory abilities and visual acuity were highly developed, close to those of *Lohuecosuchus megadontos*, a sympatric and coeval allodaposuchid.

The ‘Ordovician explosion’ of land plants

Thomas Servais¹, Borja Cascales-Miñana¹, Christopher J. Cleal², David A. T. Harper³ and Philippe Steemans⁴

¹CNRS UMR 8198, Université de Lille, France

²Amgueddfa Cymru – National Museum Wales, UK

³Durham University, UK

⁴University of Liège, Belgium

Molecular clock data suggest, with high probability, a Cambrian origin for Embryophyta (land plants), indicating that their terrestrialization most probably started around 500 Ma.



The fossil record of the ‘Cambrian explosion’ was limited to marine organisms and is not visible in the plant fossil record. The most significant changes in early land plant evolution occurred during the Ordovician. For instance, the earliest bryophyte-like cryptospores and the oldest fragments of the earliest land plants (and possibly spores from tracheophytes) are from the Middle and Late Ordovician, respectively. Organic geochemistry studies of biomarker compositions hint at a transition from green algae to land plants during the Great Ordovician Biodiversification Event. The colonization of the terrestrial realms by land plants clearly had an impact on marine ecosystems. Interactions between the terrestrial and marine biospheres have been proposed and the radiation of land plants potentially impacted CO₂ and O₂ concentrations and global climate. In addition, the shift of strontium isotope values during the Ordovician is probably linked to changing terrestrial landscapes, affected by the first massive land invasion by eukaryotic terrestrial life. An escalation of life on the continents took place in the Ordovician, leading to the ‘Ordovician explosion’ of land plants.

Africa’s earliest pioneers? Subaerial footprints from the Ordovician Graafwater Formation of South Africa

Anthony P. Shillito^{1,2}, Neil S. Davies² and Cameron R. Penn-Clarke³

¹*University of Oxford, UK*

²*University of Cambridge, UK*

³*Council for Geoscience, South Africa*

⁴*University of the Witwatersrand, South Africa*

The earliest records of animals walking on land come from the late Cambrian and Ordovician, with footprints known from North America, Europe and Australia. However, the record from the rest of Gondwana is more uncertain due to a lack of continental deposits from this interval, and the comparative lack of studies on African and South American strata. The Ordovician Graafwater Formation of South Africa records a succession of tidally-deposited sandstones with a moderately diverse ichnofauna of trackways and vertical and horizontal burrows. Some of the trace-bearing strata contain evidence for emergence and subaerial exposure, such as adhesion marks and raindrop impressions. Combining ichnological and physical sedimentary surface textures, this poster presents the earliest evidence of footprints in subaerial strata from Africa, within the context of these emergent tidal deposits. The ichnofauna of the Graafwater Formation is comparable to that of the Ordovician–Silurian Tumbago Sandstone of Western Australia, also thought to be deposited in a tidal environment and at a similar palaeolatitude. This poster discusses the implications of the similarities between these ichnofaunas, and what can be inferred about the ecology of low latitude shallow marine faunas in the Ordovician–Silurian.



Shedding synchrotron light on the architecture and evolution of conodont feeding apparatuses

***Bryan Shirley**^{1,3}, **Carlos Martínez-Pérez**² and **Philip C. J. Donoghue**³

¹*University of Erlangen–Nuremberg, Germany*

²*University of Valencia, Spain*

³*University of Bristol, UK*

Conodonts are the first vertebrates to have developed mineralized tissues, forming microscopic teeth-like structures known as elements. They are ubiquitous in marine rocks originating from the late Cambrian to Late Triassic. Due to the rarity of soft tissue preservation, the majority of specimens are disarticulated and leave no insight into the structure of the original oral apparatus. The scarcity of information on 3D structures of the apparatus hinders reconstructions of the evolution of this hyperdiverse group and limits our understanding of its functional morphology. Architectural reconstructions of conodont apparatuses can be obtained from clusters of diagenetically fused elements that preserve the relative positions of elements. We employ synchrotron radiation X-ray tomographic microscopy (SRXTM) to produce virtual models of the apparatus of the conodont clusters from the Kokomo Limestone of Indiana, USA. These models help resolve homology among element positions, quantitatively test hypotheses on the feeding mechanisms of conodonts, and thus on their ecological role in marine ecosystems. Furthermore, defining these positions enables us to establish character-based phylogenies. Constraining functional morphology by character-based phylogenies is essential to reconstruct the evolution of feeding ecology. This, in turn, allows testing hypotheses on the evolution of early marine ecosystems and their trophic structures.

The find of haem derivatives in vertebrate fossils from the Messel pit, Germany

Sandra Siljeström¹, **Volker Thiel**² and **Andrew Steele**³

¹*RISE Research Institutes of Sweden, Sweden*

²*University of Göttingen, Germany*

³*Carnegie Institution of Science, USA*

Organic molecules preserved in fossils may provide a wealth of new information about the history of life. Finds of almost unaltered organic molecules in well-preserved fossils raise the question of how common such occurrences are in the fossil record and what promotes such preservation. The aim of this study is to identify fossils with porphyrins preserved and to investigate the conditions that might promote preservation of porphyrins and other organic molecules in fossils. We have investigated several fossils from the Eocene Messel pit, Germany, using a variety of techniques including time-of-flight secondary ion mass spectrometry (ToF-SIMS), pyrolysis gas chromatography mass spectrometry (GC-MS), scanning electron microscopy/energy dispersive X-ray spectroscopy (SEM/EDX) and Raman spectroscopy. Several different organic molecules were detected, including only slightly diagenetically altered haem, which may originate from the fish fossil. Further analyses showed that pyrite, aluminium silicates and calcium phosphates are intermixed with the organic material. This suggests that several different taphonomic processes are involved in the preservation of the fossil and the organic molecules associated with it. Our investigations are now being extended to fossils from other locations such as the Oligocene Enspel, Germany where initial results show haem associated with the fossils.



The evolution of thecideid brachiopod shell microstructure from Triassic to modern times

***María del Mar Simonet Roda**¹, **Sara Milner**², **Tamás Müller**³, **Erika Griesshaber**¹, **Hana Jurikova**⁴, **Claire Rollion-Bard**², **Lucia Angiolini**⁵, **Facheng Ye**⁵, **M. Aleksandra Bitner**⁶, **Daniela Henkel**⁴, **Adam Tomašových**³, **Anton Eisenhauer**⁴, **David A. T. Harper**⁷, **Ulrich Jansen**⁸ and **Wolfgang W. Schmahl**¹

¹Ludwig-Maximilians University of Munich, Germany

²Institut de Physique de Globe de Paris, France

³Geological Institute SAS, Slovakia

⁴GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany

⁵Università degli Studi di Milano, Italy

⁶Institute of Paleobiology (PAN), Poland

⁷Durham University, UK

⁸Naturmuseum Senckenberg Frankfurt, Germany

The investigation of thecideidine shell morphology and structure has been the subject of research for several decades and has revealed the distinctiveness of this group of brachiopods relative to species of other extinct and modern brachiopod genera. Shell microstructure and texture in modern brachiopod orders show that thecideid brachiopod shells do not have an obvious mineral unit organization compared to that of modern rhynchonellid and terebratulid brachiopods. In this study we trace the formation and evolution of thecideid shell microstructure and texture from their first appearance in the Late Triassic to modern times. We used two modern representatives (*Pajaudina atlantica* and *Kakanuiella chathamensis*) as controls. They present a heterogranular microstructure consisting of highly irregularly-shaped mineral units, with calcite being assembled with a low degree of co-orientation. We investigate with different techniques, such as EBSD and AFM, the relationship between fibrous, granular and acicular fabrics, e.g. the progressive disappearance of fibres and the emergence of granules. We imaged and measured the shell microstructure and texture of selected taxa, differentiating the crystal morphologies within the individual microstructures and following their abundance through time. We observed major changes between the Jurassic and Cretaceous specimens.

Testing the biochemical fidelity of fossil feathers using sulfur speciation

***Tiffany Slater**¹, **Nick Edwards**², **Samuel Webb**², **Richard Unitt**¹ and **Maria E. McNamara**¹

¹University College Cork, Ireland

²Stanford Synchrotron Radiation Lightsource (SSRL), USA

Fossil feathers provide key information on macroevolutionary events such as the dinosaur-bird transition and the origins of flight. Despite extensive research, there is no consensus on whether the primary biomolecular component of feathers – keratin – can preserve in fossils. Here we use sulfur X-ray absorption near-edge structure (XANES) spectroscopy to explore changes in feather chemistry – in particular, the keratin disulfide bond – during taphonomic experiments. Black and orange feathers from *Gallus gallus* and white feathers from *Egretta garzetta* were decayed for up to 12 months and matured at temperatures of up to 250°C. Our results show that decay has minimal impact on sulfur chemistry and that progressive maturation is associated with progressive oxidation of sulfur. Notably, the extent of oxidation differs in feathers of different colour under the same conditions.



All fossil feathers analysed show peaks for sulfonate, a relatively oxidised sulfur species, but some feathers also show peaks for reduced sulfur species, suggesting less extensive degradation. These data demonstrate that sulfur speciation is a key proxy for assessing the extent of keratin degradation in fossils and can act as an independent tool for testing the biochemical fidelity of fossil feathers.

Tree shape and disparity: two sides of the same coin?

***Thomas Smith¹, Mark N. Puttick^{1,2}, Joseph E. O'Reilly¹, Davide Pisani¹ and**

Philip C. J. Donoghue¹

¹University of Bristol, UK

²University of Bath, UK

Analyses of morphological disparity attempt to capture the range of phenotypic variation exhibited by clades and determine how and why they vary over time. However, most such studies consider evolutionary singularities, hindering discrimination between credible causal hypotheses and just-so post hoc explanations of a clade's disparity. In an attempt to derive a null model for such analyses, we explore through simulation the impact of phylogenetic tree properties on the perception of evolving phenotypic disparity, measured in terms of mean pairwise distance, sum of ranges, sum of variances, and mean distance from centroid. Specifically, we consider the effects of tree symmetry and branch length distribution, characteristics sensitive to taxon sampling. We demonstrate that tree shape predictably impacts upon perceived disparity. When mean-based measures are deployed, datasets capturing the phylogenetic signal of fossil trees exhibit higher disparity than extant equivalents, with synapomorphies contributing most to the phenotypic variation recorded. Conversely, the sum of ranges metric is most affected by the evolution of autapomorphies; its magnitude is dependent on external branch length. These simulation-based results are corroborated through analyses of empirical datasets. Altogether our results highlight the need for careful consideration of tree shape and taxon sampling when interpreting disparity analyses of cladistic datasets.

Late Early Miocene mammals from the Laguna del Laja, Cura-Mallín Formation, south central Chile

***Andres Solorzano¹, Alfonso Encinas¹ and René Bobe²**

¹Universidad de Concepción, Chile

²University of Oxford, UK

The Cura-Mallín Formation consists of a series of Upper Oligocene to Middle Miocene volcanic and sedimentary rocks deposited in continental settings that crop out in the Andean Cordillera of Chile and Argentina. Recent field-trips to beds of the Cura-Mallín Formation, cropping out in the Laguna del Laja region with radiometric ages constrained between 17.9–16.4 Ma (late Early Miocene; Santacrucian SALMA), have resulted in the discovery of several new specimens of fossil mammals, reported here for the first time. These include caviomorphs (*Phanomys mixtus*, *Prolagostomus* sp., *Neoreomys* sp., and undescribed species of *Protischomys* and *Luantus*), notoungulates (*Adinotherium* sp., *Pachyrukhos* cf. *P. moyanoi*, *Hegetotherium* sp., and *Protypotherium* sp.), an undescribed genus of mylodontid sloth, armadillos (two indeterminate Dasypodidae), marsupials (Palaeothentidae indeterminate) and litopterns (Proterotheriidae indeterminate). Several of these taxa (e.g. *P. mixtus*) are reported from Chile for the first time and contribute to a



more complete understanding of the palaeodiversity of the country. While a few of these taxa likely represent undescribed species and even genera, most resemble taxa already known from the Early Miocene faunas from Patagonia (Argentina), and support a wide distribution of Santacrucian faunas in the south of South America.

Biotic and abiotic factors driving the diversification dynamics of Crocodylia

***Andres Solorzano¹, Mónica Nuñez-Flores^{1,2}, Oscar Inostroza-Michael¹ and Cristián H. Hernández¹**

¹*Universidad de Concepción, Chile*

²*Universidad de Sevilla, Spain*

Species diversity patterns, governed by complex interactions among biotic and abiotic factors over time and space, essentially result in long-term diversification dynamics. Previous studies suggest that temporal variations in global temperature drove long-term diversity changes in crocodylians (Crocodylia). Using a large database of fossil occurrences (192 spp.) and body mass estimations, following a taxic approach, we characterize the global diversification dynamics of crocodylians and their correlation with multiple biotic and abiotic factors in a Bayesian framework. The diversification dynamic of crocodylians is characterized by several phases with high extinction and speciation rates within a predominantly low long-term mean rate. Their long-term diversification dynamics is a complex process driven by a combination of biotic and abiotic factors. Higher crocodylian extinction rates are related to low body mass disparity, indicating selective extinctions of taxa at both ends of the body mass spectrum. Speciation rate slowdowns are noted when the self-diversity of the clade is high and the warm temperate climatic belt is reduced. Therefore, temporal variations of body mass disparity, self-diversity, and the warm climate belt size provided more direct mechanistic explanations for crocodylian diversification than do proxies of global temperature.

Multi-dimensional ecological proxies for all: application of homology-independent metrics to dietary analysis in phylogenetically distant clades

Christopher Stockey¹, Thomas H. P. Harvey¹, Philip C. J. Donoghue², Duncan J. E. Murdock³ and Mark A. Purnell¹

¹*University of Leicester, UK*

²*University of Bristol, UK*

³*Oxford University Museum of Natural History, UK*

Palaeobiological inferences of dietary preference have traditionally focused on the morphology of feeding structures and, in particular, dental complexity has been shown to correlate with diet. However, most studies have been one dimensional – analysing a single aspect of morphology to infer diet and trophic niche. Furthermore, this approach has been largely restricted to vertebrate dentitions. Here we demonstrate the effectiveness of an emerging technique, multi-proxy dental morphology analysis (MPDMA), in reconstructing trophic guilds in invertebrate taxa. MPDMA combines multiple one-dimensional metrics, generating a holistic measurement of complexity comparable between distantly related clades. MPDMA has previously only been applied to crown-mammals and reptiles. Here we test the hypothesis that MPDMA applied to non-homologous dental tools tracks dietary differences in other groups. To achieve this we analysed the mandibles of *c.* 50 species



of extant orthopterans (grasshoppers and crickets), for which diet is well-constrained. Our results show that MPDMA successfully predicts dietary properties in orthopterans, demonstrating that MPDMA has applicability beyond the teeth of jawed vertebrates, and can be extended to non-homologous dental tools in other groups, including extinct taxa. This is crucial for analysis of trophic and ecosystem-level responses to perturbation events in deep time.

Aragonitic fossil otoliths: debating their pristine preservation

Jarosław Stolarski¹, Ismael Coronado^{1,2} and Urszula Radwańska³

¹*Institute of Paleobiology (PAN), Poland*

²*University of León, Spain*

³*University of Warsaw, Poland*

Teleost otoliths are organo-mineral structures composed mostly of aragonite (sagitta and lapillus otoliths) or vaterite (asteriscus otoliths) and organic components formed in the inner ear, and are used for balance and/or hearing. Otoliths are composed of CaCO₃ crystals that radiate from the inner otolith region and show daily growth increments. The thickness and compositional variations between these growth increments are influenced by the circadian cycle and environmental parameters, making otoliths suitable for a broad range of applications in sclerochronology and palaeoenvironmental studies. Exceptionally well-preserved fossil aragonitic otoliths allow the extension of palaeoenvironmental reconstructions deep into the Mesozoic, assuming that aragonite is an indicator of primary mineralogy of the most commonly used sagittal otoliths. Here we present results of comprehensive structural (SEM), crystallographic (EBSD, XRD) and geochemical (EMPA) studies of fossil aragonite sagitta otoliths from several Cretaceous, Eocene and Miocene deposits from Poland, and comparative extant specimens aimed to assess pristine/secondary features of fossil otolith aragonite. Variations in fossil aragonite preservation have been observed in trace element composition and the amount of porosity, as well as in their crystallographic properties (lattice parameters and kernel misorientation). Although some of these changes can be signatures of non-actualistic seawater parameters or fish palaeophysiology, in some exceptional cases, aragonite is recrystallized keeping the original mineral phase but losing its 'biogenic' features.

Morphology of the petrosium of the Late Miocene cetaceans *Kurdalagonus*

Konstantin Tarasenko

Borissiak Paleontological Institute, RAS, Russia

Findings of Miocene cetaceans in the North Caucasus or Ciscaucasia region are numerous. Initially, the morphology of the bone labyrinth of the Late Miocene cetacean genera *Zygiocetus* and *Kurdalagonus* was described from four samples. New material supplemented the study on petrosal morphology of representatives of the genus *Kurdalagonus*. The preliminary data obtained make it possible to assess the degree of variability of some signs of the stony bone labyrinth for representatives of the genus *Kurdalagonus*. In *Kurdalagonus*, a characteristic narrowing of the wall of the canal of the facial nerve anterior to pars cochlea is observed, passing into the fissure. A few morphological features of the vestibular labyrinth and the degree of their variability were also noted. This is of great importance for determining fragmentary finds of cetaceans, many of which are represented by isolated petrosal bones.



Oligocene and early Miocene shallow marine and mudflat-associated molluscs of the Mesohellenic Basin (NW Greece)

***Danae Thivaïou¹, Efterpi Koskeridou¹, Mathias Harzhauser² and Hara Drinia¹**

¹National and Kapodistrian University of Athens, Greece

²Natural History Museum Vienna, Austria

The Mesohellenic Basin (northwestern Greece) has been of interest because of its fossiliferous sediments of middle-late Oligocene to early Miocene ages. Fossiliferous localities of these ages are scarce in the Mediterranean realm, thus the material recovered here is considered rare. In the present work, we focus on new fossil finds from the Mesohellenic Basin, corresponding to the eastern part of the Proto-Mediterranean, with the aim of defining and analysing marine environments of the late Oligocene–early Miocene. Localities included in the present study are rich in molluscs and particularly gastropods. A taxonomic analysis revealed more than 100 species of gastropods and some 20 species of bivalves. Multivariate analyses reveal similarities of the faunas with adjacent regions, including taxonomic composition and environment type. The closeness between the brackish faunas recovered with equivalent faunas from the eastern Atlantic, Switzerland, Germany and Turkey is noted. Mangrove vegetation seems to be present in the studied basin, as attested by mudflat-dwelling species of gastropods (*Granulolabium plicatum*, *Mesohalina margaritacea*) and species of the mangrove associated gastropod *Terebralia*. The results of this work contribute to the knowledge of the taxonomic diversity, biogeographic affinities, and connectivity with adjacent basins (Atlantic, Proto-Mediterranean, Paratethys, Indian Ocean).

Stable carbon isotope composition of macroalgal, invertebrate and vertebrate fossils: implications from the Kalana Lagerstätte

Oive Tinn, Leho Ainsaar, Liisa Lang and Viirika Mastik

University of Tartu, Estonia

Stable carbon isotope composition of sediments has long been used as a tool in stratigraphic correlations as well as a proxy for palaeoenvironmental changes in the carbon cycle. Several studies have demonstrated that various rock components, such as carbonate fossils or organic matter of different taxonomic groups, show carbon isotope compositions which differ from that of the surrounding sedimentary rock. Here we present results of carbon isotope analyses from completely or partially organically-preserved invertebrate fossils such as crinoids, sponges and worms, but also hemichordate and vertebrate fossils from the Kalana Lagerstätte, Estonia of Aeronian (Llandovery, Silurian) age. In the present study we sampled thalli of red and green (dasycladalean) algae, crinoids, periderms of graptoloid and dendroid graptolites, and an agnathan fish. The $\delta^{13}\text{C}_{\text{org}}$ analyses of individual fossils were supplemented with whole-rock $\delta^{13}\text{C}_{\text{carb}}$ and dispersed organic material $\delta^{13}\text{C}_{\text{org}}$ analyses from the same rock slabs. The acquired data were compared with the published values from previous studies from different Lagerstätten.



Step by step, using dinosaur footprints as tools for education and outreach

Angelica Torices, Pablo Navarro-Lorbés, Raul San Juan Palacios and Mireia Ferrer Ventura
Universidad de La Rioja, Spain

La Rioja's extraordinary fossil record has been used as an educational tool for the development of a summer course programme at the University of La Rioja, Spain from 1980 until 2014 under the supervision of Dr Félix Pérez Lorente. This course was reinstated in 2017 and has gained popularity in these last two years. During the course, undergraduate and graduate students learn techniques in restoration and preservation of palaeoichnological sites, applying them directly to the sites under supervision. Students have the opportunity to learn photogrammetry and lead their own research projects to be developed at the site. As a part of the course they are encouraged to present their research results at young researchers' conferences and seminars. The course takes place at palaeontological sites located very near to towns and on tourist routes so we can combine palaeontological outreach with fieldwork. We complement the course with a series of conferences where national and international researchers share their work and offer the students the possibility of networking. Therefore, this summer course is an opportunity to gain experience of fieldwork and research but also an opportunity to promote palaeontology as a useful tool for outreach and economic development of the region through tourism.

Who left this footprint? Application of augmented reality in palaeoichnological sites

Angelica Torices¹, Jose Manuel Valle Melon², Alvaro Rodriguez Miranda², Garbiñe Elorriaga Agirre², Francisco Gasco³, Pablo Navarro-Lorbés¹, Raul San Juan Palacios¹ and Mireia Ferrer Ventura¹

¹*Universidad de La Rioja, Spain*

²*Universidad del Pais Vasco, Spain*

³*Universidad Nacional de Educacion a Distancia, Spain*

The exceptional palaeontological heritage of La Rioja, Spain is one of the main natural resources of the region that can be used in several ways: scientific research, education, outreach and economic development through tourism. Extrapolation of the track-makers via the footprints is a difficult task and sometimes visitors find difficulty in making a connection between the footprints and the animal that produced them. Over the years, panels, statues and other educational tools have been used at the sites to provide an enjoyable and educational experience for the visitor. La Virgen del Campo palaeontological site is one of the most emblematic sites of La Rioja and one of the most visited. At this site, two trackways have been interpreted as produced by crocodiles. We developed a free app that allows the visitor, through augmented reality, to observe, through their smartphones or tablets, 3D models of the crocodiles over the trackways on the site. In this way, the visitor can have a more enriched and educational experience as they can see the animals over their footprints on site. This is the first step in the development of a virtual guide to La Rioja palaeoichnological sites.



Craniodental and postcranial characters in Pterosauria result in significantly different inferred phylogenetic relationships

***Tom Trapman**^{1,2}, **Matthew A. Wills**¹ and **Natalie Cooper**²

¹University of Bath, UK

²Natural History Museum, London, UK

Morphological data still have an important role for phylogenetic inference, and are usually the sole source of information for fossil taxa. However, fossils are often incomplete or poorly preserved, and this determines the suites of characters that can be analysed. Moreover, different regions of the body can be subject to divergent selection pressures and variable rates of character change. Previous studies of craniodental versus postcranial characters in vertebrates in general and non-avian dinosaurs in particular have demonstrated that optimal trees inferred from these regions are significantly at odds, much more often than we would expect. Here we test if the same phenomenon occurs for another remarkable group of archosaurs: Pterosauria. We analysed 42 of the most inclusive morphological matrices from the last 20 years using both incongruence length difference (ILD: tree length based) and incongruence relationship difference (IRD: tree shape based) tests. A majority yielded significant incongruence. Our results imply that the inferred relationships of incomplete pterosaur fossils should be treated with caution, particularly where data are concentrated within a single region of the skeleton (*e.g.* skulls, postcrania) rather than sampled broadly from multiple body regions.

Timing Lochkovian (Lower Devonian) conodont bioevents: the Pyrenean experience

José Ignacio Valenzuela Ríos and **Jau-Chyn Liao**

University of Valencia, Spain

Lochkovian (Lower Devonian) strata from eight Pyrenean sections recorded several conodont evolutionary lineages, which have proved to be instrumental for subdividing the Lochkovian. Members of various groups report different types of global bioevents, which are critical for the most detailed zonation and even further subdivision of zones. Relevant in this endeavour are the innovation and radiation of the genera *Ancyrodelloides*, *Lanea*, *Flajsella* and *Masaraella*. The quick evolutionary steps of the former led to the successive appearance of seven taxa in less than three million years, which reinforces their value in detailed subdivision of the interval. This kind of record permits testing the pace of bioevents for different conodont genera and analysis of their value for global correlations. The integration of these analyses with cyclostratigraphic techniques will be essential for understanding the role that astronomical factors could have played in the evolution of ecosystems, and we will explore these relations within the frame of the UNESCO-IGCP-652.

Patterns of morphological and genetic disparity in mammalia

***Conrad van den Ende**, **Mark N. Puttick**, **Araxi Urrutia** and **Matthew A. Wills**

University of Bath, UK

At the macroevolutionary scale, the relationship between morphological and genetic change is opaque, yet understanding this relationship is a central objective of evolutionary biology. By examining the relative variance in morphology of taxa, known simply as disparity,



we can understand the patterns and processes that underlie phenotypic macroevolution in the fossil record. Here we explore possible meanings of the term ‘genetic disparity’, and propose some indices for its quantification. We test ancestral state reconstruction by quantifying the variance between the ancestral and extant sequences as well as performing a branch length comparison of maximum likelihood trees. We explore these relationships in Mammalia which represent an excellent focal group of study: mammalian diversity is strongly heterogeneous across higher taxa; there is a well-studied conflict between morphological and genetic phylogenetic analyses; and there is extensive genomic data available for many species. Our results show that metrics of genetic disparity correlate with each other in mammalian subclades. However, the correlation between genetic and morphology is weaker, although it is significant for some genes. We corroborate previous studies to show there is no correlation between morphological disparity and diversity, and extend this to show there is no relationship between genetic disparity with diversity.

Spinophorosaurus nigerensis (Middle ? Jurassic, Niger): mosaic morphofunctional evolution on early branching Eusauropoda

Daniel Vidal¹, Pedro Mocho^{1,2}, José Luis Sanz³ and Francisco Ortega¹

¹Universidad Nacional de Educacion a Distancia, Spain

²Universidade de Lisboa, Portugal

³Universidad Autónoma de Madrid, Spain

Sauropods evolved from bipedal cursorial dinosaur ancestors with grasping hands and long necks of medium size to become large graviportal quadrupeds with columnar limbs and even more elongated necks. How this transition occurred is not completely known, as many early branching sauropods are known either from fragmentary specimens or have not been studied in detail yet. The remarkably complete holotype of *Spinophorosaurus nigerensis* was digitized to build a virtual skeleton for detailed study. Its morphofunctional capabilities were studied and compared with earlier branching sauropodomorphs and more deeply nested Neosauropods. *Spinophorosaurus* shows several characters regarding its feeding and locomotion capabilities evolved at different rates. Unlike earlier branching sauropodomorphs, it had a strongly wedged sacrum that makes the presacral spine slope anterodorsally and gives a substantially more dorsoventral osteological range of motion in the neck, suggesting high browsing capabilities. On the other hand, sauropodomorphs had become obligatory quadrupeds, which use hind and forelimbs as forward thrust during locomotion, before the origin of sauropods. *Spinophorosaurus*, however, has osteological correlates for caudofemoral musculature proportionately larger than large bipedal theropods, comparable to *Plateosaurus*, despite having well-developed pectoral girdle and forelimb musculature. This occurs in many non-neosauropods, suggesting the retention of a basal condition for caudal musculature.

Tackling the demise of the dinosaurs using a novel phylogenetic method

Maria Volkova^{1,2}, Rachel C. M. Warnock², Marc Manceau², Timothy Vaughn² and Tanja Stadler²

¹Sechenov University, Russia

²ETH Zürich, Switzerland

Some controversy remains surrounding the demise of the dinosaurs. Although the K-Pg impact event is widely accepted to have resulted in the extinction of all non-avian species,



the status of dinosaur diversity prior to this event remains disputed. A recent study based on a large dinosaur phylogeny concluded that the group were in decline 50 million years prior to the K-Pg boundary. This analysis used a regression approach, meaning there are hidden assumptions that are potentially problematic. Here we present the results of a novel Bayesian phylogenetic approach to estimating species richness, which uses an explicit birth–death process to model speciation, extinction and sampling. We addressed whether available supertrees do provide statistical evidence for a decline in dinosaur diversity preceding the impact event. Our results indicate speciation was overall higher than extinction during the Cretaceous, which suggests that dinosaurs were potentially thriving. Similarly, estimates of diversity do not show evidence of a decline during this interval. However, we also show that estimates of parameter values are sensitive to the assumptions we make about the fossil recovery process. Extensions of our approach could take advantage of additional evidence in constraining estimates of diversity.

Quantifying conodont disparity at the P-T boundary

Nicola Vuolo and Nicolas Goudeband

Université Claude Bernard Lyon 1, France

Since organisms' morphological variability is the result of the interaction between developmental and environmental constraints, the study of morphological disparity of fossil assemblages is essential to macroevolutionary process reconstructions. We present a quantitative study of conodont disparity at the Permian–Triassic boundary based on P1 elements of 23 genera selected from the Upper Permian to the Lower Triassic. The two main obstacles in conodonts disparity quantification are: 1) the conodont elements accretionary growth and 2) their high intergeneric morphological variability. To overcome those difficulties, we used the modern techniques of X-ray microtomography that have revolutionized the field of palaeontology in recent decades: 3D virtual models of the P1 elements that can be manipulated, sectioned and measured with no damage for the original material. To quantify conodont intergeneric disparity we used a combination of different techniques (such as landmark-based geometric morphometrics and outline analysis) working with both 2D and 3D models. The protocol we developed can be extended to conodont genera from different time intervals, and we applied it to 2D images from literature, exploring their problems and potentials as sources of data for conodont morphological disparity studies.

Body organization in scorpions changing through time: a quantitative approach

***Philipp Wagner, Joachim T. Haug and Carolin Haug**

Ludwig-Maximilians University of Munich, Germany

Scorpions are predatory representatives of Euchelicerata with about 2,300 extant species and various fossil occurrences, the oldest ones dating back to the Silurian (~430 Ma). Morphological diversity in scorpions is not only represented by size differences, but also by differences of body organization. The segmented body of scorpions is organized into functional units (tagmata), which are specialized morphologically to perform different functional tasks, such as walking or food uptake. In Euchelicerata, especially the transition area between the anterior and the next tagma shows a high morphological variability. In scorpions, this transition area is highly compressed with obscured segment borders. For a better understanding of this transition area and its evolution, a morphospace-based



approach was used. Morphospaces are multi-dimensional spaces representing the shape of structures of an organism based on measurements, including different lengths and widths of the specimen, e.g. the maximum width of the prosomal shield or the length of the trunk. After size correction these measurements can be plotted as a morphospace which yields information about the body organization and tagmatization. Including specimens from different geological periods, as well as different ontogenetic stages, provides information about changes of morphological diversity through evolutionary history and individual development.

A feat of clay: palaeontology engagement through art

Elspeth Wallace^{1,2}, Anthea R. Lacchia^{1,3}, Elaine Harrington⁴, Fergus McAuliffe¹, Emma A. Morris^{1,3} and Peter D. W. Haughton^{1,3}

¹*Irish Centre for Research in Applied Geosciences (iCRAG), Ireland*

²*The University of Manchester, UK*

³*University College Dublin, Ireland*

⁴*University College Dublin Parity Artist in Residence, Ireland*

Palaeontology is possibly the most effective tool to engage the public with Earth sciences. However, the audiences reached by palaeontological engagement are often limited to recurring groups, such as families with young children and adults with a pre-held interest in the science. Here we have taken a novel approach to broadening the audiences reached by palaeontological engagement through collaboration with the arts. University College Dublin seed funding has enabled a pilot workshop to be developed and run with UCD Parity Artist in Residence Elaine Harrington. In the workshop, participants were introduced to a range of fossils and the geoscience involved in producing clay for ceramics. They were then encouraged to create a fossil-inspired artwork from the provided clays. Participants actively engaged with and were inspired by the palaeontological material. The 2.5-hour workshop was held on a Saturday afternoon at a community centre in rural western Ireland with low levels of scientific engagement. Attendees (25 people) were predominantly females between the ages of 30 and 60, which suggests the workshop was successful in broadening engaged audiences. We intend to build on this success in future events and expand the project by creating transportable ceramic models. Suggestions for future workshops are welcomed.

Origin of ecdysis: fossil evidence from 535-million-year-old scalidophoran worms

***Deng Wang¹, Jean Vannier¹, Isabell Schumann³, Xing Wang⁴, Xiao-Guang Yang², Tsuyoshi Komiya⁵, Kentaro Uesugi⁶, Jie Sun² and Jian Han²**

¹*Université Claude Bernard Lyon 1, France*

²*Northwest University, China*

³*University of Leipzig, Germany*

⁴*Qingdao Institute of Marine Geology, China*

⁵*University of Tokyo, Japan*

⁶*Japan Synchrotron Radiation Research Institute (JASRI), Japan*

With millions of extant species, ecdysozoans (Scalidophora, Nematoida and Panarthropoda) constitute a major portion of present-day biodiversity. All ecdysozoans secrete an exoskeletal cuticle which must be moulted periodically and replaced by a larger one.



Although moulting (ecdysis) has been recognized in early Palaeozoic panarthropods such as trilobites and basal groups such as anomalocaridids and lobopodians, the fossil record lacks clear evidence of ecdysis in early scalidophorans, largely because of difficulties in recognizing true exuviae. Here we describe two types of exuviae in microscopic scalidophoran worms from the lowermost Cambrian Kuanchuanpu Formation (c. 535 Ma) of China and reconstruct their moulting process. These basal scalidophorans moulted in a manner similar to that of extant priapulid worms, extricating themselves smoothly from their old tubular cuticle or turning their exuviae inside out like the finger of a glove. This is the oldest record of moulting in ecdysozoans. We also discuss the origin of ecdysis in light of recent molecular analyses and the significance of moulting in the early evolution of animals.

Are we reaching gender parity among *Palaeontology* authors?

Rachel C. M. Warnock¹, Emma Dunne², Sam Giles^{2,3}, Erin E. Saupe³, Laura C. Soul⁴ and Graeme T. Lloyd⁵

¹*ETH Zürich, Switzerland*

²*University of Birmingham, UK*

³*University of Oxford, UK*

⁴*Smithsonian Institute, USA*

⁵*University of Leeds, UK*

We examine whether the proportion of women publishing in palaeontology is approaching parity, using data from the journal *Palaeontology* as a proxy for the discipline. This work was motivated by the sense that, despite increased representation of women, articles on palaeontological subjects almost never appear to have 50 % female authorship, regardless of the journal. Indeed, we find that <20 % of authors are female and, perhaps more surprisingly, an insubstantial increase in the proportion of women contributing to the journal over the past 20 years. We highlight important barriers that remain for women and other under-represented groups in science, and we make several recommendations to help improve their representation in palaeontology.

Spatangoid body size during the Late Mesozoic and Cenozoic: implications for present-day global warming

***Ceri Webster^{1,2} and Richard J. Twitchett²**

¹*University College London, UK*

²*Natural History Museum, London, UK*

Anthropogenic climate change is causing, and is predicted to cause, a number of changes to marine ecosystems, reducing biodiversity and elevating extinction rates. Using fossil records, we can identify evolutionary trends from previous periods of global temperature change to test some of the hypotheses related to present-day warming. One example is the prediction that marine animals will become smaller in response to current warming. In this study, we use fossil collections to test this hypothesis in spatangoid echinoids. Three morphometric parameters (test length, height and width) were measured in a total of 1,863 specimens spanning the late Mesozoic and Cenozoic. Our results show a significant decrease in the body size of the genus *Hemiaster* across the Cenomanian/Turonian boundary, associated with an episode of global warming. Furthermore, a significant body size increase is recorded across the Eocene/Oligocene boundary in the genera *Schizaster* and



Eupatagus, which is associated with global cooling. Both of these results are consistent with the hypothesis that present-day warming will cause a reduction in the sizes of spatangoid echinoids, and we can use these results to predict some of the impacts that warming climates may have on the wider marine ecosystem.

A new Cambrian echinoderm from the Kinzers Formation informs on the evolution and development of the skeleton in early echinoderms

Samuel Zamora¹, Imran A. Rahman² and Jeffrey R. Thompson³

¹*IGME, Instituto Geológico y Minero de España, Spain*

²*Oxford University Museum of Natural History, UK*

³*University College London, UK*

Echinoderms possess a calcite skeleton composed of multiple plates with a mesh-like microstructure called stereom. This distinctive microstructure is underpinned in modern echinoderms by a number of specific transcription factors and signalling molecules regulating the expression of numerous biomineralization genes. We report a new Cambrian echinoderm from the Kinzers Formation (Cambrian Series 2, Stage 4) of Pennsylvania, USA, which shows clear differentiation in body plan structure. Energy dispersive X-ray spectroscopy confirms that the axial part of the body is iron-rich, and was likely calcified in life; the extraxial part of the body has abundant carbon, suggesting this was originally organic material. The ambulacra in this new animal consists of five erect feeding appendages with large flooring plates with podial pores and multiple series of cover plates. The theca is preserved in soft tissue with no obvious plating. This unique combination of characters, with calcified axial elements and non-calcified extraxial portions, suggest that a module of genes responsible for skeleton formation in early echinoderms was expressed in two independent spatial contexts. Future work on the evolution and development of the echinoderm skeleton should explore the possibility of context-dependent biomineralization gene batteries controlling skeleton formation in axial and extraxial body regions.

Identifying changes in brachiopod community structures and correlating type sections from the Upper Ordovician in the Eastern Baltics

***Aija Valentīna Zāns**

Vilnius University, Lithuania

The position of the area of modern-day Latvia and Lithuania was located in the central part of the Baltic palaeobasin during the Ordovician and Silurian periods. Due to several sea transgressions and regressions many different marine facies zones are found in this region. The main deposits are limestones, marlstones and mudstones, but dolomites, argillites and clays are also commonly found. Currently, three major issues remain in the eastern Baltic Upper Ordovician formations: 1) incomplete type section correlations; 2) the lack of detailed brachiopod community structures; and 3) a thorough understanding of brachiopod bioevents in Baltica. In a preliminary attempt to solve some of these issues, brachiopods from drill core samples from the Mežciems Formation (Upper Ordovician) in Latvia were studied in detail in a 2014 thesis. Further research into analogous formations and palaeoenvironments, and significant brachiopod genera occurring in the Mežciems Formation, such as the orthids *Dalmanella*, *Howellites*, *Horderleyella*, and *Platystrophia*; strophomenids *Sowerbyella*, *Longvillia*, and *Leptaena*; and the billingsellid *Vellamo*,



have led to a greater understanding of the palaeoenvironmental conditions that lead to changes in brachiopod community structures, which will also assist in further defining the stratigraphic borders of the Upper Ordovician in the Eastern Baltics.

Identifying characteristics of crown group in a ctenophore specimen from the early Cambrian Chengjiang biota

***Yang Zhao, Peiyun Cong, Fan Wei, Yujing Li and Xianguang Hou**

Yunnan University, China

Ctenophores are a rare phylum in modern oceans with no more than 150 extant species, of which the unique bodyplan and evolutionary history have provoked intense debates. Fossil ctenophores, especially those from the Cambrian explosion, are contributing fundamentally to our understanding of the morphology and evolution of this group. By now, at least twelve Cambrian taxa have been identified as ctenophores, all of which, though, have been pinned into the stem groups, while the earliest known crown group of ctenophores is from the early Devonian. Here, we re-investigate a Cambrian specimen from the Chengjiang biota, China, which displays a series of new structures that relate to the crown group of ctenophores. The specimen is laterally compressed and well-preserved in detail, consisting of a dome with statolith inside, and external comb rows that can be detached from the body. In addition, a pair of dark brownish patches can be observed at the central part of the body, which we interpret as possible tentacle sheaths based on their size and topology. These paired tentacle sheaths imply a biradial symmetry, and altogether rule out the previous explanation that it represents the ctenophore *Maotianoascus octonarius* but allude to a phylogenetic position of crown group for this Chengjiang ctenophore.

Chancelloriid scleritomes from the early Cambrian Guanshan biota, eastern Yunnan, China

Jun Zhao^{1,2}, Guobiao Li² and Paul A. Selden^{3,4}

¹*Yunnan University, China*

²*China University of Geosciences, China*

³*University of Kansas, USA*

⁴*Natural History Museum, London, UK*

Chancelloriids are a group of sessile problematic metazoans that are characterized by a sac-like body covered with spiny sclerites. Despite the cosmopolitan distribution of their isolated sclerites in the Cambrian small shelly fossils, scleritomes of chancelloriids are only known in Cambrian Burgess-Shale-Type fossil Lagerstätten. A detailed investigation on abundant specimens of chancelloriids from the Guanshan Lagerstätte of eastern Yunnan, China, confirmed that only two genera, *Allonnia* and *Nidelric*, are present, exactly the same as its stratigraphic precursor, the Chengjiang biota. The Guanshan *Allonnia* (*A. tenuis*) shows that its body can shrink/stretch laterally and top-down, implying that chancelloriids might use a feeding mechanism by contracting their sac-shaped body. *Nidelric*, a chancelloriid-like animal previously only known from the Chengjiang biota by very rare specimens, is quite abundant in the Guanshan biota. It is revealed for the first time that the single-element spine of *Nidelric* is hollow, thus reinforcing its affinity as an unusual chancelloriid.



posters

**The
Palaeontological
Association**

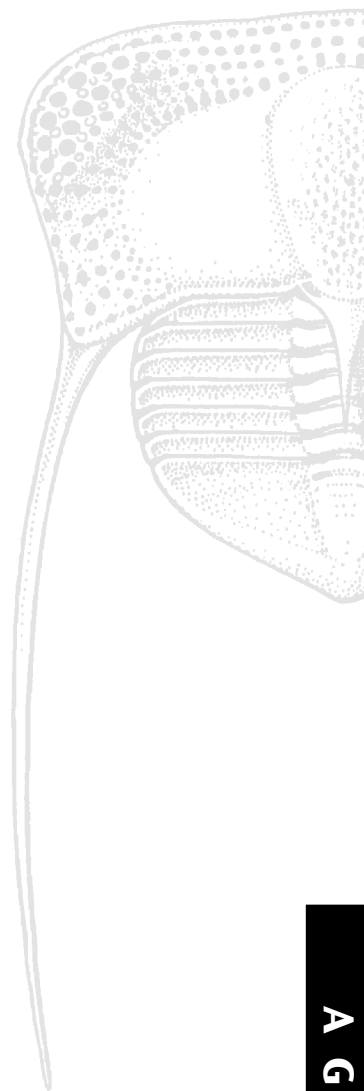
**Annual
General
Meeting**

14.45

Thursday

19th December

Papers





Annual Meeting 2019 and AGM

This will be held at the University of Valencia, Spain, on Thursday 19th December 2019, following the scientific sessions.

AGENDA

1. Apologies for absence
2. Minutes of the 62nd AGM, University of Bristol
3. Trustees Annual Report for 2018
4. Accounts and Balance Sheet for 2018
5. Election of Council and vote of thanks to retiring members
6. Report on Council Awards
7. Annual address

DRAFT AGM MINUTES 2018

Minutes of the Annual General Meeting held on Saturday 15th December 2018 at the University of Bristol, UK.

- 1. Apologies for absence.** None.
- 2. Minutes.** The minutes of the 2017 AGM were agreed a true record by unanimous vote.
- 3. Trustees Annual Report for 2017.** The report was agreed by unanimous vote of the meeting.
- 4. Accounts and Balance Sheet for 2017.** The accounts were agreed by unanimous vote of the meeting. The proposal to reappoint M.R. Corfield of Corfield Accountancy Ltd as Association financial examiner was also agreed by unanimous vote.
- 5. Election of Council and vote of thanks to retiring members.**
 - 5.1** Prof. M.P. Smith extended a vote of thanks to the following members of Council who were retiring from their positions this year: Dr A.B. Smith, Dr L.G. Herringshaw, Prof. R.J. Twitchett; Council thanked Prof. M.P. Smith, who also retired following the AGM.
 - 5.2** The following members were elected to serve on Council: President: Prof. C.H. Wellman, Vice-Presidents: Dr C.J. Buttler and Prof. T.R.A. Vandenbroucke, Treasurer: Dr P. Winrow, Secretary: Dr C.T.S. Little; Editor-in-Chief: vacant; Editor Trustees: Dr B.H. Lomax and Prof. M.A. Purnell, Newsletter Editor: Dr G.T. Lloyd, Book Review Editor: Dr T.J. Challands, Publicity Officer: Dr S.J. Lydon, Education Officer: Dr M.E. McNamara, Outreach Officer: Dr L.M.E. McCobb, Internet Officer: Dr A.R.T. Spencer, Meetings Coordinator: Dr U. Balthasar, Diversity Officer: Dr R.C.M. Warnock, Ordinary Members: Dr D.P.G. Bond, Dr A.M. Dunhill, Prof. A.S. Gale and Ms Z.E. Hughes.
- 5.3** Dr C. Martínez Pérez and colleagues will organize the Annual Meeting in 2019 at the University of Valencia, Spain.

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

- 6.1** The Lapworth Medal was awarded to Prof. D.J. Siveter (Oxford University Museum of Natural History).
- 6.2** The President's Medal was awarded to Prof. E.J. Rayfield (University of Bristol).
- 6.3** The Hodson Award was presented to Dr X. Ma (Natural History Museum, London).
- 6.4** The Mary Anning Award was presented to Mr N. Chase (Isle of Wight, UK).
- 6.5** The Gertrude Elles Award for public engagement was jointly presented to Ms E. Dunne, University of Birmingham, and Mr R. Barnett, University of Durham, for their efforts in the Scholars Programme of the Brilliant Club.
- 6.6** Research Grants were awarded to: Dr K. Agiadi, National and Kapodistrian University of Athens, *Time resolution of fish death assemblages on the Eastern Mediterranean shelf*; Dr P.E. Jardine, University of Münster, *A chemical clue to an abominable mystery? Chemotaxonomy of basal angiosperm pollen and cuticles*; and Dr I.A. Rahman, Oxford University Museum of Natural History, *Studying the soft tissues of exceptionally preserved Carboniferous crinoids with high-resolution X-ray microtomography*.
- 6.7** Under the Small Grants Scheme, the following awards were announced: the Whittington Award to Mr T.J. Raven, NHM, London and University of Brighton, *The evolutionary history of North American nodosaurid ankylosaurian dinosaurs*; the Callomon Award to Mr A. Elgorriaga, Universidad de Buenos Aires, *A new window on Jurassic Patagonian gymnosperm diversity: the exquisitely preserved "Pomelo" taphoflora of Chubut, Argentina*; Stan Wood awards to Ms E. Coombs, University College London, *Investigating cranial morphology in two geographically distinct groups of Oligocene cetaceans*, and Dr P. Cruzado-Caballero, Universidad Nacional de Río Negro, *Patagonian Ornithomimid dinosaurs and the conquest of Western Gondwana*; and Sylvester-Bradley awards to Mr A. Dhungana, University of Cambridge, *Ecology of Silurian deep-water coral communities*, Ms E. Long, Durham University, *Reconstructing the early development of segmented animals in 3D*, Mr N. Mongiardino Koch, Yale University, *Merging genomics and phenomics to understand macroevolution: a case study using echinoid body size*, Dr L. Pérez, Museo de La Plata, *Oligocene/Miocene Bryozoans from southern South America: a taxonomic and biogeographic perspective*, and Mr J. Prowting, University of Portsmouth, *Palaeoclimatic variation in the Adriatic Sea during the Late Pleistocene Heinrich Event 1 (18–14 Kys BP)*.
- 6.8** Undergraduate Research Bursaries were awarded to: Ms F. Butler, University of Birmingham, supervised by Dr T. Dunkley Jones, *The Evolution of Alkenone-producing Coccolithophore Algae*; Mr S. Cross, University of Bristol, supervised by Prof. M.J. Benton, *Reconstructing the limbs and girdles of the Ichthyosaurs of Strawberry Bank, Somerset*; Ms J. Farrant, University of Birmingham, supervised by Dr K.M. Edgar, *Biotic disturbance in the latest Eocene – impact events and climate cooling*; Ms S. Glasgow, Liverpool John Moores University, supervised by Dr P.L. Falkingham, *Regionalization of cervical vertebrae in plesiosaurs*; Mr T. Gray, University of Leicester, supervised by Prof. M.A. Purnell, *The grit problem: environmental signals in tooth microwear and implications for reconstructing diets of fossil mammals*; Ms E. Griffiths, University of Oxford, supervised by Prof. R.B.J. Benson, *Postcranial anatomy of a new plesiosaur from the Oxford Clay*; Mr T. Henton, University of Birmingham, supervised by Dr I.J. Sansom, *The oldest urolith? Investigating a possible*



kidney stone from the Kimmeridgian (Jurassic) of Dorset; Ms E. Hunt, Imperial College, London, supervised by Dr P.D. Mannion, *A new crocodylomorph from the early Late Cretaceous Kem Kem beds of Morocco*; Mr S. Webb, University of Birmingham, supervised by Prof. R.J. Butler, *Macroevolutionary patterns of tetrapod evolution during the Carboniferous–Permian transition: evidence from fossil footprints*; and Mr G. Willment, University of Oxford, supervised by Dr S. Giles, *Endocranial anatomy of a durophagous Permian actinopterygian*.

6.9 Engagement Grants were awarded to Ms E. Panciroli for ‘Scottish fossil workshops in rural schools’, and Mr D. Marshall for the project ‘Palaeocast Gaming Network’.

6.10 The 2018 Best Paper Awards were presented to Prof. R.B.J. Benson and colleagues for their paper entitled ‘Cope’s rule and the adaptive landscape of dinosaur body size evolution’ (*Palaeontology*), and to Drs C. Ji and H. Bucher for ‘Anisian (Middle Triassic) ammonoids from British Columbia (Canada): biochronological and palaeobiogeographical implications’ (*Papers in Palaeontology*).

6.11 The President’s Prize was presented to Ms E. Panciroli (University of Edinburgh and National Museums Scotland).

6.12 The Council Poster Prize was presented to Ms N.M. Murales García (University of Bristol).

7. Annual Address. The Annual Address entitled ‘Ice in a greenhouse world – 60 Ma and 2060’ was given by Prof. Dame Jane Francis (British Antarctic Survey).

Trustees Annual Report 2018

The Trustees present their report with the financial statements of the charity for the year ended 31 December 2018. The Trustees have adopted the provisions of *Accounting and Reporting by Charities: Statement of Recommended Practice* applicable to charities preparing their accounts in accordance with the Financial Reporting Standard applicable in the UK and Republic of Ireland (FRS 102) (effective 1 January 2015).

1. OBJECTIVES AND ACTIVITIES

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

1.2 Risk register. In 2018 Council developed a 31-point risk register for the Association, with defined risk owners. This document will serve as a reference point for future activities of the Association.

1.3. Finances. At a separate awayday in October, Council discussed Association finances, based on a financial review by the Treasurer and the Executive Officer. In order to secure the Association



finances for the future (in addition to the planned 2019 increase to annual subscription fees), Council agreed to the following for 2019 onwards: to ensure that all Annual Meetings are cost-neutral to the Association; to reduce overall expenditure on Research Grants, Undergraduate Research Bursaries and Grants-in-aid; to reduce the Public Engagement Group budget, including a re-balance of expenditure with a reduction in financial support to Fossil Festivals.

1.4 Grants-in-aid for meetings and workshops: The Association provided funds to support the following meetings and workshops: 4th International Meeting of Early-Stage Researchers in Palaeontology (4th IMERP) (Mr F. Blanco, Museum für Naturkunde, Berlin); 13th International Symposium on Fossil Cnidaria and Porifera (Prof. F. Bosellini, Università degli Studi di Modena e Reggio Emilia); Crossing the Palaeontological–Ecological Gap (Dr A.M. Dunhill, University of Leeds); The 10th European Palaeobotany and Palynology Conference (EPPC2018) (Prof. J.C. McElwain, Trinity College Dublin); Uncovering Yorkshire’s Jurassic (Dr L. Herringshaw, University of Hull); Palaeontological excavations at an exceptional site: the diversity of life 125 million years ago (Dr H. Martín-Abad, Universidad Autónoma de Madrid); 1st Palaeontological Virtual Congress (Dr C. Martínez Pérez, Universitat de Valencia); Journées de rencontre autour du patrimoine minier de la Corniche angevine (JRPM 2018) (Dr C. Strullu-Derrien, Natural History Museum, London); 18th International Bryozoology Association Conference (Dr K. Zágoršek, Technická Universita Liberec).

1.5 Public meetings: Two public meetings were held in 2018, and the Association extends its thanks to the organizers and host institutions of these meetings.

62nd Annual Meeting. The Association’s Annual Meeting is its flagship meeting and this year was held on 14–17 December at the University of Bristol. Dr J. Vinther, together with local support from colleagues and PhD students, organized the meeting, which included a symposium on ‘Frontiers and Advances in Dinosaur Palaeobiology’ and comprised a programme of internationally recognized speakers. There were 314 attendees. The Annual Address was entitled ‘Ice in a greenhouse world – 60 Ma and 2060’ and was given by Prof. Dame Jane Francis (British Antarctic Survey). The President’s Prize for best oral presentation by an early-career researcher was awarded to Ms E. Panciroli (University of Edinburgh and National Museums Scotland). The Council Poster Prize for best poster presentation by an early career researcher was presented to Ms N.M. Murales García (University of Bristol).

Progressive Palaeontology. This is an annual, open meeting for research students in palaeontology and allied sciences to present their work to an audience of their peers. The 2018 meeting was organized by Ms E. Wallace and a team of other students, and held at the University of Manchester and Manchester Metropolitan University on 7–9 June. There were 89 attendees.

1.6 Publications: The journals *Palaeontology* and *Papers in Palaeontology* are produced by Wiley. During 2018, the following volumes were published: *Palaeontology* volume 61, comprising six issues; and *Papers in Palaeontology* volume 4, comprising four issues. Council thanks Mr N. Stroud for assistance with the typesetting and production of the *Palaeontology Newsletter*.

1.7 Research Grants: A total of 20 applications for Palaeontological Association Research Grants were received. Three were recommended for funding in 2018, totalling £19,378, and were awarded to: Dr K. Agiadi, National and Kapodistrian University of Athens, ‘Time resolution of fish death assemblages on the Eastern Mediterranean shelf’; Dr P.E. Jardine, University of Münster, ‘A chemical



clue to an abominable mystery? Chemotaxonomy of basal angiosperm pollen and cuticles'; and Dr I.A. Rahman, Oxford University Museum of Natural History, 'Studying the soft tissues of exceptionally preserved Carboniferous crinoids with high-resolution X-ray microtomography'.

1.8 Small Grants Scheme: The scheme received 14 applications. Nine were recommended for funding in 2018, totalling £11,540.09. Small grants were awarded as follows: Mr T.J. Raven (NHM, London and University of Brighton) received the Whittington Award; Mr A. Elgorriaga (Museo Paleontológico Egidio Feruglio) received the Callomon Award; Ms E.J. Coombs (University College London) and Dr P. Cruzado-Caballero (Universidad Nacional de Río Negro) received Stan Wood awards; Mr A. Dhungana (University of Cambridge), Ms E.J. Long (Durham University), Mr N. Mongiardino Koch (Yale University), Dr L. Pérez (Museo de La Plata), and Mr J. Prowting (University of Portsmouth) received Sylvester-Bradley awards.

1.9 Undergraduate Research Bursary Scheme: The scheme attracted 17 applications, of which ten were recommended for funding in 2018, totalling £21,920. The awardees were as follows: Ms F. Butler, University of Birmingham, supervised by Dr T. Dunkley Jones; Mr S. Cross, University of Bristol, supervised by Prof. M.J. Benton; Ms J. Farrant, University of Birmingham, supervised by Dr K.M. Edgar; Ms S. Glasgow, Liverpool John Moores University, supervised by Dr P.L. Falkingham; Mr T. Gray, University of Leicester, supervised by Prof. M.A. Purnell; Ms E. Griffiths, University of Oxford, supervised by Prof. R.B.J. Benson; Mr T. Henton, University of Birmingham, supervised by Dr I.J. Sansom; Ms E. Hunt, Imperial College London, supervised by Dr P.D. Mannion; Mr S. Webb, University of Birmingham, supervised by Prof. R.J. Butler; and Mr G. Willment, University of Oxford, supervised by Dr S. Giles.

1.10 Publicity, outreach and engagement: The Association continues to promote Palaeontology and its allied sciences to the national print media, radio and television. The Association is a major financial supporter of the Lyme Regis Fossil Festival and the Yorkshire Fossil Festival (held in University of Hull in 2018, as part of the Hull Science Festival). At both festivals the Association had displays and activities for the public on the theme of fossilization, organized and staffed by members of Council, the Executive Officer and volunteers. The Public Engagement Group (PEG), consisting of the Outreach Officer, Education Officer, Publicity Officer, Executive Officer, President and Treasurer decided on expenditure of the group budget (£30,000 for 2018), supporting recurring festival activities, Engagement Grants and commissioned projects.

1.11 Engagement Grants: The scheme received a total of six applications in 2018, of which two were recommended for funding, totalling £3,961.88. These were awarded to Ms E. Pancioli for 'Scottish fossil workshops in rural schools' and Mr D. Marshall for the project 'Palaeocast Gaming Network'.

1.12 Diversity study: In 2017 the Association commissioned a diversity study of the Association and field of palaeontology, which was undertaken by Parigen Ltd. in 2018, at a cost of £17,609. The contractors presented their findings to Council in May, and an action plan was drawn up by Council in October. The findings of the study and the action plan were presented at the 2018 AGM by the President. The action points include the following: create a new Council post of Diversity Officer with specific roles in the Diversity Group; develop programmes with disadvantaged schools/communities and investigate a school-level research placement scheme; continue to monitor the proportion of male to female authors in Association publications and to consider actions to improve



this imbalance; enhance the Association mentoring scheme and evaluate outcomes; include additional career talks at Progressive Palaeontology; introduce guidelines relating to dependent children at the Annual Meeting; introduce a Carers Bursary scheme for the Annual Meeting; encourage Annual Meeting organizers to have diverse session chairs, including a balanced female to male ratio; establish a working group to look at the nomination and voting processes for the Association prizes and awards; and continue to monitor diversity and maintain diversity as a live project.

1.13 Diversity Group: In order to deliver the diversity study action points in 1.12, the Association formalized a Diversity Group that will be led by the new Diversity Officer, and comprises the President, Executive Officer, Publications Officer, and a sub-group of other Council members. The Diversity Group will work closely with the Public Engagement Group and will report to Council through the meetings, and the membership via the *Newsletter* and social media.

1.14 Palaeontological Association Exceptional Lecturer scheme: In order to promote palaeontology to the wider academic community and public, and to recognize excellence in research among palaeontologists, in 2018 the Association introduced a new scheme called the Innovations in Palaeontology Lecture Series, to be given by the PalAss Exceptional Lecturer, who is selected in a competitive process. The Exceptional Lecturer will give at least five lectures at five different institutions over a nine-month period. The first PalAss Exceptional Lecturer has now been selected and will give their lectures in 2019.

1.15 Online activities: The online activities of the Association continue to expand with greater emphasis on social media (Facebook, Twitter). The Association continues to be the sole host for the online-only journal *Palaeontologia Electronica*, as well as continuing to host websites for other societies (The Palaeontographical Society, International Organisation of Palaeobotany), palaeontological online resources (EDNA fossil insect database, the Kent Fossil Database, SPIERS Software), palaeontological networking sites (European Coalfield Conservation Opportunities) and online outreach projects (Palaeontology [Online]). The listserv PaleoNet also continues to be hosted. The Association continues to run its internet actives on cloud-based services provided by AWS located on EU-based servers. At the end of 2018 members of the PalAss Facebook group numbered 1,591 and the @ThePalAss Twitter account had 5,000 followers.

1.16 Awards: The Lapworth Medal, awarded to people who have made a significant contribution to the science by means of a substantial body of research, was presented to Prof. Derek J. Siveter (Oxford University Museum of Natural History). The President's Medal, awarded to a palaeontologist within 15 to 25 years of their PhD in recognition of outstanding contributions in their earlier career, coupled with an expectation that they will continue to contribute significantly to the subject in their further work, was presented to Prof. Emily J. Rayfield (University of Bristol). The Hodson Award, for a palaeontologist within ten years of award of their PhD who has made an outstanding contribution to the science through a portfolio of original published research, was awarded to Dr Xiaoya Ma (Natural History Museum, London). The Mary Anning Award, for an outstanding contribution by an amateur palaeontologist, was made to Mr Nick Chase (Isle of Wight, UK). The inaugural Gertrude Elles Award for high-quality, amateur or institutional, public engagement projects that promote palaeontology was awarded to Ms E. Dunne (University of Birmingham) and Dr R. Barnett (University of Durham) for their efforts in the Scholars Programme of the Brilliant Club. The 2018 Best



Paper Awards in *Palaeontology* and *Papers in Palaeontology* were given respectively to Prof. R.B.J. Benson and colleagues for their paper entitled 'Cope's rule and the adaptive landscape of dinosaur body size evolution', 61(1), 13–48; and Dr C. Ji and colleague for their study on 'Anisian (Middle Triassic) ammonoids from British Columbia (Canada): biochronological and palaeobiogeographical implications', 4 (4), 623–642. Council also awards undergraduate prizes to outstanding students in university departments where palaeontology is taught beyond Level 1; a total of 23 were awarded throughout the year.

1.17 Forthcoming plans: The Association will continue to make substantial donations from General and Designated funds to promote the charitable aims of the Association. Resources will be made available to continue a similar programme of grants, meetings, outreach and public engagement activities. As agreed at the 2017 AGM, from 2019 subscription fees will be: Ordinary Membership £40 (up from £30), Retired/Student Membership £20 (up from £15). Action points from the Diversity Study will be implemented during 2019, including a new Carers Bursary scheme for the Annual Meeting, and the establishment of a working group to look at the nomination and voting processes for the Association prizes and awards. A small group has been set up to investigate soliciting additional legacies for the Association. The first 'Innovations in Palaeontology' lecture series will be given by the inaugural PalAss Exceptional Lecturer. The 63rd Annual Meeting will be held in December 2019 at the University of Valencia. The 2019 Progressive Palaeontology conference will be held at the University of Birmingham. The Association's website will continue to evolve in 2019, with all applications and nominations to be via online forms. Volume 62 of *Palaeontology* and volume 5 of *Papers in Palaeontology* will be published. Two additions to the *Field Guides to Fossils* series are in production and with publication expected in 2019. A book entitled *Trilobites, Dinosaurs and Mammoths* written by palaeoartist Mr J. McKay, with substantial input from Association members, will be published in 2019 and is expected to launch at the Lyme Regis Fossil Festival. The Public Engagement Group is in the process of developing initial content for a new Association YouTube channel, to be launched late in 2019. A tender process will be initiated for the filming and editing of the channel.

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

2. ACHIEVEMENTS AND PERFORMANCE

2.1 Meetings support: During 2018, the Association agreed to support a total of nine palaeontological meetings, symposia or workshops worldwide (held in the Czech Republic, France, Ireland, Italy, Spain and the UK). In addition, our Postgraduate Travel Grant scheme supported ten postgraduate students to present their work at national and international conferences: Ms Bethany Allen (University of Leeds), Mr Yul Altolaguirre (Senckenberg Research Institute, Frankfurt), Mr Nicolas Baird (Natural History Museum, London), Mr Adam Bermingham (Northumbria University), Mr Alfio Alessandro Chiarenza (Imperial College London), Ms Paige de Polo (University of Edinburgh), Ms Karen Halsall (University of Liverpool), Ms Roxana Pirnea (University of Bucharest), Mr Omar Rafael Regalado Fernandez (University College London) and Ms Emily Roberts (University of Portsmouth). The Association also awarded £11,600 in travel grants to assist 28 student members presenting at the 5th International Palaeontological Congress in Paris in July 2018. The



Association's support enabled the worldwide dissemination of research to the benefit of the global palaeontological community.

2.2 Publications: During 2018, 276 papers were submitted to either *Palaeontology* or *Papers in Palaeontology*. Of these, 147 (53 %) were considered to be within scope by the Editorial Board and 90 (32 %) were subsequently accepted following peer review; a further 31 papers are still awaiting submission of a revised manuscript before a final decision is made. There was a further improvement in the Impact Factor of *Palaeontology*, which increased from 3.132 to 3.73. The Impact Factor of *Papers in Palaeontology* is now 2.156. The number of downloads of articles via Wiley Online Library was 8.7 % higher in 2018 relative to 2017 for *Palaeontology* and 122 % higher for *Papers in Palaeontology*. The Association continues to support data archiving by sponsoring Dryad data records; in the 2018 volumes 52 papers had associated data files, representing 58 % of all papers published (a similar proportion to 2017).

2.3 Support for research: In 2018 the Association agreed to fund the research activities of 19 early-career researchers based in three countries (Argentina, the UK and USA). Apart from directly benefitting the career development of the individuals concerned, the Association's funds continue to enable more palaeontological research to be undertaken worldwide than would otherwise be the case. Overall, the number grants funded in 2018 increased slightly from 2017 (from 19 to 22). Compared to 2017, applications for Research Grants increased substantially, from 15 to 20, and thus the success rate decreased again from 20 % to 15 %. The applications to the Small Grants Scheme decreased substantially (from 34 to 14), and the success rate consequently increased from 24 % to 64 %. Applications to the Undergraduate Research Bursary Scheme increased in 2018 compared to 2017 (from ten to 17) and the success rate decreased to 59 %.

2.5 Mentoring scheme for early career palaeontologists: In 2017 the Association devised a mentoring scheme for early career palaeontologists, to have a particular focus on palaeontologists at post-doctoral level in the first instance. After receiving offers from palaeontologists willing to act as mentors the scheme was publicized in the *Newsletter* and on social media in 2018. Nine postdoctoral palaeontologists applied to take part in the scheme and all have been assigned mentors. Guidelines have been developed to aid the relationships between mentors and mentees and we will consider methods to assess the scheme in 2019.

2.6 Outreach, education and public engagement: During 2018, the Association supported two major fossil festivals in the UK, in Lyme Regis and Hull, which attracted respectively an estimated 8,000 and 3,000 members of the general public of all ages. Workshops were delivered to around 150 primary school children by PalAss volunteers, as part of the Lyme Regis Fossil Festival schools' day, which involved scientists going out into the community. During 2018, we awarded two Engagement grants (see 1.9). Continued use of social media, in particular the Association's Twitter and Facebook accounts, has enabled the rapid and regular dissemination of research news, including of new publications, meetings and other information, to a growing audience (see section 1.15).

3. FINANCIAL REVIEW

3.1 Reserves: As of 31st December 2018, The Association holds reserves of £729,511 in General Funds, which enable the Association to generate additional revenue through investments, and thus to keep subscriptions to individuals at a low level, whilst still permitting a full programme of



meetings to be held, publications to be produced, and the award of research grants and Grants-in-aid. They also act as a buffer to enable the normal programme to be followed in years in which expenditure exceeds income, and allow new initiatives to be pursued. The Association holds £132,172 in Designated Funds, which contribute interest towards the funding of the Sylvester-Bradley, Hodson, Callomon, Whittington and Stan Wood awards and towards the Jones-Fenleigh fund. Total funds carried forward to 2019 totalled £861,043.

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

3.3 Summary of expenditure: Total charitable expenditure, through grants to support research, scientific meetings and workshops in 2018 was £407,105. Governance costs were £44,557. Total resources expended were £473,652. The Association continues its membership of the International Palaeontological Association and remains a Tier 1 sponsor of *Palaeontologia Electronica*, and the *Treatise on Invertebrate Paleontology*.

4. STRUCTURE, GOVERNANCE AND MANAGEMENT

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

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

4.3 Membership: Membership on 31st December 2018 totalled 1,189 (1,173 at end 2017). Of these, 602 were Ordinary Members, 181 Retired Members, 20 Honorary Members, 358 Student Members and 28 Institutional Members. There were 45 institutional subscribers to *Papers in Palaeontology*. Wiley also separately manage further Institutional subscribers and arrange online access to publications for those Institutional Members on behalf of the Association.

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



A number of external websites and their associated databases are hosted on the Association's server and an Internet Hosting Service Agreement was drawn up in 2016 to minimise risk and signed by most parties during 2017. The final outstanding agreements were signed in early 2018.

5. REFERENCE AND ADMINISTRATION

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

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

5.3 Trustees: The following members were elected at the AGM on 18th December 2017 to serve as Trustees in 2018:

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

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

Approved by order of the Board of Trustees on 28th June 2019.



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

I report to the trustees on my examination of the accounts of the above charity for the year ended 31st December 2018 set out on pages 9 to 14.

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

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

The charity's gross income exceeded £250,000 and I am qualified to undertake the examination by being a qualified member of ACA and ACMA.

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

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

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

Ms M. R. Corfield ACA ACMA
Corfield Accountancy Limited
Chartered Accountants
Myrick House
Hendomen
Montgomery
Powys SY15 6EZ
Date: 29th June 2019



THE PALAEOLOGICAL ASSOCIATION

Statement of Financial Activities
for the Year Ended 31 December 2018

	Notes	Unrestricted funds £	Designated funds £	31.12.18 Total funds £	31.12.17 Total funds £
INCOME AND ENDOWMENTS FROM					
Donations and legacies		59,896	2,655	62,551	56,328
Charitable activities					
Public Meetings		48,536	—	48,536	37,314
Publications		318,458	—	318,458	322,556
Investment income	2	<u>12,550</u>	<u>1,975</u>	<u>14,525</u>	<u>13,978</u>
Total		439,440	4,630	444,070	430,176
EXPENDITURE ON					
Raising funds	3	39,599	—	39,599	32,164
Charitable activities					
Public Meetings		72,542	—	72,542	168,056
Grants & Awards		52,390	13,476	65,866	60,126
Administration		55,756	—	55,756	44,603
Publications		195,332	—	195,332	120,575
Governance Costs		44,557	—	44,557	23,093
Total		<u>460,176</u>	<u>13,476</u>	<u>473,652</u>	<u>448,617</u>
Net gains/(losses) on investments		(27,017)	—	(27,017)	60,340
NET INCOME/(EXPENDITURE)		(47,753)	(8,846)	(56,599)	41,899
RECONCILIATION OF FUNDS					
Total funds brought forward		<u>776,624</u>	<u>141,018</u>	<u>917,642</u>	<u>875,743</u>
TOTAL FUNDS CARRIED FORWARD		<u>728,871</u>	<u>132,172</u>	<u>861,043</u>	<u>917,642</u>

CONTINUING OPERATIONS

All income and expenditure has arisen from continuing activities.

The notes form part of these financial statements.



THE PALAEOLOGICAL ASSOCIATION

Balance Sheet

At 31 December 2018

	Notes	Unrestricted funds £	Designated funds £	31.12.18 Total funds £	31.12.17 Total funds £
FIXED ASSETS					
Investments	7	584,477	40,992	625,469	661,561
CURRENT ASSETS					
Debtors	8	189,454	—	189,454	185,839
Cash at bank		<u>125</u>	<u>91,180</u>	<u>91,305</u>	<u>105,140</u>
		189,579	91,180	280,759	290,979
CREDITORS					
Amounts falling due within one year	9	<u>(45,185)</u>	<u>—</u>	<u>(45,185)</u>	<u>(34,898)</u>
NET CURRENT ASSETS		144,394	91,180	235,574	256,081
TOTAL ASSETS LESS CURRENT LIABILITIES		<u>728,871</u>	<u>132,172</u>	<u>861,043</u>	<u>917,642</u>
NET ASSETS		<u>728,871</u>	<u>132,172</u>	<u>861,043</u>	<u>917,642</u>
FUNDS					
Unrestricted funds	10			<u>861,043</u>	<u>917,642</u>
TOTAL FUNDS				<u>861,043</u>	<u>917,642</u>

The notes form part of these financial statements.

The financial statements were approved by the Board of Trustees on 28th June 2019.



THE PALAEOLOGICAL ASSOCIATION

**Notes to the Financial Statements
for the Year Ended 31 December 2018****1. ACCOUNTING POLICIES****Basis of preparing the financial statements**

The financial statements of the charitable company, which is a public benefit entity under FRS 102, have been prepared in accordance with the Charities SORP (FRS 102) 'Accounting and Reporting by Charities: Statement of Recommended Practice applicable to charities preparing their accounts in accordance with the Financial Reporting Standard applicable in the UK and Republic of Ireland (FRS 102) (effective 1 January 2015)', Financial Reporting Standard 102 'The Financial Reporting Standard applicable in the UK and Republic of Ireland' and the Companies Act 2006. The financial statements have been prepared under the historical cost convention with the exception of investments which are included at market value, as modified by the revaluation of certain assets.

Income

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

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

Expenditure

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

Allocation and apportionment of costs

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

Taxation

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

Fund accounting

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



THE PALAEOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2018

1. ACCOUNTING POLICIES – continued

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

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

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

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

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

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

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

2. INVESTMENT INCOME

	31.12.18 £	31.12.17 £
Deposit account interest	99	34
Investment Income	<u>14,426</u>	<u>13,944</u>
	<u>14,525</u>	<u>13,978</u>

3. RAISING FUNDS

	31.12.18 £	31.12.17 £
Investment Management Costs:		
Stockbroker Fees	<u>4,118</u>	<u>3,780</u>
	<u>4,118</u>	<u>3,780</u>

4. SUPPORT COSTS

	31.12.18 £
Governance Costs:	<u>26,948</u>



THE PALAEOLOGICAL ASSOCIATION

**Notes to the Financial Statements – *continued*
for the Year Ended 31 December 2018****5. TRUSTEES' REMUNERATION AND BENEFITS**

There were no Trustees' remuneration or other benefits for the year ended 31 December 2018 nor for the year ended 31 December 2017.

Trustees' expenses

The total travelling expenses reimbursed to 19 Members of Council (2017:18) was £16,810 (2017: £14,983).

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

	£ 2018	£ 2017
Salaries	81,750	80,032
Social Security Costs	5,975	5,094
Pension Costs	<u>8,175</u>	<u>7,494</u>
Total	<u>95,900</u>	<u>92,620</u>

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

	2018	2017
Publications	1	1
Administration	<u>1</u>	<u>1</u>
	<u>2</u>	<u>2</u>

No employees received emoluments in excess of £60,000.

7. FIXED ASSET INVESTMENTS

Investments are initially recognized at their transaction value and subsequently measured at their fair value as at the balance sheet date. The statement of financial activities includes the net gains and losses arising on revaluation and disposals throughout the year.

8. DEBTORS: AMOUNTS FALLING DUE WITHIN ONE YEAR

	£ 2018	£ 2017
Sundry Debtors	<u>189,454</u>	<u>185,839</u>



THE PALAEOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2018

9. CREDITORS: AMOUNTS FALLING DUE WITHIN ONE YEAR

	31.12.18 £	31.12.17 £
Trade creditors	27,945	18,714
Subscriptions in advance	<u>17,240</u>	<u>16,184</u>
	<u>45,185</u>	<u>34,898</u>

10. MOVEMENT IN FUNDS

	At 1.1.18 £	Net movement in funds £	At 31.12.18 £
Unrestricted funds			
General fund	776,624	(47,753)	728,871
Sylvester-Bradley	26,394	(5,321)	21,073
Jones-Fenleigh	27,713	(210)	27,503
Hodson	1,719	(1,425)	294
Callomon	4,519	(1,151)	3,368
Whittington	13,974	(1,000)	12,974
Stan Wood	<u>66,699</u>	<u>261</u>	<u>66,960</u>
TOTAL FUNDS	<u>917,642</u>	<u>(56,599)</u>	<u>861,043</u>

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

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
Unrestricted funds				
General fund	439,440	(460,176)	(27,017)	(47,753)
Sylvester-Bradley	652	(5,973)	—	(5,321)
Jones-Fenleigh	1,370	(1,580)	—	(210)
Hodson	1	(1,426)	—	(1,425)
Callomon	349	(1,500)	—	(1,151)
Whittington	500	(1,500)	—	(1,000)
Stan Wood	<u>1,758</u>	<u>(1,497)</u>	<u>—</u>	<u>261</u>
TOTAL FUNDS	<u>444,070</u>	<u>(473,652)</u>	<u>(27,017)</u>	<u>(56,599)</u>



THE PALAEOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2018

10. MOVEMENT IN FUNDS — *continued*...**Comparatives for movement in funds:**

	At 1.1.17 £	Net movement in funds £	At 31.12.17 £
Unrestricted Funds			
General fund	728,484	48,140	776,624
Sylvester Bradley	29,665	(3,271)	26,394
Jones-Fenleigh	26,313	1,400	27,713
Hodson	3,301	(1,582)	1,719
Callomon	5,476	(957)	4,519
Whittington	14,883	(909)	13,974
Stan Wood	<u>67,621</u>	<u>(922)</u>	<u>66,699</u>
TOTAL FUNDS	<u>875,743</u>	<u>41,899</u>	<u>917,642</u>

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

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
Unrestricted funds				
General fund	422,731	(434,931)	60,340	48,140
Sylvester Bradley	1,465	(4,736)	—	(3,271)
Jones-Fenleigh	2,836	(1,436)	—	1,400
Hodson	53	(1,635)	—	(1,582)
Callomon	543	(1,500)	—	(957)
Whittington	585	(1,494)	—	(909)
Stan Wood	<u>1,963</u>	<u>(2,885)</u>	<u>—</u>	<u>(922)</u>
TOTAL FUNDS	<u>430,176</u>	<u>(448,617)</u>	<u>60,340</u>	<u>41,899</u>



THE PALAEOLOGICAL ASSOCIATION

Notes to the Financial Statements – *continued* for the Year Ended 31 December 2018

10. MOVEMENT IN FUNDS — *continued*...

A current year 12 months and prior year 12 months combined position is as follows:

	At 1.1.17 £	Net movement in funds £	At 31.12.18 £
Unrestricted funds			
General fund	728,484	387	728,871
Sylvester Bradley	29,665	(8,592)	21,073
Jones-Fenleigh	26,313	1,190	27,503
Hodson	3,301	(3,007)	294
Callomon	5,476	(2,108)	3,368
Whittington	14,883	(1,909)	12,974
Stan Wood	<u>67,621</u>	<u>(661)</u>	<u>66,960</u>
TOTAL FUNDS	<u>875,743</u>	<u>(14,700)</u>	<u>861,043</u>

A current year 12 months and prior year 12 months combined net movement in funds included in the above are as follows:

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
Unrestricted funds				
General fund	862,171	(895,107)	33,323	387
Sylvester Bradley	2,117	(10,709)	—	(8,592)
Jones-Fenleigh	4,206	(3,016)	—	1,190
Hodson	54	(3,061)	—	(3,007)
Callomon	892	(3,000)	—	(2,108)
Whittington	1,085	(2,994)	—	(1,909)
Stan Wood	<u>3,721</u>	<u>(4,382)</u>	<u>—</u>	<u>(661)</u>
TOTAL FUNDS	<u>874,246</u>	<u>(922,269)</u>	<u>33,323</u>	<u>(14,700)</u>



THE PALAEOLOGICAL ASSOCIATION

**Notes to the Financial Statements – *continued*
for the Year Ended 31 December 2018****11. RELATED PARTY DISCLOSURES**

There were no related party transactions for the year ended 31 December 2018.

12. INVESTMENT GAINS AND LOSSES

All gains and losses are taken to the Statement of Financial Activities as they arise. Realised gains and losses on investments are calculated as the difference between sales proceeds and their opening carrying value or their purchase value if acquired subsequent to the first day of the financial year.

Unrealised gains and losses are calculated as the difference between the fair value at the year end and their carrying value. Realised and unrealised investment gains and losses are combined in the Statement of Financial Activities.

Investment Gains/Losses	31st December 2018	31st December 2017
	£	£
Realised Gain/(Loss)	(498)	4,605
Unrealised Gain/(Loss)	<u>(26,519)</u>	<u>55,735</u>
Total per Statement of Financial Activities	<u>(27,017)</u>	<u>60,340</u>

13. INVESTMENT PORTFOLIO 2018

See pages 22–23.



Detailed Statement of Financial Activities for the Year Ended 31 December 2018

	31.12.18 Unrestricted funds £	31.12.17 Total funds £
INCOME AND ENDOWMENTS		
Donations and legacies		
Donations	7,461	5,732
Subscriptions	55,090	50,596
	62,551	56,328
Investment income		
Deposit account interest	99	34
Investment Income	<u>14,426</u>	<u>13,944</u>
	14,525	13,978
Charitable activities		
Scientific Journals	314,201	318,416
Special Papers	828	698
Newsletter	243	87
Field Guides	2,944	2,872
Distribution	242	483
Scientific Meetings	<u>48,536</u>	<u>37,314</u>
	<u>366,994</u>	<u>359,870</u>
Total incoming resources	444,070	430,176
EXPENDITURE		
Raising donations and legacies		
Administration	35,481	28,384
Investment management costs		
Stockbroker Fees	4,118	3,780
Charitable activities		
Scientific Journals	56,630	70,627
Newsletters	18,265	19,479
Marketing	632	1,193
Publication Costs	81,825	85,222
Editorial Costs	37,980	34,160
Public Meetings & Costs	72,542	77,950
Grants & Awards	53,772	41,393
Research Grants	12,094	18,733
Administration	55,756	44,603
Consultancy	<u>17,609</u>	<u>—</u>
	407,105	393,360
Support costs		
Governance costs		
Trustees' expenses	16,810	14,983
Accountancy and legal fees	595	595
Administration	<u>9,543</u>	<u>7,515</u>
	<u>26,948</u>	<u>23,093</u>
Total resources expended	<u>473,652</u>	<u>448,617</u>
Net expenditure before gains and losses	(29,582)	(18,441)
Realised recognised gains and losses		
Realised gains/(losses) on fixed asset investments	<u>(27,017)</u>	<u>60,340</u>
Net (expenditure)/income	<u>(56,599)</u>	<u>41,899</u>

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



Palaeontological Association year ended 31st December 2018.

Nominal	Holding	Cost (bought pre 2018) £	Value end 2017 £
£10,000	UK 4.5% Gilt 07/03/19 GBP 0.01	10,046.50	10,622.00
£10,000	UK 4.5% Gilt 07/03/19 GBP 0.01	10,046.50	10,622.00
£18,000	UK 4.75% Stock 07/03/20 GBP 100	18,145.87	19,955.00
49,685.81	COIF Charities Fixed Interest Fund	65,807.52	68,839.69
1,425	BP Ord 25c shares	5,047.35	7,448.00
600	Royal Dutch Shell B shares	4,422.42	15,051.00
600	BHP Billiton \$0.5 shares	4,341.48	9,135.00
180	CRH ord EUR 0.32	4,426.82	4,783.00
1,400	Smith(DS) ord GBP 0.10	4,569.69	5,693.00
500	Halma ord GBP 0.10	5,232.04	6,300.00
437	IMI Ord 25p shares	4,267.00	5,825.00
420	Experian Ord 10C	3,444.95	6,871.00
300	Diageo Ord GBP 0.28	5,826.00	8,175.00
200	Persimmon Ord 10p	2,258.00	5,476.00
70	Reckitt Benckiser Group ord GBP 0.10	5,325.75	4,843.00
300	Unilever PLC Ord GBP 0.031111	4,326.21	12,377.00
170	Astrazeneca Ord 25c	8,145.00	8,706.00
450	Glaxo Smithkline Ordinary 25p shares	7,083.98	5,951.00
300	Relx Olc GBP 0.1444	4,438.20	5,217.00
175	Carnival Plc Ord USD 1.66	3,996.49	8,561.00
1,000	BT Group Ordinary 5p shares	3,446.05	2,717.00
2,277	Vodafone Group Ord USD 0.11428571	3,434.00	5,351.00
641	National Grid Ord GBP 0.12431289	3,648.26	5,609.00
2,250	Barclays 25p Ord shares	4,867.00	4,570.00
1,465	HSBC Holdings Ordinary 0.5 US Dollar shares	4,534.00	11,235.00
982	Great Portland Estates Ord GBP0.15263157894	8,503.00	7,849.00
6,000	Mercantile Investment Tst Plc(The) ord GBP0.025	10,171.60	13,074.00
425	Findlay Park Partners US Smaller Companies	6,158.47	33,975.00
2,825	Ishares S&P 500 GBP	20,319.63	56,094.00
4250	Fidelity EUR Value Ordinary 25P shares	4,059.07	9,635.00
6,600	Fund Partners Ltd Crux European Spl Situation	7,140.00	15,358.00
30	Roche Hldgs Ag Genusscheine Nvp	3,335.33	5,620.00
9,000	Baillie Gifford & Co Japanese Income Growth W4 Dis	11,977.02	12,042.00
1,007	Eastspring Investments SICAV Japan Dynamic FGDY GBP	7,837.74	10,265.00
26	Veritas Funds Plc Veritas Asian D GBP Inc	8,182.27	16,977.00
900	JPMorgan Am UK Ltd Emerging Markets I Instl	5,043.10	8,240.00
650	RIT Capital Partners Ordinary £1 shares	4,903.90	12,753.00
800	BH Global Ltd ord GBP	10,226.25	10,912.00
4,400	Invesco Fund Managers Targeted Y Acc	9,770.33	9,914.00
37	Marshall Wace UCITS Funds Plc MW Tops UCITS G GBP	4,849.70	5,141.00
4,443	Aberdeen Investment Property Trust B	4,681.00	5,296.00
9,000	Charities Property Fund Income	11,043.28	11,393.00
1,021.54	COIF Charities Investment Fund Acc Units	59,678.69	157,089.46
	Total	399,007.45	661,560.15



Schedule of Investments (Note 13 to the Accounts).

Proceeds (sold in 2018) £	Cost (bought in 2018) £	Gain realised during 2018 £	Value end 2018 £	Gain unrealised during 2018 £
			10,210.00	-412.00
10,124.13		-497.87	19,112.00	-843.00
			66,246.09	-2,593.60
			7,067.00	-381.00
			14,040.00	-1,011.00
			9,910.00	775.00
			3,728.00	-1,055.00
	1,050.00		4,190.00	-1,503.00
			6,820.00	520.00
			4,125.00	-1,700.00
			8,001.00	1,130.00
			8,385.00	210.00
			3,860.00	-1,616.00
			4,209.00	-634.00
			12,326.00	-51.00
			9,984.00	1,278.00
			6,710.00	759.00
			4,850.00	-367.00
			6,585.00	-1,976.00
			2,381.00	-336.00
			3,482.00	-1,869.00
			4,899.00	-710.00
			3,387.00	-1,183.00
			9,477.00	-1,758.00
			6,472.00	-1,377.00
			10,530.00	-2,544.00
			35,864.00	1,889.00
			55,218.00	-876.00
			8,798.00	-837.00
			12,699.00	-2,659.00
			5,829.00	209.00
			11,052.00	-990.00
			8,854.00	-1,411.00
			14,924.00	-2,053.00
			7,313.00	-927.00
			12,415.00	-338.00
			11,860.00	948.00
			9,538.00	-376.00
			4,990.00	-151.00
			5,386.00	90.00
			11,711.00	318.00
			158,032.03	942.57
10,124.13	1,050.00	-497.87	625,469.12	-25,469.03



Nominations for Council

At the AGM in December 2019, the following vacancies will occur on Council:

- President-elect
- Vice President
- Chair of the Editorial Board
- Editor Trustee
- Outreach Officer
- Internet Officer
- Ordinary Members (4 vacancies)

Nominations are as follows:

- President-elect: Prof. P.J. Orr*
- Vice President: Dr F.L. Gill*
- Chair of the Editorial Board: Dr B.H. Lomax*
- Editor Trustee: Prof. N.J. Butterfield*
- Outreach Officer:
 - Ms Z.E. Hughes*
 - Ms E. Wallace
- Internet Officer: Dr R. Garwood*
- Ordinary Members (4 vacancies):
 - Dr T. Clements
 - Dr S. Giles*
 - Dr T.H.P. Harvey*
 - Dr E.A. Hide

* denotes Council nominations

No other nominations were received by the deadline.



Notes...



Notes...