

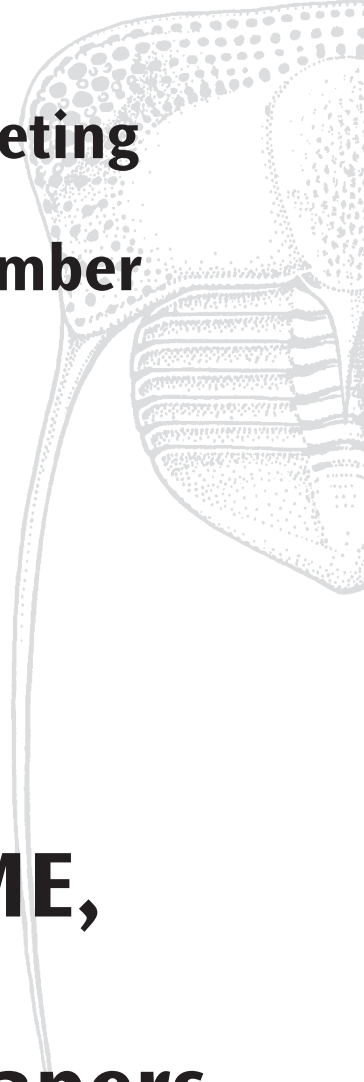
**The  
Palaeontological  
Association**

**60th Annual Meeting**

**14th–17th December  
2016**

***Université Claude  
Bernard Lyon 1  
Lyon, France***

**PROGRAMME,  
ABSTRACTS  
and AGM papers**



## 1. Laënnec Building

*(All talks & posters, ice breaker)*

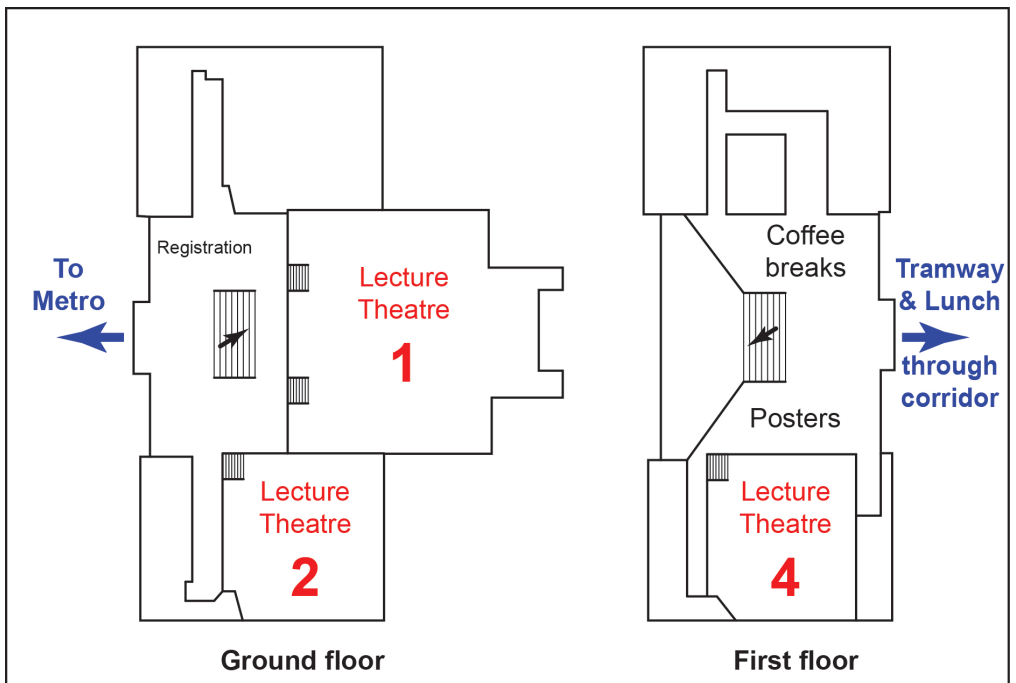
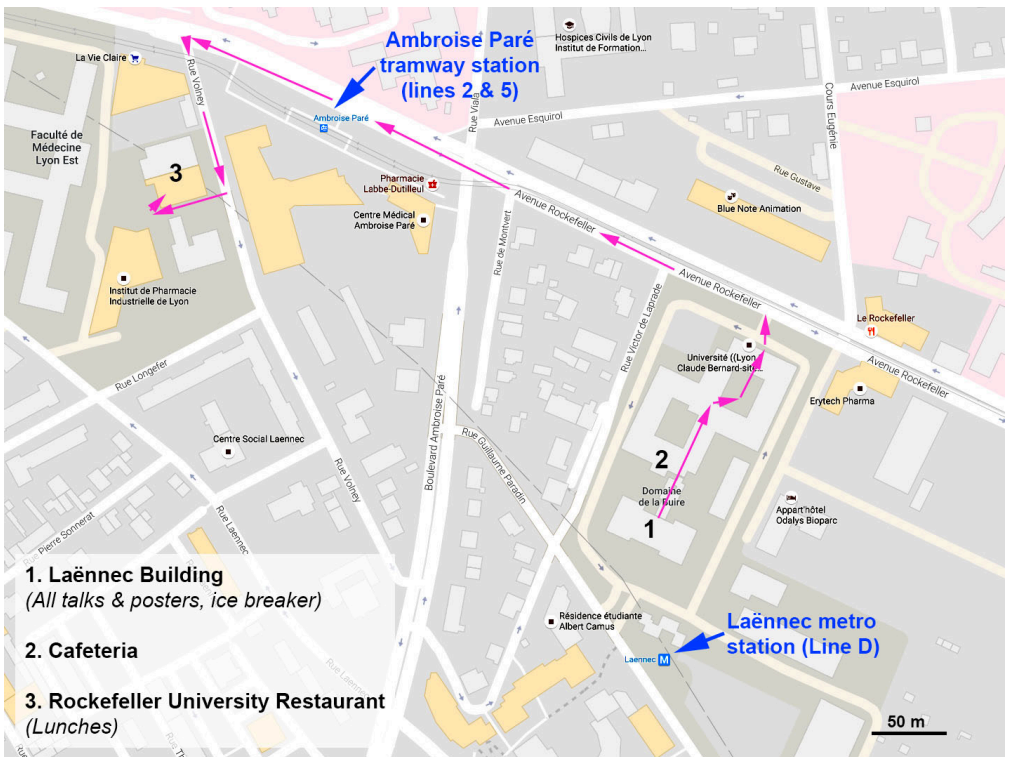
## 2. Gare Part Dieu (train station)

(Terminus airport shuttle)

### 3. Musée des Confluences

#### 4. Bellona Restaurant (boat) (Annual dinner)







# The Palaeontological Association

## 60th Annual Meeting

### 14th–17th December 2016

#### Université Claude Bernard Lyon 1

#### Lyon, France

The programme and abstracts for the 60th Annual Meeting of the Palaeontological Association are provided after the following information and summary of the meeting.

#### Venue

The Conference takes place at the Laënnec Campus, Domaine de la Buire, Université Claude Bernard Lyon 1 (Metro line D, station 'Laënnec'; tram T2 or T5, stop 'Ambroise Paré') in the eastern part of Lyon.

#### Oral Presentations

All speakers (apart from the symposium speakers) have been allocated 15 minutes. You should therefore present for only 12 minutes to allow time for questions and switching between speakers. We have a number of parallel sessions in adjacent theatres so timing is especially important. All of the lecture theatres have an A/V projector linked to a large screen. All presentations should be submitted on a memory stick and checked the day before they are scheduled. This is particularly relevant for Mac-based presentations as UCBL is PC-based.

#### Poster presentations

Poster boards will accommodate an A0-sized poster presented in **portrait** format only. Materials to affix your poster to the boards are available at the meeting.

#### Travel grants to student members

Students who have been awarded a PalAss travel grant should see the Executive Officer, Dr Jo Hellawell (e-mail <[executive@palass.org](mailto:executive@palass.org)>) to receive their reimbursement.

#### Lyon

Lyon (<[www.onlylyon.com/en/visit-lyon.html](http://www.onlylyon.com/en/visit-lyon.html)>), capital of Gaul, is an ancient Roman city and a UNESCO World Heritage Site. It is also a capital of gastronomy with, among many others, Paul Bocuse Michelin-starred restaurants. It is situated near famous vineyards (*e.g.* Beaujolais, Côtes du Rhône). The world-renowned Fête des Lumières (festival of lights) will take place a few days prior to the Meeting (8–11 December).





## *Schedule*

### **Wednesday 14th December: Registration, symposium and reception**

Registration will open at 12.00 in the entrance hall of the **Laënnec Building**.

The Annual Meeting will begin with a symposium in the afternoon (at 13.15) in Lecture Theatre 1 of the **Laënnec Building**. The theme of the symposium is “Assessing palaeoenvironments and palaeobiology through geochemistry”.

Following the symposium there will be an icebreaker reception at 18.00 in the main hall of the **Laënnec Building**.

### **Thursday 15th December: Conference, AGM, Annual Address and Dinner**

Registration will be open from 7.45 to 17.30 in the entrance hall of the **Laënnec Building**.

The conference will start at 8.45 in the **Laënnec Building** with a full day of talks and posters, followed by the Association AGM (at 16.15) and the Annual Address (at 16.45) given by Prof. Manolo Gouy (Université Claude Bernard Lyon 1). The morning sessions will be in Lecture Theatre 1. The parallel afternoon sessions will be in Lecture Theatre 2 and the nearby Lecture Theatre 4, both in the **Laënnec Building**. Posters will be on display throughout the meeting in the main hall of the **Laënnec Building**, where tea breaks will be held.

In the evening there will be a nocturnal visit to the **Musée des Confluences** (a new science centre and anthropology museum) at 18.30, followed by the Annual Dinner at 20.15 on the banks of the river Rhône (**Bellona Restaurant**, located on a boat). People wearing an orange University T-shirt will be there to help you during the transfer.

### **Friday 16th December: Conference**

The registration desk will remain open from 7.45 until 12.00.

The second day of the Conference will begin with a poster session from 8.15–9.15 in the main hall of the **Laënnec Building**, where tea, coffee and cakes will be served. Oral presentations will start at 9.15, with parallel sessions in Lecture Theatre 2 and the nearby Lecture Theatre 4 in the **Laënnec Building**. The final session of the day will be held in the main lecture theatre of the **Laënnec Building** and will be followed by a wine and local products tasting session in the main hall of the building.

### **Saturday 17th December: Field-trip**

Price €30 including transport and lunch in a local restaurant.

The field-trip starts at 7.00 at the front of the **Laënnec Building**, returning to Lyon by 19.30. The number of participants is limited to 45.

We will visit the **Natural History Museum in Autun** as well as the type localities for the **Autunian** in the area, which have yielded, among many other fossils, the temnospondyl *Onchiodon (Actinodon) frossardi*. Access to the collections of the Museum, which hosts the fossils from the Montceau-les-Mines Lagerstätte, can be arranged for those who are interested and who will not take part in the field excursion.



# Schedule of events and timetable of presentations

## Wednesday 14th December

*Taylor and Francis workshop: “Publishing in Academic Journals: tips to help you succeed”*

Lecture Theatre 1, Laënnec Building

11.00 – 12.00 Andrew Kelly (Managing Editor, Earth & Environmental Sciences, Taylor & Francis Group)

*Thematic Symposium: “Assessing palaeoenvironments and palaeobiology through geochemistry”*

Lecture Theatre 1, Laënnec Building

Underlined author denotes designated speaker.

13.15 – 13.50 **Deep-sea barnacle shells: geochemical signal and microstructure**  
Ana-Voica Bojar and Hans-Peter Bojar

13.50 – 14.25 **Reconstructing Ordovician (Floian) conodont ecology and Laurentian seawater temperatures using oxygen isotopes**  
James R. Wheeley, Phillip E. Jardine, Robert J. Raine, Ian Boomer and M. Paul Smith

14.25 – 15.00 **Isotope perspectives in vertebrate palaeobiology**  
Jeremy E. Martin, Théo Tacail and Vincent Balter

15.00 – 15.35 **Non-traditional isotopic approaches to study the physiology of biomineralizing organisms**  
Robert A. Eagle

15.35 – 16.05 **Tea/coffee break**

16.05 – 16.40 **Isotopic aspects of dinosaur reproduction**  
Romain Amiot, Christophe Lécuyer, Xiaolin Wang, Xing Xu, Jinyou Mo, Zhonghe Zhou, François Fourel, Shuo Wang and Jean-Michel Mazin

16.40– 17.15 **The foraging ecology of pterosaurs – implications from stable isotope analysis**  
Thomas Tütken and David W. E. Hone

17.15 – 17.50 **Carnivoran resource and habitat use in the context of a Late Miocene faunal turnover episode**  
Laura Domingo, M. Soledad Domingo, Paul L. Koch, Jorge Morales and M. Teresa Alberdi

## Reception

Laënnec Building, main hall

18.00 – 21.00 **Icebreaker reception**



## Thursday 15th December

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

Underlined author denotes designated speaker.

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

07.30 – 08.45 Poster set-up.

#### **Session 1 (Lecture Theatre 1, Laënnec Building)**

08.45 – 09.00 **Opening of the Annual Meeting** by Marie-France Joubert, Vice-Président of formal and natural sciences at UCBL and Emanuela Mattioli, Director of the Geology Department.

09.00 – 09.15 **How good are your palaeodiversity measurements?**

Abel Barral, Bernard Gomez, Juan M. Zorrilla, José M. Serrano, Johan Yans, Véronique Daviero-Gomez and Christophe Lécuyer

09.15 – 09.30 **A fossilized birth-death model for the reliable estimation of speciation and extinction rates**

Rachel C. M. Warnock, Tracy A. Heath and Tanja Stadler

09.30 – 09.45 **Mass extinctions: towards an understanding of how, why and when ecosystems collapse**

David P. G. Bond

09.45 – 10.00 **Why we are looking at the wrong phase of life – palaeontology beyond the adult paradigm**

Joachim T. Haug

10.00 – 10.15 **Feeding in chelicerate arthropods – diverse and far from ‘primitive’**

Carolin Haug

10.15 – 10.30 **The importance of fossils in dating the Tree of Life: from exceptional preservation to complete absence**

Joanna M. Wolfe

#### **Laënnec Building, main hall**

10.30 – 11.00 **Tea/coffee break and posters**

#### **Session 2a (Lecture Theatre 4, Laënnec Building, in parallel with session 2b)**

11.00 – 11.15 **The Weeks Formation fauna (Utah, USA) and the evolution of marine animal communities during the late Cambrian**

Rudy Lerosey-Aubril, Robert R. Gaines, Thomas A. Hegna, Bertrand Lefebvre, Javier Ortega-Hernández, Peter Van Roy, Carlo Kier and Enrico Bonino





11.15 – 11.30 **Preservation and phylogeny of Cambrian ecdysozoans tested by experimental decay of *Priapul***

Robert Sansom

11.30 – 11.45 **Cambrian bivalved arthropods and the origin of mandibulates**

\*Cedric Aria and Jean-Bernard Caron

11.45 – 12.00 **Can phosphatic microfossils constrain Cambrian climates?**

\*Thomas W. Hearing, Thomas H. P. Harvey, Mark Williams, Sarah E. Gabbott, Philip R. Wilby and Melanie J. Leng

12.00 – 12.15 **Mineralogical insights into the tissues of Burgess Shale animals**

\*Ross P. Anderson, Nicholas J. Tosca, Stuart L. Kearns and Derek E. G. Briggs

12.15 – 12.30 **Comparison of the postembryonic development in the family Paradoxididae (Trilobita)**

\*Lukáš Laibl, Jorge Esteve and Oldřich Fatka

#### Session 2b (Lecture Theatre 2, Laënnec Building, in parallel with session 2a)

11.00 – 11.15 **Variable preservation of fruit flies in *Pinus* and *Wollemia* resin**

\*Victoria E. McCoy, Carmen Soriano, Arnoud Boom and Sarah E. Gabbott

11.15 – 11.30 **What can spores and pollen tell us about taphonomic bias at the Permian–Triassic boundary in the Eastern and Southern Alps?**

\*Hendrik Nowak, Evelyn Kustatscher, Guido Roghi, Massimo Bernardi and Karl Krainer

11.30 – 11.45 **Recent new discoveries from the upper Ediacaran of western Mongolia**

Tatsuo Oji, Stephen Q. Dornbos, Hitoshi Hasegawa, Sersmaa Gonchigdorj, Keigo Yada, Akihiro Kanayama, Takafumi Mochizuki, Hideko Takayanagi and Yasufumi Iryu

11.45 – 12.00 **The (incomplete) Phanerozoic fossil record of major phytoplankton lineages**

Thomas Servais and Ronald E. Martin

12.00 – 12.15 **The effect of climate on equatorial late Palaeozoic floral transitions in the limnic Muse and the paralic Mengkarang Formations. Two sides of the same coin?**

Isabel M. van Waveren, Menno Booij, Christopher J. Cleal, Mike J. Crow, Fauzie Hasibuan, Pierre Pellenard, Mark D. Schmitz and Ellen Stolle

12.15 – 12.30 **The early aquatic angiosperm *Montsecchia* from the Barremian of Spain**

Bernard Gomez, Véronique Daviero-Gomez, Clément Coiffard, Abel Barral, Carles Martin-Closas and David L. Dilcher

#### University Restaurant Rockefeller

12.30 – 14.00 **Lunch**



**Session 3a (Lecture Theatre 4, Laënnec Building, in parallel with session 3b)**

- 14.00 – 14.15 **Modern brains and their Cambrian antecedents: evolutionary stability, genealogical correspondence and evolved loss**  
Nicholas J. Strausfeld, Xiaoya Ma and Gregory D. Edgecombe
- 14.15 – 14.30 **Palaeoecology of an Upper Ordovician submarine cave-dwelling fauna in northern Kentucky, USA**  
Caroline J. Buttler and Mark A. Wilson
- 14.30 – 14.45 **Freshly-moulted trilobites from the Fezouata Lagerstätte of Morocco**  
\*Harriet B. Drage, Thijs R. A. Vandenbroucke, Peter Van Roy and Allison C. Daley
- 14.45 – 15.00 **Modelling enrolment mechanisms in Ordovician trilobites**  
Jorge Esteve, Juan-Carlos Gutierrez-Marco, Pedro Rubio and Isabel Rabano
- 15.00 – 15.15 **Burgess Shale-type fossils in the Middle Ordovician of the Barrandian area (Czech Republic)**  
Oldřich Fatka
- 15.15 – 15.30 **The diversification of early Asterozoa: resolving a palaeontological quandary**  
Aaron W. Hunter
- 15.30 – 15.45 **Ecological fitting within sheet-forming skeletal metazoans and the Ordovician rise of reef ecosystems**  
Björn Kröger, André Desrochers and Andrej Ernst
- 15.45 – 16.00 **Biostratigraphic assessment of the uppermost Ordovician in the central Anti-Atlas (Morocco)**  
Enrique Villas, Jorge Colmenar, Juan C. Gutiérrez-Marco, Sofia Pereira, José-Javier Álvaro, Diego García-Bellido and Saturnino Lorenzo

**Session 3b (Lecture Theatre 2, Laënnec Building, in parallel with session 3a)**

- 14.00 – 14.15 **Revision of the imbricate eocrinoid *Vyscystis* from the Middle Cambrian of the Barrandian area (Czech Republic)**  
Martina Nohejlová, Oldřich Fatka and Elise Nardin
- 14.15 – 14.30 **Is a 'one size fits all' taphonomic model appropriate for Mazon Creek?**  
\*Thomas Clements, Mark A. Purnell and Sarah E. Gabbott
- 14.30 – 14.45 **Preferential origin of calcitic cephalopod shell structures during calcite seas**  
Kenneth De Baets and Munnecke Axel
- 14.45 – 15.00 **Prospects and limitations of ecological studies of a fossil reef community (Aferdou el Mrakib, Middle Devonian, Morocco) based on fore-reef talus**  
Michał Jakubowicz, Jan J. Król, Mikołaj K. Zapalski and Blazej Berkowski



- 15.00 – 15.15 **Palaeoecological and palaeoenvironmental significance of Brigantian *Gigantoproductus* brachiopod beds, Derbyshire carbonate platform, UK**  
\*Leah Nolan, Lucia Angiolini, Giovanna Della Porta, Vanessa J. Banks,  
Sarah J. Davies, Flavio Jadoul, Melanie J. Leng and Michael H. Stephenson
- 15.15 – 15.30 **Phylogenetic analysis implies early diversification of tetrapods in the Tournaisian**  
Jennifer A. Clack, Marcello Ruta and Timothy R. Smithson
- 15.30 – 15.45 **Where to find the Carboniferous terrestrial fauna: recent discoveries in Romer's Gap point the way**  
Timothy R. Smithson, Carys E. Bennett, Jennifer A. Clack, Neil D. L. Clark,  
Sarah J. Davies, Gregory D. Edgecombe, Timothy I. Kearsey, John E. A. Marshall,  
Dave Millward, Andrew J. Ross and Janet E. Sherwin
- 15.45 – 16.00 **The Capitanian biodiversity crisis among tetrapods**  
Michael O. Day

#### Laënnec Building, main hall

- 16.00 – 16.15 **Tea/coffee break and posters**

#### Lecture Theatre 1, Laënnec Building

- 16.15 – 16.45 **Annual General Meeting (AGM)**

### *Annual Address*

#### Lecture Theatre 1, Laënnec Building

- 16.45 – 17.45 **Molecular thermometers: ancestral sequence reconstruction uncovers the history of adaptation to environmental temperature along the tree of life**  
Manolo Gouy

### *Museum Nocturnal Visit & Annual Dinner*

#### Musée des Confluences

- 18.30 – 20.00 **Nocturnal visit to the Museum**

#### Restaurant Bellona

- 20.15 – 00.00 **Annual Dinner**



## Friday 16th December

### *Conference & Poster session*

#### Session 4 (Laënnec Building, main hall)

08.15 – 09.15 **Poster Session, with tea/coffee and cakes**

#### Session 5a (Lecture Theatre 4, Laënnec Building, in parallel with session 5b)

09.15 – 09.30 **Palaeopsychrospheric ostracods during the Late Palaeozoic–Middle Triassic: the key to surviving mass extinction events?**

Sylvie Crasquin, David J. Horne and Marie-Béatrice Forel

09.30 – 09.45 **Mass extinctions as drivers of increased faunal cosmopolitanism on the supercontinent Pangaea**

David J. Button, Richard J. Butler, Graeme T. Lloyd and Martin D. Ezcurra

09.45 – 10.00 **The enigmatic archosaurs *Mandasuchus* and *Teleocrater* from the Middle Triassic of Tanzania and their implications for archosaur evolution**

Paul M. Barrett, Sterling J. Nesbitt, Alan Charig and Richard J. Butler

10.00 – 10.15 **Ammonoids from the Griesbachian (Early Triassic) of northeastern Greenland: taxonomy and biostratigraphy**

David Ware and Hugo Bucher

10.15 – 10.30 **Looking snappy: quantifying convergence in cranial morphology between phytosaurs and crocodylomorphs**

\*Andrew Jones, Pedro L. Godoy and Richard J. Butler

#### Session 5b (Lecture Theatre 2, Laënnec Building, in parallel with session 5a)

09.15 – 09.30 **Early Cambrian ostracoderms and the trials and tribulations of total evidence dating**

\*Joseph N. Keating, Richard Dearden and Philip C. J. Donoghue

09.30 – 09.45 **A new Burgess Shale polychaete from Marble Canyon (British Columbia)**

\*Karma Nanglu and Jean-Bernard Caron

09.45 – 10.00 **Reconstructing anomalocaridid feeding appendage dexterity sheds light on radiodontan ecology**

Giacinto De Vivo, Stephan Lautenschlager and Jakob Vinther

10.00 – 10.15 **Appendicular nature of gnathobase-like structures in Cambrian radiodontans**

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

10.15 – 10.30 **Contributions to the ongoing work on the International Chronostratigraphy of the Cambrian: preliminary data from the Terreneuvian of Iran and Series 2 of Mexico**

Léa Devaere, Sébastien Clausen, Dieter Korn, Abbas Ghaderi, Ulrich Struck, Juan J. Palafox-Reyes, Blanca E. Buitrón-Sanchez and Daniel Vachard

**Laënnec Building, main hall**

10.30 – 11.00 Tea/coffee break and posters

**Session 6a (Lecture Theatre 4, Laënnec Building, in parallel with session 6b)**

11.00 – 11.15 **Testing niche versus neutral models of Ediacaran community assembly**

\*[Emily G. Mitchell](#), Charlotte G. Kenchington, Alexander G. Liu, Simon J. Harris,  
Philip R. Wilby and Nicholas J. Butterfield

11.15 – 11.30 **The Chronicles of *Charnia*: developmental biology and phylogenetic inference from an Ediacaran rangeomorph**

\*[Frankie Dunn](#), Philip R. Wilby, Philip C. J. Donoghue and Alexander G. Liu

11.30 – 11.45 **On the agglutinated nature of Ediacaran palaeopascichnids from northern Siberia**

\*[Anton V. Kolesnikov](#)

11.45 – 12.00 **Critically accessing the depositional setting of the Ediacaran Mistaken Point biota**

\*[Jack J. Matthews](#)

12.00 – 12.15 **The palaeobiology of Ediacaran rangeomorphs: reproduction, environmental sensitivity and ecological succession**

[Charlotte G. Kenchington](#) and Philip R. Wilby

**Session 6b (Lecture Theatre 2, Laënnec Building, in parallel with session 6a)**

11.00 – 11.15 **Vision in fossil polychelidan lobsters**

[Denis Audo](#), Joachim T. Haug, Carolin Haug, Sylvain Charbonnier,  
Günter Schweigert, Carsten H. G. Müller and Steffen Harzsch

11.15 – 11.30 **Synchrotron X-ray spectroscopy reveals burial conditions and fossilization in a Cretaceous freshwater Lagerstätte**

[Pierre Gueriau](#)

11.30 – 11.45 **Arms race or feeding competition? The mid-Palaeozoic origins of cephalopod and vertebrate jaws**

[Christian Klug](#), Linda Frey, Dieter Korn, Romain Jattiot and Martin Rücklin

11.45 – 12.00 **Within-guild niche partitioning in sympatric species: how ecologically sensitive is texture analysis of tooth microwear?**

[Mark A. Purnell](#), Christopher Nedza and Leszek Rychlik

12.00 – 12.15 **Macroevolution of Mesozoic lepidosaurs**

\*[Jorge A. Herrera Flores](#), Michael J. Benton and Thomas L. Stubbs

**University Restaurant Rockefeller**

12.15 – 13.45 **Lunch**



**Session 7a (Lecture Theatre 4, Laënnec Building, in parallel with session 7b)**

- 13.45 – 14.00 **The pattern of ecological radiation of mammals across the K-Pg boundary**  
*\*Gemma L. Benevento*, Matt Friedman and Roger B. J. Benson
- 14.00 – 14.15 **The death of dinosaurs and rise of mammals in the San Juan Basin of New Mexico, USA**  
*Stephen L. Brusatte*, Thomas E. Williamson, Matthew T. Heizler, Daniel J. Peppe, Ross Secord, Adam Davis, C. Will Fenley, Andrew Flynn, Caitlin Leslie and Sarah L. Shelley
- 14.15 – 14.30 **Identifying patterns and drivers of coral diversity in the Central Indo-Pacific marine biodiversity hotspot**  
*Morana Mihaljevic*, Chelsea Korpany, Willem Renema and John M. Pandolfi
- 14.30-14.45 **Exploring the drivers of ecological and evolutionary turnover in the Caribbean**  
*Paola G. Rachello-Dolmen*, Ethan L. Grossman, Kenneth G. Johnson, Jonathan A. Todd and Aaron O'Dea
- 14.45-15.00 **A new fossil *Bramoides* from the Eocene London Clay, re-aligned with the enigmatic modern genus *Gasterochisma* (Teleostei: Scombridae)**  
*Hermione T. Beckett*, Zerina Johanson, Mark Graham and Matt Friedman

**Session 7b (Lecture Theatre 2, Laënnec Building, in parallel with session 7a)**

- 13.45 – 14.00 **Exploring the morphological diversity and hydrodynamic performance of extinct jawless vertebrates**  
*Carlos Martínez Perez*, Humberto G. Ferron, Imran A. Rahman, Victor Selles de Lucas, Philip C. J. Donoghue and Hector Botella
- 14.00 – 14.15 **The origins of colour patterns in fossil insects: insights from trace element chemistry**  
*\*Nidia Alvarez Armada*, Maria E. McNamara, Sam Webb and Fiona L. Gill
- 14.15 – 14.30 **Testing turbulent waters: palaeoecological implications of the durability and preservation potential of soft-bodied organisms in sediment-density flows**  
*\*Orla Bath Enright*, Nicholas J. Minter and Esther J. Sumner
- 14.30 – 14.45 **Using melanosomes to discriminate between tissues in vertebrate eyes**  
*\*Christopher S. Rogers* and Maria E. McNamara
- 14.45 – 15.00 **The influence of taphonomic bias on Bayesian estimation of clade ages using morphological data**  
*Joseph O'Reilly* and Philip C. J. Donoghue

**Laënnec Building, main hall**

- 15.00 – 15.30 **Tea/coffee break** (take down posters)



**Session 8 (Lecture Theatre 1, Laënnec Building)**

- 15.30 – 15.45 **Fossilized nuclei from the Ediacaran Weng'an Biota (Doushantuo Formation, South China)**  
John A. Cunningham, Zongjun Yin, Kelly Vargas, Stefan Bengtson and Philip C. J. Donoghue
- 15.45 – 16.00 **Ultrastructure and chemistry of integumentary structures in an ornithischian dinosaur**  
Maria E. McNamara, Pascal Godefroit, Danielle Dhouailly, Michael J. Benton, Sofia M. Sinita, Yuri L. Bolotsky, Alexander V. Sizov and Paul Spagna
- 16.00 – 16.15 **Environmental partitioning and differential growth in species of the thyreophoran dinosaur *Stegosaurus* in the Upper Jurassic Morrison Formation, USA**  
Susannah C. R. Maidment, D. Cary Woodruff and John R. Horner
- 16.15 – 16.30 **Diets of giants: the nutritional value of herbivorous dinosaur diet during the Mesozoic**  
Fiona L. Gill, Juergen Hummel, A. Reza Sharifi, Alexandra P. Lee and Barry H. Lomax
- 16.30 – 16.45 **Reappraisal of *Compsognathus longipes* (Saurischia; Theropoda) skull anatomy and endocast shape by synchrotron imaging and virtual reconstruction**  
Vincent Beyrand, Paul Tafforeau, Stanislav Bureš and Oliver W. M. Rauhut
- 16.45 – 17.00 **Phylogenetic diversity as a palaeobiodiversity metric: new evidence for a Cretaceous decline in Mesozoic dinosaurs**  
Graeme T. Lloyd, David W. Bapst, Matt Friedman and Katie E. Davis

**Closing of the meeting (Lecture Theatre 1, Laënnec Building)**

- 17.15 – 17.30 **Presentation by London 2017 organizing committee**
- 17.30 – 17.45 **Presentation of the President's Prize and Council Poster Prize, followed by closing remarks**

**Wine and local products tasting session (Laënnec Building, main hall)**

- 17.45-19.00 **Wine and local products tasting session**



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

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Université de Lyon





# Abstracts of symposium presentations:

## Assessing palaeoenvironments and palaeobiology through geochemistry

### Isotopic aspects of dinosaur reproduction

**Romain Amiot<sup>1</sup>, Christophe Lécuyer<sup>1</sup>, Xiaolin Wang<sup>2</sup>, Xing Xu<sup>2</sup>, Jinyou Mo<sup>3</sup>, Zhonghe Zhou<sup>2</sup>, François Fourel<sup>1</sup>, Shuo Wang<sup>4</sup> and Jean-Michel Mazin<sup>1</sup>**

<sup>1</sup>CNRS UMR 5276, Université de Lyon and Ecole Normale Supérieure de Lyon, France

<sup>2</sup>Institute of Vertebrate Paleontology and Paleoanthropology, CAS, China

<sup>3</sup>Natural History Museum of Guangxi, China

<sup>4</sup>Beijing Capital Normal University, China

A key factor that constrains the spatial and temporal distribution of land vertebrates is their ecological capability for breeding. Because of their large variation in body size and latitudinal distribution, non-avian dinosaurs must have developed various strategies to ensure successful reproduction, such as the selection of optimal egg-laying environment, time period, and egg-brooding strategy to keep incubation temperature at an ideal range. In order to investigate this latter aspect, incubation temperature of oviraptorosaur embryos have been estimated using the recently updated phosphate-water temperature scale, applied here to calculate the temperature at which embryo apatite precipitates from egg fluids. Whereas the apatite  $\delta^{18}\text{O}_p$  value can be measured directly from preserved embryo bones, the egg fluids  $\delta^{18}\text{O}_{ew}$  value can be estimated from the oxygen isotope composition of eggshell calcite by applying the fractionation factors determined between eggshell calcite and egg fluids of extant birds. Using these relationships, the oxygen isotope composition of three oviraptorosaur eggshell calcites and their embryo apatite have been measured. These fossil eggs have been recovered from the Late Cretaceous Nanxiong Formation of China. Calculated embryo incubation temperature lies within the 33-40°C range, which is likely above environmental temperatures at that time and consistent with brooding behaviour.

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### Deep-sea barnacle shell: geochemical signal and microstructure

**Ana-Voica Bojar<sup>1</sup> and Hans-Peter Bojar<sup>2</sup>**

<sup>1</sup>University of Salzburg, Austria

<sup>2</sup>Universalmuseum Joanneum, Austria

One of the largest hydrothermal fields of the Manus Spreading Center, Papua New Guinea is Hydrothermal Field 1 (Vienna Woods). The heterogeneous fauna collected at this site consists of gastropods, barnacles, bythograeid crabs, bresiliid shrimps, vestimentiferans and sea anemones. Barnacles are crustaceans adapted to a sessile existence and that cement to substrates by proteins. Less than 2% of barnacle species are found at depths between 100 m and 2,500 m, most inhabiting shallow marine environments. In the present study, we have investigated shell microstructure in addition to minor elements (Mg, Na, S, Sr) and stable isotope distributions of barnacles collected at depths of 2,500 m from the Vienna Woods hydrothermal field. Stable isotopes as well as the elemental composition of *Eochionelasmus ohtai manusensis* were retrieved along profiles perpendicular to growth lines. Preliminary data indicate that within one shell, oxygen isotope values show



variations of up to 0.6%. According to calculated temperatures, *Echionelasmus* populated sites with temperatures between 2°C and 5°C, in agreement with the habitat from the North Fiji and Lau Basins, where temperatures of max. 6°C are documented for the environment of *Echionelasmus*. Calculated and measured temperatures indicate input of hydrothermal fluid, with barnacles occupying a niche in a marginal position with respect to active vents.

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## Carnivoran resource and habitat use in the context of a Late Miocene faunal turnover episode

**Laura Domingo<sup>1,3</sup>, M. Soledad Domingo<sup>2</sup>, Paul L. Koch<sup>3</sup>, Jorge Morales<sup>4</sup> and M. Teresa Alberdi<sup>4</sup>**

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We investigate resource and habitat use by apex predators through stable isotope analysis on two Spanish Late Miocene localities: Los Valles de Fuentidueña (~9.6 Ma, LVF) and Cerro de los Batallones (~9.1 Ma, BAT). The temporal window represented by LVF and BAT was crucial in the shaping of the current Iberian mammalian structure. It corresponds to the initial stages of a faunal turnover episode and regional environmental change at ~9.5–8.5 Ma (Vallesian–Turolian transition) associated with an increase in the seasonality of precipitation. Herbivore and carnivore  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values do not indicate significant changes in either the vegetation cover or the hydrological regime during the time lapse represented between LVF and BAT. From the standpoint of predator–prey interactions, LVF and BAT large active carnivores encountered high levels of interspecific competition, although some genera, such as the amphyconid *Magericyon* and the hyaenid *Lycyaena*, seemed to avoid competition by taking prey from more open habitats. We propose that apex predator sympatry may have been favoured if a low seasonality of precipitation, as inferred for the onset of the Vallesian–Turolian turnover event, promoted high levels of primary productivity with a direct impact on biomass availability at different trophic levels.

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## Non-traditional isotopic approaches to study the physiology of biomineralizing organisms

**Robert A. Eagle**

*University of California, Los Angeles, USA*

Recent research has focused on non-traditional isotope systems as tracers of the physiology of biomineralizing organisms. In particular, isotopic ordering in fossil vertebrate biominerals can function as an indicator of body temperatures or taphonomy. In modern teeth and in eggshells,  $^{13}\text{C}$ – $^{18}\text{O}$  bond abundance in the carbonate moiety reflects body temperature of the organism. The technique therefore has the potential to unlock information on the body temperature and physiology of extinct vertebrates and of palaeoenvironments, but in some fossil taxa and localities, this isotopic signal has been altered during diagenesis. Another area of recent research uses boron isotope ( $\delta^{11}\text{B}$ ) measurements to reveal aspects of the biology of marine calcifying organisms. Traditionally used as a palaeoceanographic proxy for ocean pH,  $\delta^{11}\text{B}$  in the carbonate shells or skeletons of diverse cultured modern marine organisms records information on their ability to modify their internal pH and buffer it with respect to seawater across a



range of atmospheric CO<sub>2</sub> concentrations. In some taxa, biological control over internal pH may compromise the use of  $\delta^{11}\text{B}$  as a palaeo-ocean pH proxy. Conversely, comparative measurements of  $\delta^{11}\text{B}$  in co-occurring marine organisms may yield information on both ocean pH and physiology.

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## Isotope perspectives in vertebrate palaeobiology

**Jeremy E. Martin, Théo Tacail and Vincent Balter**

*CNRS UMR 5276, Université de Lyon and Ecole Normale Supérieure de Lyon, France*

The recent development of multi-collector inductively coupled plasma mass spectrometry (MC-ICPMS), notably in the disciplines of Earth sciences, now allows the measurement of precise isotope ratios, even under low concentration. Non-traditional isotope systems, such as alkaline earth (Ca, Mg) and transition (Cu, Fe, Zn) metals, are now being measured in a variety of biological tissues, including bones and teeth. Although our understanding of the environmental and biological mechanisms behind the fractionation of such elements is still in its infancy, some of these isotopes are suspected to fractionate along the food chain as has been reported in the literature for Ca, Mg and Zn. Other geochemical methods, such as concentration analyses, permit a prior assessment of diagenesis in the fossils to be analysed and such approaches allow us to recognize that, in some circumstances, not only enamel but also dentine or bone can preserve its original biogenic composition. The aims here are to review current knowledge surrounding these isotopic tools, to address their potential preservation in biological apatite, to provide the palaeobiologist with a guide to the different toolkits available, and to discuss their potential applications in vertebrate palaeobiology.

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## The foraging ecology of pterosaurs - implications from stable isotope analysis

**Thomas Tütken<sup>1</sup> and David W. E. Hone<sup>2</sup>**

*<sup>1</sup>University of Mainz, Germany*

*<sup>2</sup>Queen Mary University of London, UK*

Means of testing the available hypotheses for the diet of many pterosaurs have proved elusive. While there is good evidence that many pterosaurs were piscivores, the location of the fossil remains of numerous species leaves open the question as to whether they fed in primarily marine or terrestrial settings. Here, using stable isotope analysis of skeletal bioapatite, we examine the potential ecological habits of 18 pterosaur taxa from more than seven different families, covering a broad spectrum of hypothesized diets as evidenced in Mesozoic marine and terrestrial deposits. Based upon the carbon and oxygen isotope compositions of both tooth and bone samples relative to the surrounding matrix, the food and water sources used by these flying reptiles are inferred and compared with existing feeding hypotheses. In general, the large range of oxygen and carbon isotope compositions indicate the consumption of water and food from isotopically distinct sources ranging from freshwater to marine settings. The stable isotope data will be discussed in the context of those from modern-day birds and reptiles with aquatic and terrestrial feeding habits to assess the foraging ecology of pterosaurs.



## Reconstructing Ordovician (Floian) conodont ecology and Laurentian seawater temperatures using oxygen isotopes

**James R. Wheeley<sup>1</sup>, Phillip E. Jardine<sup>2</sup>, Robert J. Raine<sup>3</sup>, Ian Boomer<sup>1</sup> and M. Paul Smith<sup>4</sup>**

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<sup>4</sup>*Oxford University Museum of Natural History, UK*

Conodont  $\delta^{18}\text{O}$  is increasingly used throughout the Palaeozoic–Triassic to reconstruct seawater temperatures, especially low–mid latitude temporal changes. Much less attention has been paid to  $\delta^{18}\text{O}$  variation for time-slices across palaeoenvironments or within sample assemblages. Furthermore, there have been few isotopic tests of conodont ecological models based on biogeographic and bio- and lithofacies distributions. Here we present the first test of the ecological model for Ordovician conodonts based on analysis and interpretation of  $\delta^{18}\text{O}$  values from a Lower Ordovician (Floian) shelf edge–slope assemblage of the Shallow Bay Formation, Cow Head Group, western Newfoundland. Nine taxa yield a 1.7–1.8‰ intra-sample variability based on mixed tissue and white matter-only analyses. This  $\delta^{18}\text{O}$  variability is equivalent to a ~8°C range. Fitting linear mixed models to the dataset demonstrates significant differences between the  $\delta^{18}\text{O}$  of some species, in both mixed and single histology analyses, supporting the interpretation that an isotopic and temperature gradient is preserved. By combining knowledge of conodont distributions in host rocks and geological setting with conodont  $\delta^{18}\text{O}$ , an integrated palaeoecological and palaeoceanographic model is proposed, with species inhabiting a range of bathymetries (epipelagic–mesopelagic) across the shelf–shelf-edge–slope palaeoenvironment. This model supports the depth stratification ecology for conodonts and their pelagic mode of life. These findings highlight the risk of using single species  $\delta^{18}\text{O}$  as representative of time-slice seawater temperatures and promote isotopic ecological analysis for temporal  $\delta^{18}\text{O}$  studies.





# Abstract of Annual Address

The Annual Address will be given on Thursday 15th December.

## **Molecular thermometers: ancestral sequence reconstruction uncovers the history of adaptation to environmental temperature along the tree of life**

**Manolo Gouy**

*Laboratoire de Biométrie et Biologie Evolutive, CNRS - Université de Lyon, France*

It has recently been recognized that the effects of environmental temperature on ancestral organisms have left genetic footprints that can be uncovered in extant genomes. These effects allow us to define “molecular thermometers” that relate ancestral environmental temperatures to the composition of ancestral molecules in nucleotides and amino acids. The accuracy of the reconstruction of ancestral molecular compositions is therefore crucial for an effective application of molecular thermometers. Recent progress in the definition of probabilistic models of the evolutionary process has improved the biological realism of these models by accounting for the variation of patterns of molecular evolution among lineages. These new non-homogeneous methods allow us to reconstruct ancestral molecular compositions more accurately than traditional homogeneous methods. Analyses of genomic data using these tools allow attempts to reconstruct the evolutionary history of the adaptation to environmental temperatures at the scale of the tree of life. The evidence supports a mesophilic lifestyle for LUCA, the last universal common ancestor, but hyperthermophilic lifestyles for LBCA and LACA, the last common ancestors of the bacterial and archaeal domains, respectively.



# Abstracts of oral presentations

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

Underlined author denotes designated speaker.

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## The origins of colour patterns in fossil insects: insights from trace element chemistry

\***Nidia Alvarez Armada<sup>1</sup>, Maria E. McNamara<sup>1</sup>, Sam Webb<sup>2</sup> and Fiona L. Gill<sup>3</sup>**

<sup>1</sup>*University College Cork, Ireland*

<sup>2</sup>*Stanford Synchrotron Radiation Lightsource, USA*

<sup>3</sup>*University of Leeds, UK*

Insects are the most diverse group of animals known and are adapted to live in almost all terrestrial, and some aquatic, biomes. The most striking adaptations of insects include colour patterns on their cuticle, which are produced primarily by pigments such as melanin. Many fossil insects also exhibit patterns on their cuticles, but which pigments are responsible for generating the patterns is unknown. We resolve these issues using synchrotron X-ray fluorescence (XRF) to characterise the spatial distributions of trace elements in patterned cuticles of fossil and modern insects. Principal component analysis (PCA) of the concentrations of these elements reveals a strong taxonomic signal: representatives of individual insect families show similar concentrations of trace elements. In at least some families, this taxonomic signal is overprinted by a pigment-related signal, whereby cuticle regions of different colours differ in trace element chemistry. Understanding pigment- and taxon-specific variation in trace element chemistry will greatly enhance our ability to interpret the original pigmentary colours of fossil insects, thus informing models of the evolution of colour and its ecological functions in insects through deep time.

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## Mineralogical insights into the tissues of Burgess Shale animals

\***Ross P. Anderson<sup>1</sup>, Nicholas J. Tosca<sup>2</sup>, Stuart L. Kearns<sup>3</sup> and Derek E. G. Briggs<sup>1</sup>**

<sup>1</sup>*Yale University, USA*

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

<sup>3</sup>*University of Bristol, UK*

Burgess Shale-type fossils are crucial to our understanding of the diversification of animals during the Cambrian explosion. There has been a substantial effort to understand their taphonomy since it is vital to biological interpretations. Clay minerals have been implicated in preservation, templating soft tissues during decay and early diagenesis. Differences in elemental abundances (and, by inference, clays) across fossil anatomy were previously attributed to contrasts in the decaying tissues. However, subsequent work suggested that the clays formed much later, with differences reflecting volatilization of tissues during different stages of metamorphism. In either case, the clays could reflect the nature of tissue chemistry, but clearly linking specific clay minerals with different tissues remains a challenge. Here we utilize selected area X-ray diffraction to identify clays non-destructively across the anatomical features of multiple specimens of *Marrella* from the Burgess Shale. These analyses revealed that the stomach and cephalic canals, and occasionally the gut trace, are differentiated from the remainder of the fossil and matrix by the presence of



kaolinite. Identifying mineral phases provides more information on their formation than elemental mapping alone and may allow us to differentiate the chemistry of the original tissues on which they precipitated, thereby revealing new biological information.

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## Cambrian bivalved arthropods and the origin of mandibulates

**\*Cedric Aria<sup>1</sup> and Jean-Bernard Caron<sup>1,2</sup>**

<sup>1</sup>*University of Toronto, Canada*

<sup>2</sup>*Royal Ontario Museum, Canada*

Although they were first believed to be related to crustaceans, a number of iconic Cambrian taxa with bivalved carapaces (such as *Canadaspis*, *Odaraia*, *Branchiocaris*) have, in the last decade, been more commonly presented as early, or even earliest, euarthropods. This view was based heavily on a lack of information on the cephalic configuration of these animals, translated into minimalist heads with one or two segments. Extraordinarily well-preserved specimens of a new branchiocarid arthropod from Marble Canyon (Burgess Shale, Kootenay National Park) and a critical reevaluation of *Branchiocaris* material from Utah and the Burgess Shale show that these animals had a mandibulate head configuration, with intercalary segment, mandibles, maxillae and maxillipeds. *Canadaspis* and *Odaraia* are also arguably part of the same clade, characterised by multisegmented, enditic basipods. This new evidence reshapes the phylogeny of panarthropods and constitutes a major step forward in unifying hypotheses of mandibulate limb evolution, notably those of Müller and Walossek, and Boxshall, with developmental studies and molecular phylogenies. Our new topology also sheds light on the significance of larval morphotypes in the Cambrian, suggesting that heterochrony played a major role in the emergence of crown features and the apparent large disparity of early arthropod body plans.

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## Vision in fossil polychelidan lobsters

**Denis Audo<sup>1,3</sup>, Joachim T. Haug<sup>2</sup>, Carolin Haug<sup>2</sup>, Sylvain Charbonnier<sup>3</sup>, Günter Schweigert<sup>4</sup>, Carsten H. G. Müller<sup>5</sup> and Steffen Harzsch<sup>5</sup>**

<sup>1</sup>*Université de Rennes, France*

<sup>2</sup>*LMU Munich, Germany*

<sup>3</sup>*CNRS UMR 7207, Muséum National d'Histoire Naturelle and Sorbonne Universités, France*

<sup>4</sup>*Staatliches Museum für Naturkunde Stuttgart, Germany*

<sup>5</sup>*Erst-Moritz-Arndt-Universität Greifswald, Germany*

Compound eyes are fascinating structures which undoubtedly play a critical role in the evolution of crustaceans. Several types of compound eyes exist: apposition eyes, with a superior resolution; three superposition eye subtypes, which trade-off resolution for sensitivity. Decapod crustaceans are probably the group with the greatest eye type diversity. The study of their visual system is complicated by the occurrence of groups in which extant species have reduced eyes, such as polychelidan lobsters, sister-group of all lobsters and crabs (Eureptantia). Our study is the first to focus on this problem by studying the eyes of Jurassic fossil polychelidan from Europe. Our results reveal that fossil polychelidans had functional eyes. Most of these were reflective superposition eyes, easily identified by their squared facets. However, for *Rosenfeldia oppeli* facets were hexagonal. *Rosenfeldia oppeli* eyes probably correspond to apposition type. We searched for variations in the size of eyes. Our results show a weak but significant taxonomic effect. Surprisingly, no



significant environmental effect was detected. More samples are now required to further our statistical analysis; these efforts have already allowed the identification of two unusual specimens: small adult *Voulteryon parvulus* with both squared and hexagonal facets.

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### How good are your palaeodiversity measurements?

**Abel Barral<sup>1</sup>, Bernard Gomez<sup>1</sup>, Juan M. Zorrilla<sup>2</sup>, José M. Serrano<sup>2</sup>, Johan Yans<sup>3</sup>,  
Véronique Daviero-Gomez<sup>1</sup> and Christophe Lécuyer<sup>1</sup>**

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<sup>2</sup>Complutense University of Madrid, Spain

<sup>3</sup>Université de Namur, Belgium

One of the main concerns in palaeontology is how large a sample should be in order to assess the diversity of a fossil assemblage. Sampling effort analyses are used in neoecology to evaluate diversity representativeness, by minimizing the bias in data acquisition and adjusting the effort needed to obtain reliable results. These methods can be very useful in palaeoecological studies, in which exhaustive sampling is usually carried out. The Clench model is a useful method as it allows for the monitoring of several parameters to examine the accuracy and reliability of diversity estimates during data acquisition: 1) a value of collected richness, associated with 2) a value of stability for the estimates produced by the model, 3) an estimate of the total richness held in the sample, and 4) a prediction of the sampling effort required to reach a given proportion of total richness. Thus, the Clench equation allows the evaluation of the trade-off between the loss of information and the amount of work required to reach the information for the whole sample. The application of the Clench equation to palaeodiversity studies gives us a great opportunity to enhance the performance of data acquisition and to provide a quality test for the resulting taxonomic inventories.

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### The enigmatic archosaurs *Mandasuchus* and *Teleocrater* from the Middle Triassic of Tanzania and their implications for archosaur evolution

**Paul M. Barrett<sup>1</sup>, Sterling J. Nesbitt<sup>2</sup>, Alan J. Charig<sup>1</sup> and Richard J. Butler<sup>3</sup>**

<sup>1</sup>Natural History Museum, London, UK

<sup>2</sup>Virginia Polytechnic Institute and State University, USA

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

The Lifua Member of the Manda Beds (Middle Triassic: Anisian) crops out in the Ruhuhu Valley, Tanzania, and has yielded a diverse fauna of terrestrial vertebrates. This fauna has had major impacts on our understanding of the establishment of clades that subsequently dominated the Mesozoic landscape. Rhynchosaur and synapsid remains are the most abundant, but archosaurs are represented by multiple specimens and taxa. Here we provide the first evaluations of two archosaur taxa that have been frequently mentioned in the literature, but never formally described, which both have important ramifications for understanding the early evolution of the clade. '*Mandasuchus*' and '*Teleocrater*' were named in an unpublished thesis 60 years ago and are each represented by several partial skeletons and isolated referred remains. This material provides a good overview of their postcranial anatomy, but cranial material is scarce. Both taxa can be diagnosed on the basis of autapomorphies and unique character combinations. Phylogenetic analysis reveals that '*Mandasuchus*' is referable to Crurotarsi, as an early-diverging member of Loricata,



whereas ‘*Teleocrater*’ is recovered within Avemetatarsalia. ‘*Teleocrater*’ forms a clade with several other previously enigmatic archosaurs from South America, India and Russia, substantially altering our knowledge of early avemetatarsalian evolution prior to the pterosaur/dinosaur split.

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### Testing turbulent waters: palaeoecological implications of the durability and preservation potential of soft-bodied organisms in sediment-density flows

**\*Orla Bath Enright<sup>1</sup>, Nicholas J. Minter<sup>1</sup> and Esther J. Sumner<sup>2</sup>**

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

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

Experiments in an annular flume tank explored the durability and preservation potential of the polychaete *Alitta virens* when transported by fast and turbulent sediment-laden flows. Understanding whether soft-bodied organisms within fossil assemblages could have been transported or not is fundamental to the study of palaeoecology. Experiments can allow us to place constraints on interpretations of transport distances from life environments. In a three-factorial experimental design, we generated fully turbulent sandy flows and tested the effects of transport duration, sediment concentration, and grain angularity on the states of bodily damage experienced by freshly euthanized *Alitta virens*. Results identified statistically significant effects of transport duration and grain angularity. Increasing sediment concentration had a significant effect with angular sediment but not with rounded sediment. Our experiments demonstrate that if soft-bodied organisms such as polychaetes were alive and then killed by a flow they would have been capable of enduring prolonged transport with little damage. Dependent upon flow conditions, specimens were capable of remaining intact over extended transport durations and distances. This has significant palaeoecological implications for fossil Lagerstätten deriving from sediment-density flows, because the organisms present may have been transported over substantial distances and thus will not represent true palaeocommunities.

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### A new fossil *Bramoides* from the Eocene London Clay, re-aligned with the enigmatic modern genus *Gasterochisma* (Teleostei: Scombridae)

**Hermione T. Beckett<sup>1</sup>, Zerina Johanson<sup>2</sup>, Mark Graham<sup>2</sup> and Matt Friedman<sup>3</sup>**

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

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

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

The London Clay Formation (Ypresian) yields a rich fauna documenting an important stage in the radiation of modern spiny-rayed teleosts. Many London Clay species show clear affinity with modern lineages, but placement of others remains uncertain. Among these is *Bramoides*, known only from isolated braincases. We recently located an unprepared, articulated skull in the Natural History Museum, London, representing the most complete *Bramoides* known. Mechanical preparation and computed tomography revealed distinctive features of the genus: high sagittal crest with a supraoccipital contribution extending anterior to the eyes, ‘box-like’ profile of the braincase in posterior view, wide vomer, and expansion of the exoccipitals into large articular facets for the vertebral column. Additionally, the specimen revealed the presence of beak-like, non-protrusible upper jaws and large cycloid scales. This distinctive combination of features is otherwise only known



in *Gasterochisma*, which represents the earliest diverging branch of Scombridae but has no fossil record. Separation of *Bramoides* and *Gasterochisma* seems merited, as several features of the Eocene taxon are less specialized than the modern form. Placement of *Bramoides* in Gasterochismatinae expands the diverse assemblage of London Clay scombroids, providing further evidence for the rapid radiation of this group in the early Palaeogene.

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## The pattern of ecological radiation of mammals across the K-Pg boundary

**\*Gemma L. Benevento<sup>1</sup>, Matt Friedman<sup>2</sup> and Roger B. J. Benson<sup>1</sup>**

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

<sup>2</sup>University of Michigan, USA

The apparent adaptive radiation of mammals following the Cretaceous–Palaeogene (K-Pg) extinction has long attracted the interest of palaeontologists. Despite this prominence, some aspects of mammalian diversification remain unclear. To date, quantitative work has either focused on mammalian subgroups (e.g. eutherians or multituberculates), examined comparatively short time intervals (e.g. Late Cretaceous–Paleocene), or explored limited trait data (e.g. body mass alone), making it difficult to assess the timing and magnitude of possible changes in ecomorphological diversity across the Mesozoic and Cenozoic. Continuous character traits were collected from direct examination of specimens and from the primary literature, with measurements selected to capture key mechanical properties. We find little increase in the morphological diversity of jaws immediately post-K-Pg, but from the Tiffanian (60 Ma) onward mammalian mandibular disparity increases in a stepwise fashion until the end of our study interval. Our results indicate that the increase in disparity was principally concentrated in larger mammals rather than in species comparable in size to those of the Mesozoic. This may suggest that the previously observed increase in mammalian upper body mass allowed Palaeogene mammals to explore novel feeding ecologies unavailable to smaller Mesozoic species, consistent with the hypothesis of ecological release following the extinction of the dinosaurs.

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## Reappraisal of *Compsognathus longipes* (Saurischia; Theropoda) skull anatomy and endocranium shape by synchrotron imaging and virtual reconstruction.

**Vincent Beyrand<sup>1,2</sup>, Paul Tafforeau<sup>2</sup>, Stanislav Bureš<sup>1</sup> and Oliver W. M. Rauhut<sup>3</sup>**

<sup>1</sup>Palacký University, Olomouc, Czech Republic

<sup>2</sup>European Synchrotron Radiation Facility, France

<sup>3</sup>Bayerische Staatssammlung für Paläontologie und Geologie, Germany

Compsognathidae is a small, basal coelurosaurian theropod with a wide distribution during the Late Jurassic and Early Cretaceous. The name-bearing taxon of the group, *Compsognathus longipes*, is based on a specimen found in the nineteenth century in the Kimmeridgian/Tithonian lithographic limestones of southern Germany. As the specimen is preserved in a slab, only the bones on the surface can be described, leading to incomplete knowledge of bone morphology and skull shape. *C. longipes* has been scanned using





the ID19 and BM05 beamlines of the ESRF (France) using propagation phase contrast microtomography. This method, currently the most powerful one to investigate internal structures in such fossils non-destructively, helped us to look at more details of the bone anatomy in the skull of *C. longipes*. Detailed segmentation allowed us to perform a virtual reconstruction of the skull and to access the endocranial anatomy of this specimen. The virtual endocast shows a rather short and wide cerebrum and unusual conformation of the olfactory tracts and cerebellum compared to most theropod dinosaurs.

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## Mass extinctions: towards an understanding of how, why and when ecosystems collapse

**David P. G. Bond**

*University of Hull, UK*

Advances in our understanding of mass extinctions have resulted from greater resolution in the fossil record, better dating, and improved proxies for palaeoenvironmental change, but we still do not know what drives extinctions. The realization that Earth is again facing stresses implicated in its past crises (global warming, anoxia, ocean acidification) has intensified research on the ultimate cause(s) of extinctions (*e.g.*, large igneous provinces and bolide impacts). There is growing evidence that volcanic eruptions might be the driver of proximal kill mechanisms, but the links between these are not well understood. Likewise, the temporal relationship between bolide impact and the Cretaceous extinction implies a causal relationship, but the mechanics of biotic losses remain unclear. This talk evaluates environmental factors implicated in major episodes of species extinctions and explores the links between killers and ultimate drivers. Experimental biology, by examining responses of species to change, is helping us understand how extinctions happen. Reduced pH, for instance, alters the efficacy of fishes' chemical receptors, leaving them less equipped to detect prey, predators and mates – invoking 'death-by-celibacy' scenarios. Experimental geobiologists and Earth scientists could together unravel the causes of past extinctions, and better inform understanding of the modern crisis.

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## The death of dinosaurs and rise of mammals in the San Juan Basin of New Mexico, USA

**Stephen L. Brusatte<sup>1,2</sup>, Thomas E. Williamson<sup>2</sup>, Matthew T. Heizler<sup>3</sup>, Daniel J. Peppe<sup>4</sup>, Ross Secord<sup>5</sup>, Adam Davis<sup>4</sup>, C. Will Fenley<sup>4</sup>, Andrew Flynn<sup>4</sup>, Caitlin Leslie<sup>4</sup> and Sarah L. Shelley<sup>1</sup>**

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The end-Cretaceous extinction (66 Ma) was a turning point in Earth history, as the dinosaur-dominated world of the Cretaceous gave way to complex mammalian faunas in the Palaeogene. The alluvial foreland basin deposits of the San Juan Basin (New Mexico, USA) document this transition in remarkable detail, particularly the early Palaeogene radiation of mammals. A new geochronology of the basin based on radioisotopic dates and magnetostratigraphy indicates that diverse dinosaur communities persisted into the last 300,000 years of the Cretaceous and the first highly diverse mammalian faunas



(Puercan 2 biozone) were established within 350,000 years of the extinction, the result of extremely high rates of evolution. Analysis of over 15,000 fossils, collected over the past 40 years and spanning c. 4 million years of the Puercan and Torrejonian biozones of the early Palaeogene, shows that mammal richness, originations and extinctions fluctuated dramatically over this time. Peak local diversity was achieved early in the Torrejonian, approximately 3 million years after the extinction, and high turnover rates and shifts in body size towards the end of the Torrejonian may have been related to climate or environmental perturbations, possibly including two short-term transient warming events ('hyperthermals') that were precursors to the Paleocene–Eocene Thermal Maximum.

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## Palaeoecology of an Upper Ordovician submarine cave-dwelling fauna in northern Kentucky, USA

**Caroline J. Buttler<sup>1</sup> and Mark A. Wilson<sup>2</sup>**

<sup>1</sup>*Amgueddfa Cymru – National Museum Wales, UK*

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

A bryozoan-dominated fauna that inhabited small caves underneath a carbonate hardground is here described from the Grant Lake Formation (Upper Ordovician, Katian) of Kentucky. The dominant bryozoan, *Stigmatella personata*, is found growing upwards in presumably well-lit waters on the exposed hardground surface and downwards from the ceilings in the gloomy caves. The cave-dwelling forms in some cases have longer zoecial tubes than its exposed equivalent. In both conditions the bryozoans formed mounds of multiple overgrowing colonies, sometimes showing changes in growth direction controlled by microenvironmental effects. The large colonies have multiple layers formed by self-overgrowth. The overgrowths are marked by thin layers of sediment infilling the upper zoecial chambers. We suggest that biofilms developed on patches of the colony where the zooids had died. Sediment adhered to these surfaces and the colony then grew on top. The bryozoan skeletons and the carbonate hardground are extensively bored by two forms of the cylindrical ichnogenus *Trypanites*. Both types preferentially penetrated along zoecial walls, suggesting that the bryozoan skeletons were not yet infilled with calcite cement. This fauna is one of few submarine examples known from the Palaeozoic, supporting the hypothesis that early cave-dwelling organisms were little differentiated from their exposed counterparts.

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## Mass extinctions as drivers of increased faunal cosmopolitanism on the supercontinent Pangaea

**David J. Button<sup>1</sup>, Richard J. Butler<sup>1</sup>, Graeme T. Lloyd<sup>2</sup> and Martin D. Ezcurra<sup>3</sup>**

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Mass extinctions have had a profound impact on the evolution of life, not only by reducing taxonomic diversity but also through influencing faunal distribution. In particular, they have been widely considered to drive increased biogeographic cosmopolitanism. The overlap between contemporaneous faunas can be quantified as the biogeographic connectedness, *i.e.* the density of links in a taxon-locality network. We quantify faunal cosmopolitanism for a global dataset of 891 terrestrial amniote species spanning the



Late Permian–Early Jurassic, using a novel phylogenetic modification of biogeographic connectedness that weights the links between taxa according to the phylogenetic distance between them. We apply our analysis to eight time bins and ten biogeographic areas, the latter defined using K-means clustering of palaeocoordinates. This interval is of key biogeographic importance, and includes the onset of fragmentation of the supercontinent Pangaea, the origins of many modern amniote groups, and both the end-Permian and end-Triassic mass extinctions. Results demonstrate an overall decline in cosmopolitanism through this interval, but significant increases occur after both mass extinction events, leading to relatively homogeneous global ‘disaster faunas’ dominated by groups that radiated in the immediate aftermath of the extinction events. These shared patterns suggest that mass extinctions have predictable influences on animal distribution.

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### Phylogenetic analysis implies early diversification of tetrapods in the Tournaisian

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Five new tetrapods from the Tournaisian of Scotland are sufficiently well preserved to be diagnosed and cladistically analysed. Some include anatomical information available only from micro-CT scan data. Several other new taxa are represented by an array of further specimens. Not sufficiently complete to be included in the analysis, these are nevertheless distinct and informative. The five new tetrapods represent new species and are spread across the tetrapod stem and into the crown group. They show no close relationship to each other and exhibit different combinations of plesiomorphic and derived characters. Some taxa cluster with Devonian forms, suggesting a possible relict fauna, whereas others appear more crownward, even clustering near the base of the crown group. They imply an early radiation of tetrapods during the Tournaisian, with an early Carboniferous date for the crown group split. These new forms also suggest a blurring of the Devonian–Carboniferous boundary in respect of tetrapod evolution, a feature also noted in tetrapod remains from Nova Scotia. The appearance of large forms about a million years later than the Devonian–Carboniferous boundary suggests rapid recovery from the extinction event, and that large size was achieved quickly rather than slowly as some recent studies have indicated.

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### Is a ‘one size fits all’ taphonomic model appropriate for Mazon Creek?

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The Late Carboniferous Mazon Creek Lagerstätte (Illinois, USA) is a world-renowned fossil deposit with a large diversity of both flora and fauna. Constraining a ‘one-size fits all’ taphonomic model for the Mazon Creek Lagerstätte is difficult because of our poor understanding of sideritic concretionary preservation, the large geographical area, the influences of fresh, brackish and saline waters during burial, and the subsequent complicated diagenetic processes. To determine whether Mazon Creek fossil organisms have undergone similar preservational pathways, we have compiled fossil morphological character data sets for three polychaete taxa: *Esconites zelus*, *Didontogaster cordylina* and *Astreptoscolex anasillosus*. We then used these data to test for variation in mode of preservation between taxa and between specific tissue types – suites of morphological



characters. We also compared fossil datasets to experimental decay data to constrain the impact of decay prior to fossilization. Our analysis indicates that there are variations in preservation potential of specific characters shared by polychaete taxa; modes of preservation, however, are consistent across all three taxa. This quantitative approach is being utilised as part of a larger ongoing investigation to elucidate the mode and timing of the preservation of 'complex' organisms preserved in the Mazon Creek deposit. This will lead to better understanding of taphonomic biases operating in this Lagerstätte.

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### Appendicular nature of gnathobase-like structures in Cambrian radiodontans

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The morphology and homology of limbs in the euarthropod stem lineage is vital to understanding the early evolution of this megadiverse phylum. Whether limbs additional to the paired frontal appendages are present in radiodontans (anomalocaridids) is a contentious issue. Here we document at least two pairs of gnathobase-like structures in *Amplectobelua symbrachiata*, the most abundant radiodontan in the Chengjiang biota, and in two unnamed radiodontan taxa from the same Konservat-Lagerstätte. The appendicular nature of these gnathobase-like structures is inferred from their paired presence, dentate morphology, and topological position relative to the frontal appendages and other cephalic structures. The superficial similarity between the gnathobase-like structures and the mandibles of some crustaceans and jaws of onychophorans indicates that their likely function was to tear and mince food captured by the frontal appendage. This observation reinforces the case that most radiodontans were predators. The discovery of these gnathal structures also explains the absence of isolated *Peytoia*-like oral cones in Chengjiang, compared to their abundance in the Burgess Shale. This new mouthpart morphology is in line with the great diversity of oral structures seen within Radiodonta, including a variety of oral cones or the complete absence of mouth plates (*Lyrarapax*).

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### Palaeopsychrospheric ostracods during the Late Palaeozoic–Middle Triassic: the key to surviving mass extinction events?

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The Late Palaeozoic palaeopsychrospheric ostracod fauna was established in the Early Devonian and survived the Frasnian–Famennian boundary crisis (Kellwasser Event) that wiped out 75% of ostracod species but affected mainly neritic taxa. Palaeopsychrospheric ostracods then diversified in the late Famennian and were abundant during the Early Carboniferous in deep basins throughout the Palaeo–Tethys realm, but data from younger strata are scarce. Our reconsideration of the Devonian faunas and their palaeoenvironmental settings leads us to suggest that, rather than being oxygen-deficient, deep waters were well-ventilated and provided extensive benthonic refugia during the shallow-water crises that caused mass extinction. The misconception that the formation of deep, cold water masses requires the existence of polar ice must also be corrected; the



sinking of cool surface waters can occur at temperatures  $<10^{\circ}\text{C}$  at a normal marine salinity, so the formation of sea ice is not a prerequisite, although it enhances the process. Some isolated discoveries show that the palaeopsychrospheric ostracod fauna persisted in the Late Carboniferous and during the Permian. The fact that Triassic palaeopsychrospheric faunas with Permian affinities have been described from the Anisian and Ladinian leads us to speculate that deep, cold, well-oxygenated refugia played an important role in the survival of podocopid ostracods during the end-Permian crisis when almost all palaeocopids became extinct.

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## Fossilized nuclei from the Ediacaran Weng'an Biota (Doushantuo Formation, South China)

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The interpretation of animal-embryo-like microfossils from the Ediacaran Weng'an Biota (*c.* 600 Ma) has proven contentious because they are among the oldest plausible claims of animals in the fossil record, but also because they preserve little more than simple geometric arrangements of cells. However, fossilization frequently extends beyond the cellular to preserve subcellular structures, including contentious large intracellular structures (LISs) that have been alternately interpreted as nuclei, other organelles, degraded cytoplasmic remains, or abiological structures. Our decay experiments demonstrate the feasibility of a fossil record of nuclei. Nuclei can survive decay over a period compatible with soft tissue mineralization and can be mineralized in taphonomy experiments. New tomographic data on LISs in Weng'an fossils include specimens that lack late-stage void-filling mineralization and therefore allow us to test between the competing interpretations. All the lines of evidence, including consistency in the number, shape, position, and relative size (LIS-to-cell ratio) of the LISs, as well as presence of internal structures and their occurrence within preserved cytoplasm, support their interpretation as cell nuclei. Together our findings reject the commonly expressed view that nuclei cannot be fossilized, improving the potential for interpreting the fossil record of early eukaryote evolution.

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## The Capitanian biodiversity crisis among tetrapods

**Michael O. Day**

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The Capitanian biodiversity crisis has been variously considered as one of the Phanerozoic's greatest mass extinction events, as an ecological crisis with only moderate taxonomic losses, or as simply a decline in originations. For tetrapods, the Capitanian–Wuchiapingian transition certainly involved high taxonomic turnover and, with this, the extinction of the most successful group of Guadalupian therapsids, the dinocephalians, paving the way for the Lopingian diversification of dicynodonts, gorgonopsians and therocephalians. Although these latter clades were already present within the Main Karoo Basin, many basal and/or stem genera were lost. The extinction is marked by a low diversity interval followed by the appearance of Lopingian taxa representing the early recovery. In Russia a similar series of



events is recorded, albeit with the immigration of groups originating in Gondwana after the extinction of dinocephalians. CA-TIMS U-Pb ages from syndepositional ash-fall tuffs allow the extinction peak to be constrained to just before 260 Ma, which suggests links with Emeishan volcanism. Cooling is now widely accepted in the Capitanian but there is as yet no direct evidence linking the tetrapod extinction event to any one cause. Nevertheless, the close temporal coincidence with the onset of Emeishan volcanism is compelling.

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### Preferential origin of calcitic cephalopod shell structures during calcite seas

**Kenneth De Baets and Munnecke Axel**

*Friedrich-Alexander University of Erlangen-Nuremberg, Germany*

Based on the aragonite composition of extant cephalopods and exceptionally preserved fossil cephalopods going back to the Palaeozoic, it is commonly assumed that externally shelled cephalopods had an aragonitic shell wall. Here we present evidence that at least two lineages of orthoconic nautiloids in the Silurian and Devonian calcite seas had an original biphasic mineralogy, which developed convergently with gastropods and bivalves. If we quantitatively analyse the timing of the evolutionary origin of these and other reliably dated carbonitic cephalopods structures in relationships with calcite or aragonite seas, we find support for a preferential origin of calcitic structures during calcite seas, particularly in the Palaeozoic. This further corroborates the hypothesis that seawater chemistry at the time a particular mineralized structure was first acquired within a lineage was particularly crucial for its mineralogy – even in pelagic organisms like cephalopods. These finds also highlight the need to verify the shell composition of exceptionally-preserved cephalopods more comprehensively – even at sites where aragonite has typically been dissolved or replaced.

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### Reconstructing anomalocaridid feeding appendage dexterity sheds light on radiodontan ecology

**Giacinto De Vivo, Stephan Lautenschlager and Jakob Vinther**

*University of Bristol, UK*

Anomalocaridids were one of the most successful animal groups in the Early Palaeozoic. They are particularly renowned for their pair of large feeding appendages used to capture and detain prey. Since the early stages of their evolution, anomalocaridids have evolved different feeding appendage morphologies, indicating an adaptive radiation into distinct niches early in their history. Here, to test different likely anomalocaridid feeding modes, their appendages have been reconstructed in 3-D and their range of movement explored. Our results indicate that *Anomalocaris canadensis* was able to catch small, agile prey, while *Hurdia victoria* and *Peytoia nathorsti* preyed upon relatively larger benthic animals. *Anomalocaris briggsi* from the Emu Bay Shale is here recognized as a filter feeder similar to *Tamisiocaris borealis*. The appendages of the Early Ordovician anomalocaridid *Aegirocassis benmoulai* show higher dexterity than previously thought, which allowed them to create a basket-like or fan-like structure. The inferred anomalocaridid prey size corresponds to the diameter of the mouth, suggesting that the prey was ingested whole. This indicates that the oral opening was able to dilate, probably by mouth eversion and expansion of the oral cavity, offering new clues to feeding mechanics in stem arthropods.





## Contributions to the ongoing work on the international chronostratigraphy of the Cambrian: preliminary data from the Terreneuvian of Iran and Series 2 of Mexico

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After several decades of intense research, the topic of the Cambrian explosion has fed an abundant literature focusing on its biodiversity and phylogenetic patterns. Our understanding of this is, however, limited by the lack of accurate dating of the fossil radiation and abiotic changes. Although efforts have been made to develop a refined timescale, the Cambrian remains one of the last systems for which series and stage boundaries have not yet been accurately defined. This can be ascribed in part to the paucity of comprehensive litho-, bio-, and chemostratigraphic studies of early-mid Cambrian successions from key regions, such as Sonora (Mexico) and Iran. Data from Sonora are essential for establishing the still incomplete although fundamental Cambrian chronostratigraphy of Laurentia, whereas Iranian Cambrian successions represent the best opportunity for correlations between the western Gondwana margin and the Yangtze Platform in South China. This study presents preliminary stratigraphic data from Sonora and Iran. Special attention has been given to the range of the abundant and widely-distributed polyphyletic small shelly fossils (SSFs) due to their high potential for the subdivision of the early Cambrian.

## Freshly-moulted trilobites from the Fezouata Lagerstätte of Morocco

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Trilobites, as arthropods, must periodically moult their protective hardened exoskeleton for growth, development, and repair. This complex process involves disassociating the epidermis and internal systems from the exoskeletal cuticle, secretion of new cuticle, and ecdysis of the old exoskeleton. Immediately post-moulting the new exoskeleton is soft and compressed (*i.e.*, the 'soft-shell stage'). This stage must necessarily be short-lived, as the individual is extremely vulnerable to predation at this time. The brevity of the stage is reflected in the paucity of soft-shelled specimens in the fossil record, accentuated by their reduced preservation potential. The few soft-shell post-moult trilobites described to date were identified based on the co-occurrence of wrinkling and flattening (indicating compressed, soft cuticle). However, preservational or tectonic deformation may also be responsible, and therefore freshly-moulted trilobites must be considered in context. We describe a rare example of soft-shell trilobite preservation from the exceptional Burgess Shale-type Lower Ordovician Fezouata Lagerstätte of Morocco. Nileid specimens illustrate



the complete moult sequence, with a putative moulted exoskeleton, several fully-hardened carcasses, and specimens showing varying degrees of the soft-shell stage. The latter show a progression in exoskeletal hardening by decreasing longitudinal wrinkling and flattening. Comparison with co-occurring arthropods excludes preservational bias. This assemblage likely represents the first described preserved-in-the-act trilobite mass moult.

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### The Chronicles of *Charnia*: developmental biology and phylogenetic inference from an Ediacaran rangeomorph

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The late Ediacaran Period (580–541 Ma) witnessed the emergence of the first complex, macroscopic organisms – the Ediacaran macrobiota – which are commonly considered to include antecedents to modern animal groups. Definitive evidence tying these organisms to the Metazoa, however, has not been convincingly demonstrated, and consequently multiple non-metazoan hypotheses of affinity have been proposed for the biota. We have investigated growth and development in an attempt to identify constraints on the phylogenetic affinity of the iconic Ediacaran macro-organism *Charnia masoni*. Previous work has considered ontogeny in *Charnia* to be irreconcilable with its most morphologically similar metazoan clade, the Pennatulacea. Our analysis of *Charnia masoni* reveals hitherto unrecorded ontogenetic characters, including a second polar growth zone, indicating that it was a bipolar organism and challenging phylogenetic interpretations that assume *Charnia* was unipolar. This and other new characters allow us to refute close phylogenetic relationships to several non-metazoan groups which do not grow in this way, and, crucially, reconcile *Charnia* as a member of total-group Metazoa. As such, the rangeomorphs inform debate surrounding the establishment of animal body plans, specifically the evolution of the principal body axes and the making and breaking of axial symmetries in Metazoa.

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### Modelling enrolment mechanisms in Ordovician trilobites

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Enrolment represents one of the most iconic behaviours described in the fossil record. Cambrian trilobites displayed very simple enrolment type and most of them simply flexed the second half of the trunk in order to cover the ventral side of the head and the anterior part of the trunk. Enrolment in trilobites was a behaviour that required high complexity, coordination and synchronization among different trunk tergites. Middle and Late Cambrian trilobites developed new ways to enrol, but Ordovician trilobites were the first to develop novel structures to close their body in a more efficient way. However, despite the complexity of enrolment some Ordovician trilobites had similar body patterns. For instance, *Neseuretus* and *Placoparia* display an ‘unrolled spiral’ and ‘inverted spiral’



respectively, but both genera had a very similar body pattern. The outstanding preservation of some Ordovician trilobites from Spain allows precise 3D reconstructions using a structured light scanner. These scanners form the basis of computer models of enrolment. These models shed light on the functional morphology and kinetics of this behaviour, with implications for the evolutionary history of different enrolment type causes that forced the trilobites to develop different ways to close the body.

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## Burgess Shale-type fossil in the Middle Ordovician of the Barrandian area (Czech Republic)

**Oldřich Fatka**

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Re-examination of the putative green alga *Krejiella putzkeri* Obrhel, 1968 shows no morphological difference from *Margaretia dorus* Walcott 1931, a fossil recently interpreted as an organic tube produced and inhabited by the enteropneust worm *Oesia disjuncta* Walcott, 1911. *Margaretia*, originally described from the mid-Cambrian Burgess Shale, has been reported from several Early to mid-Cambrian Lagerstätten in Laurentia (e.g. Latham, Kinzers, Marjum, USA), Siberia (as *Aldanophyton* in the Sinsk Lagerstätte, Russia), and East Gondwana (Guashan Lagerstätte, China). Geographic distribution of *Margaretia* indicates a possible latitudinal control, as all occurrences are obviously restricted to tropical to subtropical belts. The herein reported occurrence of *Krejiella* in the Barrandian area extends the record of organic tubes supposedly produced by enteropneusts to the Middle Ordovician cold-water areas of West Gondwana. *Krejiella* represents the first Burgess Shale-type fossil in the Middle Ordovician of the Barrandian area.

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## Diets of giants: the nutritional value of herbivorous dinosaur diet during the Mesozoic

**Fiona L. Gill<sup>1</sup>, Juergen Hummel<sup>2</sup>, A. Reza Sharifi<sup>2</sup>, Alexandra P. Lee<sup>3</sup> and Barry H. Lomax<sup>3</sup>**

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A major uncertainty in estimating energy budgets and population densities of extinct animals is the carrying capacity of their ecosystems, constrained by net primary productivity (NPP) and digestible energy content of that NPP. The hypothesis that increases in NPP of land plants due to elevated atmospheric CO<sub>2</sub> contributed to the unparalleled size of the sauropods, the largest ever land animals, has recently been rejected based on modern studies on herbivorous insects. However, the nutritional value of plants grown under elevated CO<sub>2</sub> levels might be very different for vertebrate megaherbivores with more complex digestive systems and different protein:energy requirements than insects. Here we show that the metabolisable energy value of five species of potential dinosaur food plants does not decline consistently with increasing CO<sub>2</sub> growth concentrations, with maxima observed at 1,200 ppm CO<sub>2</sub>. Our data potentially rebut the hypothesis that CO<sub>2</sub> levels were constraints on herbivore diet quality in the Mesozoic.



## The early aquatic angiosperm *Montsechia* from the Barremian of Spain

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*Montsechia vidalii* (Zeiller) Teixeira has been reported in several localities from the Barremian of Spain. The vegetative parts are of two types: one has relatively long, opposite-decussate leaves, and the second has tiny, spirally-arranged leaves. The two types are never connected and are without roots. Besides being more frequent in the second, both types bear pairs of fruits at the top of leafed stems. Fruits are closed, even when found dispersed on rock slabs, except for a tiny rounded hole at the tip, and contain a single orthotropous pendant seed. Palaeontological and sedimentological evidence suggest that it grew in freshwater lakes or ponds. Its closest phylogenetically affinity is with *Ceratophyllum*. Together with its palaeoecology, *Montsechia* is the youngest early aquatic angiosperm known so far. Plant fossils, such as *Archaeofructus* and *Montsechia*, open the possibility that aquatic plants were locally common at a very early stage of angiosperm evolution and that aquatic habitats may have played a major role in the diversification of some early angiosperm lineages.

## Synchrotron X-ray spectroscopy reveals burial conditions and fossilization in a Cretaceous freshwater Lagerstätte

**Pierre Gueriau**

CNRS USR 3461 and SOLEIL Synchrotron, France

The Cenomanian (~95 Ma) Djebel-Oum-Tkout Lagerstätte comprises a unique freshwater fauna of molluscs, insects, crustaceans and fish. The fossils exhibit finely mineralized soft-tissues and are found in association with microbial mats, suggesting microbially induced phosphatization. Synchrotron micro-X-ray spectroscopy techniques have provided unexpected information regarding the chemistry of the burial environment, allowing the precise reconstruction of a taphonomic scenario in agreement with recent decay experiments. X-ray fluorescence provides semi-quantitative concentrations of rare earth elements, and therefore an indirect assessment of the redox conditions through the 'cerium anomaly', X-ray absorption allows direct access to the oxidation state of the redox-sensitive Ce and Fe, and X-ray diffraction allows us to identify the minerals that compose the fossils. While anaerobic conditions were previously shown to rapidly establish in decaying carcasses, our analyses reveal the presence of oxidized Ce(III) and Fe(III), pointing to slightly oxidative burial conditions at Djebel-Oum-Tkout. Instead of an anaerobic, reducing environment, an oxidizing microenvironment attributed to microbial activity was formed inside the carcasses. This is consistent with recent decay experiments that showed that the microenvironments generated by microbial mats turn oxic after initial anaerobic conditions. Non-invasive synchrotron X-ray spectroscopy shows great promise for characterizing burial conditions in different fossilization contexts.



## Feeding in chelicerate arthropods – diverse and far from ‘primitive’

**Carolyn Haug**

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Euarthropods include two main modern lineages. On the one side are insects, myriapods and other crustaceans, such as shrimps, crabs and their smaller relatives. On the other side are chelicerates, including spiders, scorpions, mites and such like. Chelicerates are often considered to be the ‘primitive’ part of the family tree. It has even been suggested that they somehow failed to evolve proper mouthparts. I will present examples of different fossil representatives of chelicerates and reconstruct the evolution of the feeding apparatus within chelicerates. This reconstruction demonstrates that feeding mechanisms within chelicerates are, in fact, highly diverse and strongly derived from the euarthropod condition. Feeding in chelicerates can therefore in no way be considered ‘primitive’. Instead, the entire body of chelicerates has become highly modified in conjunction with changes of the feeding apparatus. Crustaceans and their relatives on the other hand have retained numerous ancestral (plesiomorphic) traits that have been lost in chelicerates. Hence, chelicerates are a prime example of the restrictions of typological thinking. Only with detailed studies of morphology interpreted in an evolutionary phylogenetic framework can we overcome simplified views on character transformation and avoid unscientific labels such as ‘primitive’.

## Why we are looking at the wrong phase of life – palaeontology beyond the adult paradigm

**Joachim T. Haug**

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It has been recognized in recent years that modern biology is adult-centred. This is even more relevant to palaeontology. Taxonomy, systematics, but also ecological interpretation is largely based on adults. The presence of an adult at a specific time slice is therefore immediately translated into the presence of a specific larva. I will present examples that demonstrate why the general adult-centered view is more than a simple misunderstanding; it represents a significant oversimplification that causes severe artefacts in any kind of reconstructions of the past. Most simply, the modern biosphere is dominated by non-adults concerning both number of individuals and biomass. Modern seas are full of planktic larval forms of which only very few individuals will survive long enough to become adult. Terrestrial ecosystems are dominated by insects, which live for many moults, of which only the final one is the adult. Many insect larvae persist for months or years, while the adults live for only a few weeks or as little as a single day. I discuss how modern palaeontology can overcome the adult paradigm and recognize fossil species as once-living organisms. This includes accepting the fact that the immature is the normal condition while being adult is something special.



## Can phosphatic microfossils constrain Cambrian climates?

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Exceptional fossil discoveries have thrown considerable light on the biological changes throughout the Cambrian metazoan radiation. However, quantitative constraints are needed to understand possible environmental causes and consequences of this dramatic radiation. There is a particular dearth of sea temperature data, which are important for constraining oceanographic and palaeoenvironmental reconstructions. We aim to begin quantifying Cambrian sea temperatures by combining the long-established stable oxygen isotope ( $\delta^{18}\text{O}$ ) palaeothermometer with novel taxa. We examined phosphatic small shelly fossils (SSFs) from the Lower Comley Limestone (Cambrian Stage 4/5, Shropshire, UK), deposited in shallow seas approximately 60°S. To minimize the influence of ecology on preserved environmental signals only taxa with well-constrained benthic lifestyles and/or modern analogues were selected, including *Rhombocorniculum*, *Torellella* and various linguliformean brachiopods. By subjecting selected specimens to a rigorous assessment of preservation using optical and scanning electron microscopy along with *in situ* chemical analyses, we found both biogenic and diagenetic microstructures and chemistries, and could distinguish a subset of well-preserved SSFs. Preliminary  $\delta^{18}\text{O}$  data provide plausible temperatures that support geological evidence for warm Cambrian climates. Carefully selected well-preserved SSFs could help fill the 50-million-year absence of quantitative palaeoenvironmental constraints in the earliest Phanerozoic Eon.

## Macroevolution of Mesozoic lepidosaurs

**\*Jorge A. Herrera Flores, Michael J. Benton and Thomas L. Stubbs**

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Lepidosauria is a group of reptiles that originated in the Early or Middle Triassic, and this group is currently divided into two orders, the Squamata and the Rhynchocephalia. Extant squamates (lizards, snakes and amphisbaenians) are well known for their high diversity that today reaches over 9,000 species, but in contrast rhynchocephalians are only represented by a single living species, the tuatara from New Zealand. Nevertheless, the fossil record shows that in the Mesozoic these relative proportions were quite different. We used geometric morphometrics in order to explore changes in morphospaces and possible evidence of competition of both orders through the Mesozoic by using a database of 2D images of lower jaws from 93 genera. Our results show that Jurassic rhynchocephalians occupied a wide morphospace while squamates formed a tight cluster. On the other hand, Cretaceous rhynchocephalians showed a considerable decrease in morphospace, while squamates had a huge expansion that overlaps most of the rhynchocephalian morphospace. Our work provides some quantifiable evidence to support the suggestion that the radiation of Cretaceous squamates was the possible cause of the decline of rhynchocephalians in the late Mesozoic.



## The diversification of early Asterozoa: resolving a palaeontological quandary

**Aaron W. Hunter**

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Our understanding of the evolution of the earliest asterozoan echinoderms has until recently been hampered by a lack of well-preserved taxa and uncertainty of the homology between the four major groups. Although the nature of the sudden appearance of primitive Asterozoa in the Ordovician remains a mystery, our understanding of their diversification has now advanced considerably in light of new discoveries from exceptionally preserved specimens from the Early Ordovician of Morocco and France, significantly increasing the scope of morphological data available for study. Exceptionally preserved 'bat-stars' from the late Tremadocian Fezouata Shale, Anti-Atlas Morocco, one of the oldest discovered asterozoan assemblages, represent at least three distinct somasteroid morphotypes. These inhabit a diverse community containing elements of Cambrian and Ordovician faunas. We have found that these communities, along with those of comparable age taxa of Australia (Tasmania) and North America (Utah), were dominated by primitive somasteroids and stenuroids, with other more derived asterozoan taxa being absent. The late Tremadocian of France (Montagne Noire), however, preserves the oldest recorded proto-ophiurids and asteroids as a minor component of this 'somasteroid-world', and by the Floian, proto-ophiurids and somasteroids are seen to have been replaced by 'true' archaic ophiurids, which persisted to the mid-Permian.

## Prospects and limitations of ecological studies of a fossil reef community (Aferdou el Mrakib, Middle Devonian, Morocco) based on fore-reef talus

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Many fossil reef communities are preserved mainly in the form of fore-reef debris deposits, with the actual reefs either not preserved at all, or affected by advanced diagenesis. This is the case for Aferdou el Mrakib (Givetian, eastern Anti-Atlas, Morocco), the largest Devonian reef of northwestern Gondwana. The core of the reef has been pervasively dolomitized, and few portions of well-preserved reef facies can be observed. The best preserved fossils are found in the talus strata and include large, platy to massive colonies of rugose and tabulate corals, domical stromatoporoids, and numerous smaller tabulates, solitary rugosans, brachiopods, amphiporids, crinoids and some algae-derived structures. Reef-derived components mix with autochthonous, off-reef fauna, composed of solitary rugosans, some branching tabulates, and brachiopods. In addition, the off-reef debris succession contains locally large blocks of the original reefal material, most likely transported by means of debris flow-type mass flows initiated by storm- or seismic-related events. The palaeontological and sedimentological data combine to give a picture of a rich, diverse palaeoecosystem that at least at some stage reached very shallow depths, challenging previous interpretations of the reef as situated below the range of the euphotic zone.



## Looking snappy: quantifying convergence in cranial morphology between phytosaurs and crocodylomorphs

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Phytosaurs were a widespread group of carnivorous archosauriform reptiles in Late Triassic ecosystems (c. 230–201 Ma), with their abundant remains demonstrating a cosmopolitan global range and ecological importance. Functional similarities between phytosaurs and crocodylomorphs have been proposed qualitatively on the basis of gross morphological similarities between the two clades, but this convergence has not yet been quantified. Here we present results from comparative shape analyses using geometric morphometrics to tease apart and quantify subtle variation in the many known phytosaur and crocodylomorph skull morphologies to aid further functional investigation. These analyses explore dorsal and lateral variation in a broad range of morphologies representative of Phytosauria and Crocodylomorpha. We use a combination of semilandmark curves and traditional landmarks to allow the accurate digitization of evolutionarily convergent features which lack directly homologous points. Results indicate that phytosaurs do overlap with crocodylomorphs in morphospace, though only with a small subset of total crocodylomorph diversity. When compared only with longirostrine crocodylomorphs, more nuanced skull variation sets phytosaurs apart from most crocodylomorphs. This variation, mainly pertaining to the supratemporal fenestra, may suggest differences in biting capability and feeding biomechanics.

## Early Cambrian ostracoderms and the trials and tribulations of total evidence dating

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The origin of jawed vertebrates is a formative episode in evolutionary history. Key to understanding this important interval are the armoured jawless ‘ostracoderms’, the relationships among which have previously been considered either in terms of clade intrarelations, or interrelations among clade exemplars. Thus, the monophyly of the putative ostracoderm plesions have yet to be adequately tested, principally because of computational limitations surmounted in the last decade. We constructed a supermatrix of 560 characters and 240 taxa, which we analysed using the MK likelihood model. The ensuing trees were compared using Bayes factors. Our results support the majority of ostracoderm clades, but resolve galeaspids and heterostracans as paraphyletic grades of stem-gnathostomes, and stem-vertebrates, respectively. Finally, we considered the role of time in topology estimation, using the fossilized birth-death model (FBD). This approach resolved heterostracans, thelodonts and anaspids as a single clade, while suggesting that ostracoderms evolved in the earliest Cambrian. This result conflicts strongly with the fossil record, suggesting that the FBD method may incorrectly estimate divergences of extinct taxa. Taken together, these results suggest that the consensus of early vertebrate relations, underpinned by the last 40 years of cladistics, does not stand up to deeper scrutiny afforded by likelihood-based phylogenetics.





## The palaeobiology of Ediacaran rangeomorphs: reproduction, environmental sensitivity and ecological succession

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The Earth has supported life for most of its 4.5-billion-year history, but the first macroscopic organisms appeared only in the Ediacaran (c. 600 Ma). Many aspects of their biology and ecology remain a mystery. Late Ediacaran fossil assemblages of Avalonia (Charnwood Forest, UK and Newfoundland, Canada) are among the oldest evidence for complex macroscopic life, and are dominated by rangeomorphs (a group characterised by 'fractal' branching). We resolve key aspects of rangeomorph palaeoecology by combining detailed petrographic analysis with multivariate statistical techniques. We demonstrate that higher taxonomic diversity is correlated with low–intermediate physical disturbance and that upright taxa (e.g. *Charnia*) and flat-lying forms (e.g. *Fractofusus*) preferentially occur on surfaces with high and low sediment input, respectively. The population demographics of several taxa show multimodality, caused by culling part of an incumbent population and by non-continuous/pulsed reproduction. Disturbance demonstrably influenced community succession: early-colonising taxa dominated horizons with low levels of disturbance, while those able to survive disturbance events dominated horizons with higher levels of disturbance, and also post-disturbance recovery populations. Based on the life history traits and environmental preferences identified for different rangeomorphs, we propose a model of ecological succession for Avalonian rangeomorph communities.

## Arms race or feeding competition? The mid-Palaeozoic origins of cephalopod and vertebrate jaws

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The oldest known cephalopod feeding structures are documented by radulae from the Ordovician, questionable opercula from the Silurian, and Late Devonian ammonoid mandibles. Based on new discoveries of latest Devonian buccal apparatuses in three different ammonoid clades, we revise the origin of mandibles in ammonoids. Their presence in four major clades argues for chitinous mandibles as a plesiomorphic character for the Ammonoidea. This hypothesis finds support in early Carboniferous Coleoidea with homologous mandibles. Accordingly, we further hypothesize the presence of mandibles in the last common ancestor of coleoids, ammonoids and recent nautilids, *i.e.* in some orthocerids, likely in the Silurian. Jawed vertebrates may have evolved as early as the late Ordovician, but certainly in the early Silurian with an initial diversification in the late Silurian, which intensified in the Devonian. The phylogenetic evidence for pre-Devonian cephalopod mandibles and synchronous diversification of jawed vertebrates in the Siluro–Devonian might have been linked ecologically. The increasing abundance of defensive structures in invertebrates may have caused a positive selection for reinforced mouthparts of invertebrate and vertebrate predators during that time.



## On the agglutinated nature of Ediacaran palaeopascichnids from northern Siberia

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The Khatyspyt Formation of the Khorbusuonka Group of northern Siberia contains one of the most fascinating Ediacaran fossils. The unique mode of fossil preservation in carbonate rocks allows us to discover new morphological features, palaeoecology and environments of preservation of problematic Ediacara-like biota. This study focuses on the problematic group Palaeopascichnida. Abundant palaeontological material from the Khatyspyt Formation gives us the opportunity to study these fossils in the finest detail and test hypotheses about the origin of Ediacaran organisms. Detailed morphological observations, conducted on thin sections with the help of both petrographic and scanning electron microscopes, revealed evidence of possible wall agglutination around the globular chambers of Palaeopascichnida. Thus, we can consider the Palaeopascichnida group as one of the oldest known macroorganisms with an agglutinated skeleton. The presence of an agglutinated skeleton places emphasis on these organisms and encourages the re-examination of other palaeopascichnid-like fossils, as well as the stratigraphic correlation of Ediacaran sequences; it also contributes to our improved understanding of the evolution and survival of the Ediacaran biota in the aftermath of the Kotlinian Crisis.

## Ecological fitting within sheet-forming skeletal metazoans and the Ordovician rise of reef ecosystems

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Sheet-forming skeletal, colonial metazoans, such as bryozoans, tabulate corals, and stromatoporoid sponges, diversified simultaneously during the Early–Middle Ordovician period and became globally the dominant Ordovician reef-builders. Based on studies from reefs of the Middle Ordovician Chazy and Mingan formations (USA and Canada), and of the Late Ordovician Vasalemma and Ärina formations (Estonia), we demonstrate that sheet-forming skeletal, colonial metazoans formed a specific type of cluster–frame reefs with a micrite-rich matrix. The accretion mechanism of these reefs is reconstructed as a combination of metazoan biomineralization and microbially-mediated organomineralization. The diversification of sheet-forming skeletal, colonial metazoans clearly lagged behind the first appearance of their respective skeletal ancestors and can be best interpreted as an ecological shift or habitat expansion of encrusters from cryptic and/or very shallow marine hard substrates onto soft-substrate and toward microbial-metazoan consortia. Their habitat expansion can be exemplified as a case of simultaneous ecological fitting, *i.e.*, the independently evolved shared traits of encrusting metazoans simultaneously were co-opted and became advantageous under globally different environmental conditions.



## Comparison of the postembryonic development in the family Paradoxididae (Trilobita)

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We reinvestigate early postembryonic stages of the Cambrian paradoxidid trilobites *Paradoxides gracilis*, *Acadoparadoxides pinus*, *Eccaparadoxides pusillus*, *E. pradoanus*, and *Hydrocephalus carens*. The protaspis and early meraspis stages of these taxa show considerable variability in morphology and dimensions. In *Paradoxides* and *Acadoparadoxides* these stages have a rather narrow glabella with quite distinct medial and lateral furrows. In *Eccaparadoxides* they share sub-elliptical glabellae with the medial furrow, and in the case of *E. pusillus* also with the lateral furrows. Early postembryonic stages of *Hydrocephalus* are characterised by a large sub-circular and effaced glabella. The earliest known stages of *Acadoparadoxides*, *Paradoxides* and *Eccaparadoxides* are around 0.9 mm long, while the earliest stages of *Hydrocephalus* reach almost 2 mm. The late meraspis development of all of these taxa includes a change in the glabellar morphology, disappearance of intergenal spines, shortening of the preglabellar field, and successive degeneration of thoracic macrospines. The variability of size, morphology and other developmental trends suggest that the earliest postembryonic stages of different taxa within Paradoxididae were influenced by different selection pressures.

## The Weeks Formation Fauna (Utah, USA) and the evolution of marine animal communities during the late Cambrian

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Exceptionally preserved fossil assemblages have proved critical to our understanding of the Cambrian explosion. Thanks to recently discovered Konservat-Lagerstätten, similarly detailed data on Ordovician marine animal communities are increasingly available. By contrast, the late Cambrian fossil record of 'soft'-bodied metazoans remains particularly scarce, with only a single diverse macroscopic fauna of that kind: the late Guzhangian Weeks Formation. Recent field investigations have greatly improved our understanding of this remarkable fauna and the environment it inhabited. Microfacies analyses revealed that intervals with exceptional preservation were deposited in a quiet, oxygen-depleted environment on a distal carbonate ramp below storm-wave base, a setting much like that of most Cambrian Lagerstätten. The biota comprises c. 80 species, belonging to nine phyla, and is dominated by arthropods, sponges and brachiopods, which is similar to older exceptionally preserved faunas. Analysis of the intra-phylum composition reveals a more complex picture. Cnidarians, hyolithids, priapulids or sponges are all represented by



taxa known from older strata. Some arthropods are also more typical of Early–Middle Cambrian times. However, other components of the fauna (*e.g.* aglaspidids, solutes), including newcomers of uncertain affinities, suggest the onset of a restructuring of marine animal communities in the early late Cambrian.

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## Phylogenetic diversity as a palaeobiodiversity metric: new evidence for a Cretaceous decline in Mesozoic dinosaurs

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Phylogenetic diversity (PD) – the sum of the branch lengths of the subtree connecting a set of taxa – is a common biodiversity metric for extant taxa, but has not been used to explore temporal changes due to the lack of sufficiently large phylogenetic hypotheses. Here we explore how PD changes over deep time using a set of simple birth–death models (BDMs) and an empirical case study: a meta-analytically derived and probabilistically time-scaled set of phylogenetic hypotheses for 960 taxa of Mesozoic dinosaur. We show that under all of our BDMs PD will continually increase over time. For most models this follows an exponential curve, although for a diversity-dependent model (carrying capacity of 50 species) a clear inflection point is seen. Empirical curves for Dinosauria and the three major subclades (Ornithischia, Sauropodomorpha, Theropoda) show much greater variation, and a general pattern of a rise to a mid-Cretaceous peak followed by a decline towards the K-Pg boundary. However, subsampling suggests this decline is largely artefactual, except in the case of the Ornithischia. Overall, PD captures aspects of diversity that richness cannot, including the selectivity of extinction, which is most apparent in the removal of ‘prosauropods’ and the subsequent re-rooting of the sauropodomorph tree.

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## Environmental partitioning and differential growth in species of the thyreophoran dinosaur *Stegosaurus* in the Upper Jurassic Morrison Formation, USA

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Two species of *Stegosaurus* are considered valid: *Stegosaurus stenops*, from Colorado, Utah and Wyoming, and *Stegosaurus mjosi*, known only from Wyoming. In 2015, a small specimen of *Stegosaurus mjosi* was excavated near Livingston, Montana. Histological examination suggests that the animal was still growing at time of death. Individuals of *Stegosaurus stenops* of a similar level of osteological maturity are larger in size, and small stature appears to be a feature common to *Stegosaurus mjosi*. The distribution of all individuals of *Stegosaurus* contemporaneous with the Livingston specimen was examined.



The ranges of *Stegosaurus mjosi* and *Stegosaurus stenops* did not overlap during the time interval in which the Livingston specimen is found. *Stegosaurus stenops* occupied the southern part of the Morrison basin, while *Stegosaurus mjosi* occupied the northern part. The southern part of the basin was more arid than the northern part, and thus segregation of the two species may have been environmental. Large body size has been suggested as an adaptation to aridity among living megaherbivores, and it is possible that the larger size displayed by *Stegosaurus stenops* may have been an adaptation to prevailing conditions in the south of the Morrison basin.

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## Exploring the morphological diversity and hydrodynamic performance of extinct jawless vertebrates

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Most extinct jawless vertebrates are characterised by the presence of a heavy cephalic shield, which has traditionally been related with poor swimming capabilities and a bottom-dwelling lifestyle. However, the huge morphological diversity of the cephalic shields suggests that these groups could be more ecologically diverse than previously thought. Interestingly, galeaspid and osteostracans show a similar range of forms, which were acquired independently in each lineage in different geographical regions. Thus, the study of such taxa provides a great opportunity to analyse whether this morphological convergence was the result of equivalent functional adaptations to similar aquatic environments. With this aim, we have created a morphospace for 70 species of galeaspid and osteostracans using geometric morphometrics and tested the hydrodynamic performance of the most extreme forms using computational fluid dynamics. Our results show that both groups occupy broadly the same areas of morphospace. In addition, comparison of their hydrodynamic performance (*i.e.* drag and lift forces and their coefficients) allowed us to better understand variations in morphology in terms of swimming strategies and modes of life. This opens up a new opportunity to investigate the ecology of these groups of early vertebrates.

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## Critically accessing the depositional setting of the Ediacaran Mistaken Point Biota

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The Mistaken Point Ecological Reserve, Newfoundland, contains some of the oldest known examples of the enigmatic Ediacaran macrobiota. The fossil assemblages, preserved on more than 100 bedding planes, provide some of the earliest evidence for both complex macroscopic eukaryotes and metazoan-style locomotion. Several depositional settings have been proposed for the strata of the Mistaken Point Formation in which many fossil taxa are found, including deep-marine and terrestrial environments. These interpretations have been



used to argue against photosynthetic biological affinities, and in favour of a lichen-affinity for the biota, respectively. In this study, detailed sedimentological analysis of the Mistaken Point Formation demonstrates that the Ediacaran organisms lived and died in subaqueous, most likely deep-marine, environments. Furthermore, the use of several geochemical proxies as indicators of palaeoenvironment is questioned. These findings categorically refute a terrestrial depositional environment for this unit, and enable constraint of the possible phylogenetic affinities for organisms in the Mistaken Point assemblages, specifically refuting the possibility that these organisms could have been lichens.

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### Variable preservation of fruit flies in *Pinus* and *Wollemia* resin

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Fossilization in amber is highly variable, ranging from exceptional examples including minute details and internal soft tissues to empty moulds. Resin (the modern precursor to amber) chemistry is also highly variable, leading to the hypothesis that these variations may contribute to different preservation in the amber inclusions. Here we use actualistic taphonomic experiments to compare decay and preservation in two different modern resins. Fruit flies (*Drosophila melanogaster*) were embedded in modern resin from either a Scots pine (*Pinus sylvestris*) or a Wollemi pine (*Wollemia nobilis*), left to decay for six months, and then external and internal morphological decay were assessed through propagation phase-contrast synchrotron microtomography. The volatile and semi-volatile components of each resin were assessed using gas chromatography. Synchrotron tomographic analysis revealed that the flies entombed in *Wollemia* resin were well-preserved, and still had most of their internal soft tissues, and external cuticle. The flies entombed in *Pinus* resin, in contrast, had very little preserved internal soft tissue and poorly preserved external cuticle which had been breached by the resin in many places. The differential preservation may be due to the different chemical composition of the two resins.

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### Ultrastructure and chemistry of integumentary structures in an ornithischian dinosaur

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Research into the evolutionary origins of feathers has been stimulated over the last twenty years by discoveries of feather-like structures in non-avian theropod dinosaurs from the Middle Jurassic to Early Cretaceous of China. Despite such intensive research, many aspects of feather evolution remain poorly understood, including the nature and significance of filamentous integumentary structures and aberrant feather types. Previous studies of



these tissues have lacked insights from tissue ultrastructure and chemistry. Here we report the preservation of diagnostic tissue structures and evidence of original biochemistry in diverse integumentary structures in the neornithischian dinosaur *Kulindadromeus zabaikalicu*, a basal neornithischian dinosaur from the Jurassic of Siberia. We analysed diverse integumentary structures, including scales, monofilaments, and compound feather-like structures, using scanning- and transmission electron microscopy, time-of-flight secondary ion mass spectrometry, and synchrotron X-ray absorption spectroscopy. The results reveal the widespread preservation of tissue ultrastructure, including keratinous tissue layers and melanosomes, in feathers and scales. Different tissue types can be discriminated on the basis of the geometry and trace element and sulfur speciation chemistry of melanosomes. Our data provide a new mechanism to determine the nature of evolutionarily important tissue types in feathered dinosaurs and will help constrain scenarios for the evolution of feathers.

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### Identifying patterns and drivers of coral diversity in the Central Indo-Pacific marine biodiversity hotspot

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Biodiversity hotspots are recognized as areas of high taxonomic and functional diversity. These hotspots are dynamic and shift geographically over time in response to environmental change. To identify drivers of the origin, evolution, and persistence of diversity hotspots, we investigated the diversity patterns of scleractinians in the Central Indo-Pacific, a marine biodiversity hotspot for the last 25 million years. We used the scleractinian fossil record (based on literature and a new fossil collection) to examine the taxonomic and functional diversity of corals from the Eocene–Pliocene, which we correlated with known environmental changes. Increases in taxonomic diversity, high origination rates, and changes in abundance of functional character states indicate that the origin of the Central Indo-Pacific hotspot occurred during the Oligocene, initially through proliferation of pre-existing taxa and then by origination of new taxa. In contrast to taxonomic diversity, overall functional diversity of Central Indo-Pacific scleractinians remained constant from the Eocene–Pliocene. Global sea level was identified as a main driver of diversity increase that, together with local tectonics, regulates availability of suitable habitats. Moreover, our results show that the marine biodiversity hotspot developed from both the accumulation of taxa from older biodiversity hotspots and the origination of new taxa.

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### Testing niche versus neutral models of Ediacaran community assembly

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Spatial analysis of *in situ* Ediacaran macrofossils can reveal key insights into the ecological dynamics of these early communities. The full potential of this approach, however, has been limited by the slow acquisition rate of large quantities of accurate data, and a focus on



only a small number of bedding surfaces. Using a high-resolution tripod-mounted laser line probe, we have overcome these logistical issues, and comprehensively mapped six of the most diverse and abundant Avalonian communities to a resolution of 50  $\mu\text{m}$ . These include the Mistaken Point 'E' Surface, Spaniard's Bay and two previously undocumented surfaces from Newfoundland, Canada, and the North Quarry and Memorial Craggs surfaces in Charnwood Forest, UK. For each community, we analysed taxa spatial distributions using pair correlation functions (PCF) and have compared the patterns with different models of known biological and habitat interactions. Preliminary analyses suggest that Avalonian communities were predominately dominated by dispersal, with only weak habitat interactions. This result stands in stark contrast to modern sessile communities where habitat or 'niche' processes dominate over dispersal or 'neutral' models of community assembly. Rapid data acquisition enables the comparison of inter-regional ecological dynamics, enabling the broader ecological patterns of the Ediacaran–Cambrian transition to be uncovered.

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### A new Burgess Shale polychaete from Marble Canyon (British Columbia)

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Most of our direct evidence regarding early annelid evolution comes from the 'middle' Cambrian Burgess Shale, which contains five out of eight of the currently known Cambrian species. Here we describe the first new Burgess Shale species in over 40 years, based on hundreds of exceptionally well-preserved specimens recently discovered from Marble Canyon (Kootenay National Park, British Columbia). The new polychaete reaches up to 25 mm in length (*c.* 25 segments) and 2 mm in width (trunk only). The biramous parapodia are large, up to half the width of their associated trunk segment, and harbor *c.* 16 notochaetae and *c.* 12 neurochaetae. The chaetae are straight, thin (approximately 10–30  $\mu\text{m}$  wide), and long, about four times the width of their chaetiger. There is no evidence of aciculae. The head bears a pair of elongate sensory palps, up to half the total body length, and a medial antenna suggesting a level of sensory complexity previously unknown in a Cambrian polychaete. Details of internal anatomy include a gut and possible neural and cardiovascular tissues. This new species helps refine our understanding of the early evolution of annelids, in particular regarding the morphology of the head and acquisition of sensory structures.

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### Revision of the imbricate eocrinoid *Vyscystis* from the mid Cambrian of the Barrandian area (Czech Republic)

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Echinoderms are abundant in the Cambrian of the Czech Republic. They are preserved mostly as disarticulated remains and occasionally as fully articulated specimens. Among them, the lepidocystid genus *Vyscystis* is currently known from less than five fairly complete specimens. The Jince Formation (Drumian Stage, Cambrian Series 3) of the Příbram–Jince Basin has recently yielded numerous beautifully preserved complete to





weakly fragmented specimens of *Vyscystis*, associated with a diverse benthic fauna (e.g. felbabkacystid and eocrinid echinoderms, trilobites, agnostids, brachiopods, hyoliths). *Vyscystis* is characterised by a slightly domed irregularly-plated oral surface, an elongate cone-shaped aboral region, and distinctive coiled biserial brachioles. It is interpreted as an epibenthic low-level suspension feeder. The new recently collected material offers us the opportunity to reassess the morphology of the genus *Vyscystis*. Study material is housed in the Palaeontological Department of National Museum Prague, in the Czech Geological Survey Prague, and also in private collections. Several excellently preserved previously unstudied specimens provide new evidence depicting allometric trends and palaeoecology of the peri-Gondwanan lepidocystids, and inferring major evolutionary patterns among early blastozoans.

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### Palaeoecological and palaeoenvironmental significance of Brigantian *Gigantoproductus* brachiopod beds, Derbyshire carbonate platform, UK

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A sedimentological and palaeoecological analysis of beds dominated by species of the brachiopod genus *Gigantoproductus* investigates the rapid colonization and success of this taxon in the Derbyshire carbonate platform. Diversification of *Gigantoproductus* has been linked to a warming climate in the late Viséan; during the Brigantian the genus thrived in the tropical and subtropical waters of Palaeotethys. Two key localities have been studied in Derbyshire. A shell bed at Ricklow Quarry comprises life assemblages (>72% of brachiopods in life position) and neighbourhood assemblages. They represent a low-moderate diversity community rapidly established in inner-middle ramp settings over relict Brigantian mud mounds. Brachiopod orientations indicate a south-directed palaeoflow. Once this community was established, the dominance of thick-shelled forms enabled baffling of mud and fine bioclasts, potentially providing localized shelter for larvae and nearby individuals. A shallower and higher energy inner ramp location, Once-a-Week Quarry, revealed a lower diversity community exclusively comprising neighbourhood assemblages (37% in life position) with no preferred shell orientation. High-resolution trace element and stable isotope data from well-preserved *Gigantoproductus* shell calcite reveal geochemical heterogeneity, potentially reflecting environmental or climatic changes. These data enable evaluation of data quality and preservation potential of palaeoenvironmental signals in deep-time specimens.



## What can spores and pollen tell us about taphonomic bias at the Permian–Triassic boundary in the Eastern and Southern Alps?

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The mass extinction at the Permian–Triassic boundary is famous for being the most severe extinction event of both marine and terrestrial faunas and one of only two mass extinctions among plants. In order to determine the importance of taphonomic bias for the observed extinction and recovery patterns, an interdisciplinary project has started to study the boundary interval in the Eastern and Southern Alps. This region contains numerous outcrops documenting coeval marine and terrestrial palaeoenvironments. Here we present the first palynological results from sections at Tesero, Bulla/Pufels and the Laurinwand. Most of the samples from the Upper Permian Bellerophon Formation yielded a rich sporomorph assemblage dominated by bisaccate taeniate and non-taeniate pollen, which were produced by conifers and seed ferns (pteridosperms). Spores of lycopsids and ferns mostly occur only sporadically. Possible algae (or fungi) of the genus *Reduviasporonites* comprise almost the entire assemblage in samples from the Tesero Member (uppermost Permian to lowermost Triassic) of the Werfen Formation at the Tesero section. Further work will be aimed at finding differences in assemblages between different depositional environments, the identification of possible biases and the reconstruction of terrestrial ecosystems over time.

## The influence of taphonomic bias on Bayesian estimation of clade ages using morphological data

**Joseph O'Reilly and Philip C. J. Donoghue**

*University of Bristol, UK*

Total-evidence divergence time estimation methods have expanded the utility of fossil data when estimating evolutionary timescales. In classic divergence-time analyses fossil data are reduced down to purely chronological data, with discrete characters being discarded. New methodology now allows for the inclusion of these data, allowing fossil morphology to refine our understanding of evolutionary history. Yet fossil morphological data are relatively incomplete, with a decidedly non-random distribution of missing data. This distribution is constrained by taphonomic processes, with soft characters likely to be poorly represented while harder, more easily fossilized characters dominate matrices. Such a bias may lead to the inaccurate estimation of divergence time estimates. We apply a series of taphonomic filters to simulate the effects of different stages of fossilization on a large and highly complete matrix. Divergence times estimated using this matrix then allow us to demonstrate the relative influence of different stages of the process of fossilization on the accuracy of divergence time estimates. We show that the loss of soft characters poses little threat to the accuracy of divergence time estimates, but that the concomitant loss of characters from different assemblages attributable to particular anatomical categories may increase age estimate error.



## Recent new discoveries from the upper Ediacaran of western Mongolia

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We have surveyed the upper Ediacaran to the lowest Cambrian of Govi-Altai and Zavkhan provinces, western Mongolia, for several years, and we have obtained interesting palaeontological data hitherto unknown from other Ediacaran sections, or not known at least from Mongolia. We will present two topics from the upper Ediacaran of these provinces. One is the existence of U-shaped burrows, possibly assignable to the ichnogenus *Arenicolites*, from the uppermost part of the Ediacaran of Bayan Gol, Govi-Altai Province. These ichnofossils occur in more than 10 horizons, and the diameter of some of their openings reach more than 1 cm. This discovery strongly suggests that bilaterians already existed by the end of the Ediacaran. The other is the occurrence of two species of algae (*Chinggiskhaania bifurcata* and *Zuunartsphyton delicatum*) from thinly laminated shale of the Ediacaran of Zuun Arts, Zavkhan Province. The shale containing these algae is considered to be a Burgess Shale-type deposit and further excavation at this site may lead to new discoveries of fossils including metazoans.

## Within-guild niche partitioning in sympatric species: how ecologically sensitive is texture analysis of tooth microwear?

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Recent work shows that tooth microwear analysis can be applied further back in time and deeper into the phylogenetic history of vertebrate clades than previously thought (e.g. niche partitioning in early Jurassic insectivorous mammals; Gill *et al.* 2014, *Nature*). Furthermore, quantitative approaches to analysis based on parameterization of surface roughness are increasing the robustness and repeatability of this widely used dietary proxy. Discriminating between taxa within dietary guilds has the potential to significantly increase our ability to determine resource use and partitioning in fossil vertebrates, but how sensitive is the technique? To address this question we analysed tooth microwear texture in sympatric populations of shrew species (*Neomys fodiens*, *Neomys anomalus*, *Sorex araneus*, *Sorex minutus*) from Białowieża Forest, Poland. These populations are known to exhibit varying degrees of niche partitioning (Churchfield and Rychlik 2006, *J. Zool.*) with the greatest overlap between the *Neomys* species. *Sorex araneus* also exhibits some niche overlap with *N. anomalus*, while *S. minutus* is the most specialized. Multivariate analysis based only on tooth microwear textures recovers the same pattern of niche partitioning. Our results also suggest that tooth textures track seasonal differences in diet. Microwear analysis clearly has the potential for very subtle dietary discrimination in fossil insectivores.



## Exploring the drivers of ecological and evolutionary turnover in the Caribbean

**Paola G. Rachello-Dolmen<sup>1,2</sup>, Ethan L. Grossman<sup>2</sup>, Kenneth G. Johnson<sup>3</sup>, Jonathan A. Todd<sup>3</sup> and Aaron O'Dea<sup>1</sup>**

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The Caribbean experienced a massive regional extinction in the Plio-Pleistocene that led to a loss of over 50% of marine species. Extinction was strongly selective against taxa better adapted to nutrient-rich environments, thus the extinction has been attributed to declining planktic nutrients in the Caribbean due to isolation from the Pacific during closure of the Isthmus of Panama. However, while nutrients declined between 4 Ma and 3 Ma the extinction occurred 1-2 million years later. In this study we dissect the ecological and environmental dynamics of this turnover. Our data include more than 500,000 specimens of molluscs, bryozoans, fish otoliths and corals from before, during and after the extinction. We measure environmental change using >4,000 stable isotope analyses from profiles of gastropod shells and explore relative abundances and co-occurrences of taxa and functional traits of organisms through this time and across space. Preliminary data suggest that functional traits provide a better predictor of turnover than taxonomic affinity. We observe that taxa that eventually go extinct tend to aggregate irrespective of taxonomic affinity, suggesting that refugia allowed doomed taxa to persist.

## Using melanosomes to discriminate between tissues in vertebrate eyes

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*University College Cork, Ireland*

The vertebrate eye contains three tissue sources of melanosomes: the retinal pigment epithelium (RPE), the choroid and the iris. These melanosome populations can be discriminated in part by their morphology. The presence of layers of melanosomes of different morphologies in the eyes of fossils has been used as evidence of the RPE and thus a vertebrate affinity. However, whether melanosomes from different tissue sources in the eye consistently differ in geometry across a range of vertebrate taxa has yet to be demonstrated. We confirm that melanosomes from different ocular tissues differ significantly in geometry both within and among taxa. Importantly, our data show that the preservation of melanosomes organized into size-specific layers could result from the superposition of melanosomes from other tissues in the eye or elsewhere in the head. Further investigation into the geometry and chemistry of melanosomes in the vertebrate eye will help constrain the extent to which the vertebrate eye can be used for phylogenetic studies.

## Preservation and phylogeny of Cambrian ecdysozoans tested by experimental decay of *Priapul*

**Robert Sansom**

*University of Manchester, UK*

The exceptionally preserved Cambrian fossil record provides unique insight into the early evolutionary history of animals. Understanding of the mechanisms of exceptional soft tissue preservation frames all interpretations of the fauna and its evolutionary significance.



This is especially true for recent interpretations of preserved nervous tissues in fossil ecdysozoans. However, models of soft tissue preservation lack empirical support from actualistic studies. Here experimental decay of the priapulid *Priapululus* reveals consistent bias towards rapid loss of internal non-cuticular anatomy compared with recalcitrant cuticular anatomy. This is consistent with models of Burgess Shale-type preservation and indicates that internal tissues are unlikely to be preserved with fidelity if organically preserved. This pattern, along with extreme body margin distortion, is consistent with onychophoran decay, and is therefore resolved as general for early ecdysozoans. Application of these patterns to phylogenetic data finds scalidophoran taxa to be very sensitive to taphonomically informed character coding, but not panarthropodan taxa. Priapulid decay also has unexpected relevance for interpretation of myomeres in fossil chordates. The decay data presented serve not only as a test of models of preservation, but also a framework with which to interpret ecdysozoan fossil anatomies and the subsequent evolutionary inferences drawn from them.

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## The (incomplete) Phanerozoic fossil record of major phytoplankton lineages

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The Phanerozoic fossil record of marine biodiversity remains an enigma. A broad range of physical and biological factors have been proposed to explain the record but none, singly or in combination, satisfactorily explain the basic patterns. One factor which has received relatively little attention with regard to the Phanerozoic fossil record is that of food. We suggest that the quantity (primary productivity) and quality (stoichiometry) of food at the base of food pyramids, *i.e.* the phytoplankton, was critical to biodiversification. Cambrian and Palaeozoic faunas are paralleled by nutrient-poor (high carbon:phosphorus ratios, 'green') lineages, whereas the modern fauna is paralleled by nutrient-rich (low carbon:phosphorus ratios, 'red') lineages. Based on studies of trophic cascades of lacustrine ecosystems, Palaeozoic macrofauna would have had to expend energy up front to 'burn off' excess carbon to obtain phosphorus (an essential macronutrient) of 'green' phytoplankton, leaving less energy for reproduction. The converse holds for modern macrofauna and 'red' lineages. However, the fossil record of phytoplankton is dramatically incomplete. A major problem in understanding the base of marine food chains is the total absence in the fossil record of the picophytoplankton (< 5 µm) that represents over 50 % of modern marine biomass.



## Where to find the Carboniferous terrestrial fauna: recent discoveries in Romer's Gap point the way

**Timothy R. Smithson<sup>1</sup>, Carys E. Bennett<sup>2</sup>, Jennifer A. Clack<sup>1</sup>, Neil D. L. Clark<sup>3</sup>, Sarah J. Davies<sup>2</sup>, Gregory D. Edgecombe<sup>4</sup>, Timothy I. Kearsley<sup>5</sup>, John E. A. Marshall<sup>6</sup>, David Millward<sup>5</sup>, Andrew J. Ross<sup>7</sup> and Janet E. Sherwin<sup>2</sup>**

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Recent exploration of the Ballagan Formation (Tournaisian) in the Tweed Basin, Scottish Borders, has revealed numerous new beds containing tetrapods and terrestrial arthropods. The most common lithology preserving this fauna is sandy siltstone. These beds usually overlie palaeosols and were deposited in seasonal flooding events as cohesive flows. This taphofacies contains the most abundant and rich fossil deposits in the early Carboniferous. It includes a diverse variety of vertebrates, bivalves, ostracods, millipedes, scorpions and other arthropods, and abundant plant remains. During the early Carboniferous the Tweed Basin was a low-lying coastal flood plain traversed by large rivers, and housed permanent and temporary freshwater lakes. Overbank flooding and periodic high rainfall provided sediment deposition in which the fauna and flora were preserved. During times of flooding, proximity to land provided refuge for the terrestrial fauna. These conditions were an ideal environment for the evolution of terrestrial ecosystems and in northern Britain were fairly stable over millions of years. Similar conditions must have prevailed throughout the Carboniferous, and basins adjacent to upland areas in which wetland palaeosols form a significant component of the succession are where we should be looking for new tetrapod and terrestrial arthropod sites.

## Modern brains and their Cambrian antecedents: evolutionary stability, genealogical correspondence and evolved loss

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The evolutionary exuberance of euarthropods is reflected in their variety of forms, behaviours and habitats. Such profusion of shapes and functions might be expected to reflect corresponding diversity of brains and nervous systems. However, contemporary studies suggest that brain and nervous system organization is constrained to a set of divergent motifs, called 'ground patterns'. Although arthropod brains comprise a rich variety of neural arrangements in defined centres, each ground pattern today typifies one of the major arthropod clades. Here we review the interpretation of discoveries deriving from exceptionally preserved fossils from China's Chengjiang and Xiaoshiba and Canada's Burgess Shale fauna that resolve these neural ground patterns as very ancient, spanning a range of about 518–505 million years. The overarching view of the panarthropod central nervous system is thus one of evolutionary stability. Four types of brain and three ventral



nervous systems found in fossils correspond to the four ground patterns of four clades of extant panarthropods. Current understanding of phylogeny and time of origin of panarthropod lineages allows allocation of divergent brain centres to each ground pattern identified in Cambrian fossils. Those times of origin tell us when transformations of sensory/motor centres are likely to have occurred.

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### The effect of climate on equatorial late Palaeozoic floral transitions in the limnic Muse and the paralic Mengkarang Formations. Two sides of the same coin?

**Isabel M. Van Waveren<sup>1</sup>, Menno Booij<sup>1</sup>, Christopher J. Cleal<sup>2</sup>, Mike J. Crow<sup>3</sup>, Fauzie Hasibuan<sup>4</sup>, Pierre Pellenard<sup>5</sup>, Mark D. Schmitz<sup>6</sup> and Ellen Stolle<sup>7</sup>**

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Two newly described uninterrupted sections from the Late Palaeozoic equatorial belt indicate apparent inverse developments of the palaeoflora. Detailed analysis of the limnic beds from the Muse Formation (Autun Basin, France) indicates a transition from peltasperm to cordaite and marattialean dominated vegetation, while the paralic Mengkarang Formation (Sumatra) displays a transition from cordaite and marattialean to peltasperm dominated vegetation. New isotopic age measurements for both formations shows their respective duration is comparable. The top and central ash bands from the Muse beds indicate 850,000 years of deposition for the metre of bituminous shales they enclose, while the top and base of the 500-metre-thick section through the paralic Mengkarang Formation indicates a duration of 630 million years. Comparison with the global eustatic sea level curve shows that the early Asselian Muse beds represent a transition from a low to a high eustatic sea level, while the middle Asselian Sumatra section shows the inverse transition. As Late Palaeozoic eustatic sea level fluctuations are related to Gondwanan glaciations, it appears that the peltasperm vegetation reflects the low eustatic sea level conditions of a glaciation while the cordaite and marattialean reflect the high eustatic sea level of global warm conditions.



## Biostratigraphic assessment of the uppermost Ordovician in the central Anti-Atlas (Morocco)

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We have revisited the stratotype area of the Lower Formation of the Second Bani Group, west of Tagounite in the Moroccan Anti-Atlas, and sampled brachiopods and trilobites from its uppermost quartzitic horizons. In addition to those brachiopods listed in previous papers on the region, we have found *Plectothyrella* sp. and *Kinnella* sp. Both genera are exclusive of the pandemic *Hirnantia* fauna, which allows confirmation of a Hirnantian age for the upper member of the Lower Second Bani Formation. By contrast, the lower member of the same unit has yielded Katian brachiopods and trilobites, such as *Eostropheodonta intermedia*, *Destombesium* sp., *Hirnantia* sp. (species other than *H. sagittifera*), *Actinopeltis* aff. *insocialis*, *Mucronaspis termieri* and *Cekovia* aff. *perplexa*. According to the lithostratigraphic framework, the Katian/Hirnantian boundary lies within the Lower Formation of the Second Bani Group and lithostratigraphically correlative horizons, such as those reported in Bou Ingarf. The latter were mainly dated as a result of lithostratigraphic and sequential correlations and, based on correlation with the Tagounite area, are in need of revision. The age of the lower part of the chitinozoan *Tanuchinita elongata* Biozone should be re-evaluated, and the suggested delayed onset of the Hirnantian glaciation reconsidered.

## Ammonoids from the Griesbachian (Early Triassic) of northeastern Greenland: taxonomy and biostratigraphy

**David Ware and Hugo Bucher**

University of Zurich, Switzerland

The Wordie Creek Formation in northeast Greenland is well known for its well-preserved and abundant Griesbachian (earliest Triassic) ammonoids. Their taxonomy is, however, still based on a very typological approach, and their biostratigraphy is based mostly on scattered occurrences and small sample size with a poor stratigraphical control. Intensive fieldwork conducted recently led to the collection of large samples collected *in situ*. These allow us, as a first step, to revise their taxonomy by studying their ontogeny and intraspecific variability. Based on this revised taxonomy, a more detailed and better substantiated biostratigraphical scheme for this area is established. The boundaries of the Griesbachian substage for this region as defined by Bjerager *et al.* (2006) are here questioned, especially concerning the *Hypophiceras triviale* zone and the *Bukkenites rosenkrantzi* zone, here considered as already Griesbachian and Dienerian in age, respectively. A new biostratigraphical scheme with nine Griesbachian zones is proposed, which clearly contrasts with the previously established five zones of Bjerager *et al.* (2006).





## A fossilized birth–death model for the reliable estimation of speciation and extinction rates

**Rachel C. M. Warnock<sup>1,2</sup>, Tracy A. Heath<sup>3</sup> and Tanja Stadler<sup>1</sup>**

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Estimating speciation and extinction rates is essential for understanding the past, present and future of biodiversity. Widespread interest in this topic has led to a divergent suite of competing approaches using stratigraphic versus phylogenetic data. The fossilized birth-death (FBD) process is a model that explicitly recognizes that the branching events in a phylogeny and the fossils sampled from the rock record were generated by the same underlying diversification process. Here we present an extension that allows the branching process to be modelled in the absence of any phylogenetic information. This eliminates the requirement for anything about the underlying phylogeny to be known, such that the model can be applied when only first and last occurrence data are available, but still allows the inherent phylogenetic structure of the data to be considered. We tested the model using simulations that incorporate non-uniform fossil preservation and compared our approach to widely implemented fossil-based alternatives. We show that our new method is both accurate and precise, but that the performance of all methods is impacted by non-uniform preservation and uncertainties in taxonomy. These represent critical areas for development among all methods that aim to recover reliable estimates of diversification rates in deep time.

## The importance of fossils in dating the Tree of Life: from exceptional preservation to complete absence

**Joanna M. Wolfe**

*Massachusetts Institute of Technology, USA*

Geological age data and molecular sequences are increasingly combined to establish a timescale for the Tree of Life. In the best case scenarios, the geological dates are derived from fossils which meet a series of criteria, such as data on their phylogenetic placement and stratigraphy. Here I empirically explore one of the absolute best cases, using a morphological dataset with over 200 arthropod fossils, mainly from Cambrian localities with exceptional preservation (thus stronger phylogenetic evidence). I also explore the worst cases, dating in ‘prokaryotes’ (Bacteria and Archaea), which generally lack a fossil record, and have divergences expected prior to the Neoproterozoic. New strategies are introduced to constrain these microbial divergences, including harnessing the horizontal transfer of genes into fossiliferous clades, and the coevolution of bacterial parasites and their fossiliferous metazoan hosts. Directly or indirectly, the fossil record remains indispensable to date any branches of the tree.



# Abstracts of poster presentations

Underlined author denotes designated presenter.

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

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## Life on a rocky shoreline: a new view of Ediacaran palaeobiology

\***Peter W. Adamson** and **Nicholas J. Butterfield**

*University of Cambridge, UK*

The Ediacaran is marked by a distinctive assemblage of large acanthomorphic acritarchs, best known from the Doushantuo Formation in South China. These fossils offer the only reasonable prospect for biostratigraphic subdivision of the early Ediacaran, though such potential seems compromised by their restriction to localized low-energy environments in chert, phosphorite, and mudstone facies. Our study of the interstices of a debris-flow conglomerate in the Ediacaran Biskopås Formation (Norway) finds conglomerate palaeosurfaces encrusted with phosphatized microbial mats containing trapped acanthomorphs. Additionally, conglomerate interstices filled with micrite (now recrystallized to microsparite) preserve ten acanthomorph species – the first documented occurrence of Doushantuo-type acritarchs preserved in carbonate. Sedimentological and palaeontological reconstruction of the Biskopås facies demonstrates that the acanthomorph-forming organisms were living in direct proximity to the actively prograding conglomerate. The discovery of carbonate-hosted acanthomorphs in a high energy environment alludes to a highly recalcitrant and eurytopic nature within shallow waters, and their possible function as the resting cysts of protists. These novel windows reveal for the first time the development of eukaryotic ecosystems along rocky coastlines during a period of major ecological and evolutionary innovation in the terminal Proterozoic, while expanding the utility of such fossils in biostratigraphically partitioning the early Ediacaran.

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## A new juvenile burnetiamorph (Therapsida: Biarmosuchia) skull from the Beaufort Group, South Africa and its role in a revision of *Lemurosaurus pricei*

**Duhamel Aliénor<sup>1</sup>**, **Julien Benoit<sup>2</sup>**, **Michael O. Day<sup>2</sup>** and **Bruce S. Rubidge<sup>2</sup>**

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The skull of a small burnetiamorph (Therapsida: Biarmosuchia) was recently discovered in the collections of the Council for Geoscience, Pretoria. The specimen (CGP MJF 22) was originally collected in the Victoria West district of Western Cape Province, South Africa, in the *Pristerognathus* Assemblage Zone (latest Guadalupian, ~260 Ma) of the Main Karoo Basin. Despite a number of new descriptions over the last 13 years, the relationships within Burnetiamorpha remain poorly understood, partly because the rarity of individual taxa and high morphological variability hinder the recognition of ontogenetic signatures. CGP MJF 22 has large orbits compared to the reduced size of the skull, clearly defined sutures and an un-ossified braincase and bony labyrinth, which together suggest that it is a juvenile. This provides an opportunity to understand growth trends in Burnetiamorpha. The juvenile specimen is similar to *Lemurosaurus pricei*; the holotype (an adult) and CGP MJF 22 are similar in size, yet the juvenile characteristics of CGP MJF 22 (lesser development of the



supraorbital bosses, absence of a frontal crest or zygomatic bosses) suggest that it is not conspecific. We provide a revision of the taxon *Lemurossaurus pricei* and in particular suggest the reassignment of referred specimen NMQR 1702.

## Upper Famennian ammonoids from the Ougarta Basin (Saoura Valley, Algeria)

**\*Ninon Allaire<sup>1</sup>, Claude Monnet<sup>1</sup>, Abdelkader Abbache<sup>2</sup> and Catherine Cr  nier<sup>1</sup>**

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The Famennian (Upper Devonian) deposits record several hypoxic events such as the global *Annulata* Event(s). These deposits outcrop in various regions of the world and often contain rich ammonoid faunas, which can be used to biostratigraphically constrain these events. The present study contributes to the description of the Upper Devonian ammonoids in Algeria, especially from the Saoura Valley. Although Upper Devonian deposits in this area were first recognized on the basis of cephalopods more than one century ago, they remain poorly studied. This study is the first comprehensive description of newly collected, abundant material from the Marhouma Formation in several sections around Beni Abb  s. In the Saoura Valley (Ougarta Basin), the Famennian part of the Marhouma Formation is characterised by deep-water facies including levels rich in ammonoids. In the Ouarourout area the ammonoid faunas are represented by 16 genera belonging to 11 families: Sporadoceratids (*Sporadoceras* and *Erfoudites*), Prionoceratids (*Prionoceras*), Tornoceratids (*Planitornoceras* and *Gundolficeras*), Posttornoceratids (*Discoclymenia*), Cyrtoclymeniids (*Cyrtoclymenia*), Cymaclymeniids (*Procyamacyclenia*, *Cymacyclenia* and *Genuclymenia*), Platyclymeniids (*Platyclymenia*), Clymeniids (*Clymenia*), Kosmoclymeniids (*Muessenbiaergia* and *Kosmoclymenia*), Sphenoclymeniids (*Sphenoclymenia*) and Gonioclymeniids (*Gonioclymenia*). This ammonoid assemblage can be correlated with ammonoid faunas from the well-known Tafilalt area (Morocco) and corresponds to the *Platyclymenia annulata* Zone (upper Famennian, UD.IV-A).

## Endocranial anatomy of two Elasmosauridae specimens (Reptilia, Plesiosauria) from the Late Cretaceous of Morocco

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Elasmosaurs were a group of marine plesiosaurians that lived during the Cretaceous period. They were agile swimmers and presumably active predators. Although the adaptations of elasmosaurs to the aquatic realm have been extensively studied from the post-cranial skeleton, the sensorial abilities supporting their adaptation to a fully aquatic lifestyle are still poorly understood. Here we present the description of CT scan-generated endocasts of two elasmosaur specimens from the Turonian of Goulmima (Morocco) in order to improve our understanding of their endocranial anatomy as well as their behaviour and sensorial adaptations. Results of the segmentation reveal enlarged optic bulbs and cerebellum suggesting neuroanatomical adaptations, allowing them to be highly mobile with developed visual capacities. The thin and long olfactory tracts do not allow interpretation of whether the specimens possessed chemoreception. The two specimens exhibit also a reduced inner ear, with small and thick semi-circular canals, as well as a bulbous vestibule, in accordance with previous observation of sensory adaptation in secondarily adapted marine tetrapods.



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## One head with two bodies: the *Onaraspis*–*Myopsolenites* trilobite conundrum

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A new fossil assemblage of Cambrian Epoch 2 (early Cambrian) redlichiid trilobites has been found in the Huérmeda Formation of the Iberian Chains, northeast Spain. This assemblage is dominated by complete specimens characterised by macropleura-bearing thoraxes close to the genera *Onaraspis* Öpik, 1968 and *Myopsolenites* Geyer and Landing, 2004, the former reported from Australia and the latter from the Mediterranean and Polish margins of Gondwana. Despite their cephalic similarities, these taxa display highly diversified thoraxes and shield-like pygidia. Although the number of segments in the trunk and the proportions allocated to the thorax and pygidium varied with ontogeny, several Iberian genera and species can be taxonomically differentiated based on trunk features. Cambrian diversification not only featured evolutionary ‘experiments’ with the constructional framework for the trilobite cephalon, but also for the trilobite trunk. The Cambrian diversification in the development of the trunk represents a wakeup call for taxonomic analyses exclusively based on disarticulated cranidia, and highly controlled by taphonomic biases.

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## A palynological investigation of the Middle Devonian of northern Spain: hunting for the Kačák event

**\*Alexander Askew and Charles H. Wellman**

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Northern Spain contains an exceptionally complete Devonian sequence, chronicling widely varying depositional environments in a Peri-Gondwana setting. We describe palynomorph assemblages from the Eifelian and Givetian age Huergas, Naranco and Gustalapedra Formations from Asturias, Castilla y León and Palencia provinces, respectively. These laterally equivalent formations represent a transect from shallow nearshore to deep offshore shelf deposits. Sandwiched between thick limestone sequences, these formations consist of large sandstone bodies interspersed with black shales, representing a period of greatly increased terrigenous input to the ocean. Samples have yielded rich assemblages of land-derived spores and marine palynomorphs (acritarchs, chitinozoans and occasional scolecodonts). Preliminary results of the quantitative analysis of this material are presented, which ultimately aim to age-constrain the formations and reveal temporal and spatial changes in the terrestrial and marine communities. A further aim is to identify any influence of the contemporary Kačák event. This widely occurring anoxic event is associated with marine extinctions and faunal turnover, though it is poorly characterised in Iberia, and its effect on terrestrial floras is little-known. We hope to identify the Kačák event in northern Spain and document its effect on the local biota, thus shedding light on potential causes of this event.



## Brachiopod shell thickness and the End-Ordovician mass extinction

**Uwe Balthasar**

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Calcareous brachiopods are among the most diverse, abundant, and best studied groups of early Palaeozoic fossils. By contrast to overall shell morphology, which has a long tradition of careful systematic study, shell thickness of brachiopods is commonly treated superficially and non-quantitatively. Here I present the first systematic study of shell thickness for brachiopods. The study looked at 181 shells of Ordovician–Silurian rhynchonelliformean brachiopods and reveals a distinct morphospace of shell thickness and shell length. When normalised for maximum shell thickness, this morphospace reveals significant differences on an order level with orthids and strophomenids having significantly thicker shells than rhynchonellids and pentamerids. The latter group is unusual in that they combine a very thick posterior shell with a paper-thin anterior shell covering the filtration chamber. Genus-level occurrence data from the Paleobiology Database show that the two thicker-shelled orders declined significantly during the End-Ordovician mass extinction whereas occurrences of thinner-shelled orders increased. This suggests that a more economical way of shell secretion might have been advantageous during the end-Ordovician mass extinction.

## Emergence of the modern freshwater food web in the early Carboniferous

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Freshwater ecosystems underwent a renovation after the extinction of many fish groups during the Hangenberg crisis. Carboniferous tetrapods, actinopterygians, dipnoans, gyracanthids and chondrichthyans occupied the niches left vacant by placoderms and porolepiformes. Change to invertebrate community structure also occurred, with bivalves and ostracods radiating from marine to freshwater environments. Little is known about changes in food webs during this transition, or vertebrate–invertebrate interactions. The radiation of ostracods and bivalves into fresh water initiated a modern food web structure and may have contributed towards the rapid diversification of many vertebrate groups. The sandy siltstone facies of the Tournaisian Ballagan Formation of Scotland was deposited in temporary floodplain lakes and contains a rich aquatic and terrestrial fauna that is populating Romer's Gap. The faunal associations of sandy siltstone beds ( $n = 122$ ), coupled with literature data (e.g. gut contents) are used to reconstruct the freshwater food web: producers comprise algae and terrestrial plant matter, consumed by ostracods, spinicaudatans and mytilid and myalinid bivalves. Second order consumers include eumalacostracans, actinopterygians, dipnoans and eurypterids, predated by gyracanthids, rhizodonts, chondrichthyans and tetrapods. Morphometric analyses of dipnoan toothplates and bivalve shells are used to infer possible dietary associations.



## Cryptic biocoenoses from the Middle Devonian of Morocco

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Three exceptionally well-preserved fossil cryptic communities composed of rugose corals and other sessile invertebrates were discovered in submarine cavities of the Middle Devonian (Givetian) mud-mound in the Hamar Laghdad area (Morocco). The studied cryptic biota is dominated by small solitary rugose corals, which encrusted the roofs of the cavities and grew predominantly in an inverted position with 'calice-in-calice' growth. Different cavities were settled by different communities of solitary rugose taxa. The rugose corals identified in the studied cryptic palaeoecosystems also occur outside of the cavities, within mound facies and/or well-bedded intermound deposits of the Givetian of the Hamar Laghdad area. The results support the hypothesis that during the middle Palaeozoic there was no distinct polarization between open-surface and cryptic faunas in relatively deep-water environments. Different taxonomic compositions of the studied cryptic ecosystems show that the regional species pool was the main determinant of the structure of these assemblages. The high density of organisms growing on each other indicates that intensive competition for space must have already existed in Devonian submarine crypts. All these observations show that the studied cryptic assemblages differed markedly from both their Palaeozoic and modern analogues.

## The family Lonchidiidae in the Early Cretaceous record of Spain

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The family Lonchidiidae Herman, 1977 (Hybodontidae) was widespread in Mesozoic non-marine environments in western Europe during the Early Cretaceous, being one of the most common hybodont sharks in the Spanish fossil record at this time. Remains of this family have been identified in almost all of the major Early Cretaceous Spanish sites. Apart from scarce articulated specimens from the Lagerstätte of La Pedrera de Rúbies (Montsech, Lleida, South-Central Pyrenees), hundreds of isolated remains of these sharks are commonly found in the rest of the Iberian Peninsula, with an Early Cretaceous palaeogeographical distribution that ranges from the Basque–Cantabrian Basin (connected to the Boreal Ocean), through all along the Iberian Basin, connected to the Alpine Tethys Ocean. Despite the abundance of lonchidiid remains (most of them teeth), the problems inherent to the parataxonomy and the scarcity of studies related to these faunas in Spain have, in most cases, prevented their proper taxonomic assignment. The study of new abundant hybodont faunas from the Enciso Group (Early Aptian, Cameros Basin) and the revision of the type material of the Spanish species *Lonchidion microselachos* and the classic European taxon '*Hybodus*' *parvidens* have permitted a new understanding of the dentition patterns of both species.



## Inferring the diets of pterosaurs and extant analogues using quantitative 3D textural analysis of tooth microwear

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Pterosaurs were a successful group of Mesozoic flying reptiles. For 150 million years they were integral components of terrestrial and coastal ecosystems, yet their feeding ecology remains poorly constrained. Postulated pterosaur diets include insectivory, piscivory and/or carnivory, but many dietary hypotheses are speculative and/or based on little evidence, highlighting the need for alternative approaches to provide robust data. One method involves quantitative analysis of the micron-scale 3D textures of worn pterosaur tooth surfaces – dental microwear texture analysis. Microwear is produced as scratches and chips generated by food items create characteristic tooth surface textures. Microwear analysis has never been applied to pterosaurs, but we might expect microwear textures to differ between pterosaurs with different diets. An important step in investigating pterosaur microwear is to examine microwear from extant organisms with known diets to provide a comparative data set. This has been achieved through analysis of non-occlusal microwear textures in extant bats and crocodilians, clades within which species exhibit insectivorous, piscivorous and carnivorous diets. The results – the first test of the hypothesis that non-occlusal microwear textures in these extant clades vary with diet – provide the context for the first robust quantitative tests of pterosaur diets.

## Reinvestigation of *Protelytron permianum* (Insecta; Early Permian; USA) as an example for applying reflectance transformation imaging to insect imprint fossils

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We reinvestigated the holotype of *Protelytron permianum*, one of the earliest putative stem-dermapteran (*i.e.* stem-earwig). We used reflectance transformation imaging (RTI) to produce exhaustive and interactive photographic data of the specimen. We identified broadenings located along veins of the hind wing vannus that form an arc, in addition to a series of radiating folds, alternatively concave and convex. Such an organization is diagnostic of Dermaptera and reflects hind wing folding mechanisms, which are particularly elaborated in these insects. We provide a foldable, paper model of the hind wing. Based on the case presented herein we anticipate that RTI-aided approaches will provide critical new data on the morphology of fossil insects preserved as imprints.



## A timescale for life's early evolution: is it time to leave behind a literal interpretation of the fossil record?

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The timescale of life's early history on Earth remains one of the last areas where literal interpretations of the fossil record guide our understanding. However, the uncertainty surrounding the early fossil record of life suggests that a probabilistic timescale could serve as a better guideline. Such a timescale can be generated by integrating fossils and genomic information using modern, relaxed, molecular clock methods. Molecular clocks rely on carefully constructed calibrations and, to date, no definitive set of calibrations for dating fundamental divergences within the tree of life has been assembled. Here we establish a suite of calibrations, employing them with the molecular clock to show that divergence times are sensitive to calibration distribution choice, and the clock model used. Integrating across the uncertainties yields a timescale that defines credibility intervals for key events in the history of life. Our probabilistic timescale, integrating fossil and genomic information, is more accurate though less precise, allowing for predictive power and simple refinements as new fossil and molecular data are revealed. It shows the Prokaryote crown lineages appearing at a similar time prior to 3 Ga, with crown Eukaryotes a late-coming clade, established around 1.8 Ga, in correspondence with the mitochondrial precursor, the Alphaproteobacteria.

## Complex post-crisis marine ecosystem during the Early Triassic

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In the aftermath of the end-Permian mass extinction, the Early Triassic (~251.9–247 Ma) represents an environmentally unstable time interval affected by several extinction events and characterised by poorly diversified marine benthic communities. However, a new, exceptional fossil assemblage from the earliest Spathian (~250.6 Ma, middle Olenekian) documents a highly diversified and remarkably complex marine ecosystem, with more than 20 distinct metazoan orders including sponges, brachiopods, molluscs, arthropods, echinoderms and vertebrates. This highly diversified assemblage represents the most





complex marine ecosystem known to date for the Early Triassic. Most unexpectedly, primitive leptomitid protomonaxonid sponges that were previously known only from Early Palaeozoic assemblages (a 200-million-year Lazarus taxon) are found together with gladius-bearing coleoid cephalopods, a common and diversified group expected to occur only since the Jurassic. Furthermore, several taxa document the earliest occurrence of derived characters in their clades, pushing their origin or diversification much earlier than previously thought. Overall, this remarkable biota shows that the diversity and dominance of the modern evolutionary fauna may have risen rapidly from complex post-crisis ecosystems with highly unexpected compositions at the dawn of the Mesozoic era.

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## Vertebral morphology and lung structure in non-avian dinosaurs; a geometric morphometric approach

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Reconstructing the respiratory system in non-avian dinosaurs is key to understanding the evolution of thermal physiology and aerobic capacity along the avian stem. In modern sauropsids, the lung's dorsal surface attaches to the vertebral bodies and proximal ribs; therefore, axial skeleton morphology provides a reliable osteological correlate of lung structure. Vertebral shape and the relative positions of the rib articulations – diapophysis and parapophysis – were quantified using 2D morphometrics in a range of non-avian dinosaurs. Living birds and crocodilians provided an extant phylogenetic bracket. Multivariate analysis of landmark data shows clear differences in vertebral morphology, associated with different lung morphologies. Birds have the parapophysis on the vertebral centrum, associated with a furrowed thoracic ceiling and rigid lungs incised by the proximal ribs. In crocodilians, the parapophysis migrates laterally onto the transverse process, producing a smooth thoracic ceiling associated with compliant lungs ventilated by the hepatic piston. Non-avian dinosaurs show an intermediate condition, and position in morphospace, where the parapophysis migrates only to the base of the transverse process. These results suggest that dinosaurs had a heterogeneously partitioned lung, with a more rigid dorsal region and compliant ventral region, but not a completely subdivided lung-air sac system as seen in birds.

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## New species of early Eocene perissodactyls from Le Quesnoy (France, MP7): evolutive and biogeographic implications

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Perissodactyls appear during the Paleocene–Eocene transition in the Northern Hemisphere. Their centre of origin is still uncertain but the Asian hypothesis is generally favoured. The locality of Le Quesnoy (Oise, France) has yielded one of the oldest and most complete fauna from the earliest Eocene of Europe (MP7). The material is very rich (290 specimens) and well-preserved compared to other MP7 localities. It includes dental and postcranial



elements which shed new light on the early evolution of perissodactyls in Europe. Two new species of perissodactyls from Le Quesnoy have been identified. A new species of the hippomorph genus *Pliolophus* is documented by abundant dental and postcranial remains, which allow us to study the intraspecific variation and the locomotor adaptations of this species. The second species is a new basal Tapiromorpha that shows dental similarities with the paraphyletic 'Isectolophidae' group. It is the oldest occurrence of Tapiromorpha in Europe, thus suggesting a major immigration event at the base of the MP7. The fossil material from Le Quesnoy provides a unique glimpse into the diversity and palaeobiogeography of basal perissodactyls.

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## Brachiopods, biomineralization and the Cambrian radiation: combined morphological and molecular systematics as a tool to infer deep lophophorate relationships

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Within Lophotrochozoa, brachiopods and allied clades are among the first biomineralized Cambrian metazoans to appear and represent a major component of the oldest known fossil record of animals, as disclosed by the tommotiids, enigmatic 'small shelly fossil' faunas of the early Cambrian. While the brachiopod fossil record is ultimately the key to determining character homology and polarity during the evolution of the brachiopod body plan, correctly reading this record has been clouded by disagreement about relationships among the crown clades. Specifically, the monophyly of brachiopods with respect to phoronids, and the relationships of the calcitic-shelled to phosphatic-shelled brachiopods. Much of this phylogenetic uncertainty stems from difficulties in rooting the tree of brachiopods, phoronids and their sister groups within the Lophotrochozoa. To this end, we are implementing the first extensive phylogenomic investigation of extant brachiopods and phoronids, which will aid resolution of the pattern of these deep evolutionary relationships. To date, combined analyses of fossils, morphology and molecular data support brachiopod monophyly and suggests the tommotiids are the sister group of linguliform brachiopods. With a robust phylogenetic backbone in place to polarize morphological characters, this will illuminate the pattern of biomineral evolution within phosphatic and calcitic brachiopods during the Cambrian radiation.

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## First report of the *Foliomena* fauna in Portugal

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The *Foliomena* fauna was first described by Sheehan (1973) from the lower Ashgill (middle Katian, Ka2 stage slice, Upper Ordovician) of Sweden. It is dominated by small, thin-shelled brachiopods frequently associated with pelagic trilobites. This community characterised the early-mid Katian deep-water faunas of low-mid latitude settings (Rong *et*



*al.* 1999 and references), but younger records (late Katian) were also documented in higher latitudes (Havlíček and Mergl 1982; Villas *et al.* 2002). However, up to now, the *Foliomena* fauna were unknown in the Iberian Peninsula. Here we report and describe for the first time a typical *Foliomena* fauna assemblage from the upper Katian (regional Kralodvorian) of Portugal. This highly diverse (~20 taxa) assemblage comes from the uppermost beds of the Porto de Santa Anna Formation (Young 1988), ranging from the middle (Ka2) to the uppermost Katian (Ka4), cropping out in several localities of the Buçaco–Penacova region (Central Iberian Zone). It is composed of the brachiopods *Jezercia*, *Aegiria*, *Christiania*?, *Dedzetina*, *Eoplectodonta* (Kozłowskites), *Eridorthis*, *Epitomyonia*, *Foliomena*, *Nicolella*, *Skenidioides*, *Ptychopleurella*, *Protozyga*?, *Bicuspina*, *Oxoplecia*, *Triplexia*, *Paracraniops*, Rafinesquinidae indet. and the trilobites *Phillipsinella*, aff. *Parillaenus* and *Cyrtometopinae* indet. A more comprehensive taxonomic study and further statistical analyses will help determine the palaeogeographic affinities of this assemblage.

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## Evaluating the phylogenetic consistency of morphological data for birds using molecular trees

**Leah Callender-Crowe, Peter Choate and Robert Sansom**

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Morphological data are fundamental for building phylogenies and thus for interpreting evolutionary history. Moreover, it is the only source of data available from fossil taxa. However, morphology is beset with problems such as subjectivity, non-independence of characters and ecologically-driven convergence. Furthermore, morphological data frequently exhibit disagreement with molecular data, which is arguably more objective and abundant. Here, the relationship between phenotype and genotype is explored in the context of phylogenetic reconstruction. Morphological data matrices of extant birds were collated and characters allocated to osteological and non-osteological partitions. Of these two regions, osteological data were found to be significantly more congruent with molecular trees as measured using ensemble retention indices (paired t-test:  $p < 0.001$  for 19 datasets). This trend indicates that morphological partitions may be subject to differing evolutionary pressures and that some aspects of morphology may be more informative with respect to evolutionary history than others.

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## The brachiopod fauna of the Fezouata Shale (Lower Ordovician) of Morocco: preliminary results

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The Fezouata Biota, located 20 km north of Zagora, in the Anti-Atlas of Morocco, was discovered some 17 years ago. Within a few years of collecting it has already yielded an incredibly diverse and exceptionally preserved fauna of shelly fossils and soft-bodied specimens. Little attention has been devoted to the brachiopod fauna, by contrast to Cambrian-like taxa or those exhibiting soft-tissue preservation. An initial study suggests that the brachiopod fauna as a whole is more diverse than previous work has indicated. Eleven species, so far, are recorded from the lower part of the Fezouata Shale (Tremadocian), at horizons ranging from the middle *murrayi* to the lower *copiosus*



biozones. Three species, two of which are common to the lower part, are recorded from the lower *protobalticus* Biozone (late Tremadocian?). Seven species are recorded from the upper part of the Fezouata Shale (Floian), from horizons ranging from the lower *jacksoni* to the *minutus* biozones. Overall the fauna is dominated by orthide and lingulide taxa. In addition, a number of species in the lower part of the Fezouata Shale (*copiosus* Biozone) represent the oldest occurrences of their respective genera. The composition of the brachiopod fauna reflects a typical western peri-Gondwanan affinity.

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### Ordovician conodonts from Peru: new data and reappraisal

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Ordovician conodont faunas are poorly known from the northern part of the Central Andean Basin, in contrast with data from the northwest of Argentina and south of Bolivia, areas located in the southern part of the same basin. A single occurrence of late Floian conodonts of the upper *Oepikodus evae* Zone was reported in 2008 from the Carcel Puncco section (Inambari River valley) of southwestern Peru, close to the Subandean Fault. Further research in the Eastern Cordillera of Peru led to the discovery of three additional occurrences of Early to Middle Ordovician conodonts, also in the San José Formation but representative of different horizons. The first of them consists of an assemblage belonging to the *Trapezognathus diprion*–*Baltoniodus cf. triangularis* zones (late Floian), and was characterised in the Kimbiri section (Apuřimac River valley). The remaining Abra de Yanacocha and Huancampa localities provided much younger assemblages, representative of the *Lenodus variabilis*–*Yangtzeplacognathus crassus* zones (early–middle Darriwilian). Early Ordovician conodonts from Peru display palaeobiogeographic affinities with similar assemblages known from Baltica, South China and northwestern Argentina, whereas the Middle Ordovician occurrences bear resemblances with coeval assemblages from Baltica, central South China and the Argentinean Precordillera.

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### Completeness of the non-avian theropod fossil record

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Changes in the quality of the fossil record through time and space can bias our interpretations of diversity, palaeoecology, biogeographical patterns and macroevolutionary processes. The completeness of fossil specimens has been previously quantified for several groups of tetrapods using the character completeness metric (CCM) and the skeletal completeness metric (SCM), and used to assess fossil record biases. CCM quantifies the phylogenetic information contained within a specimen (*i.e.* the proportion of phylogenetic characters it can be scored for), and SCM quantifies the proportion of a complete skeleton that a specimen preserves. Specimen-level SCM scores were collected from the literature for over 300 non-avian theropod species that have been included in previous phylogenetic



analyses. A time series of the average completeness per geological stage was compared statistically to non-avian theropod diversity, sampling proxies (*e.g.* dinosaur-bearing formations) and sea level through time. Preliminary results show that non-avian theropod completeness is at its lowest during the latest Triassic, has two peaks in the Early and Late Jurassic, and declines throughout the Cretaceous. Theropod completeness was not significantly correlated with diversity, sampling or sea level change, but does show similarities to completeness estimates for another major dinosaur group, sauropodomorphs.

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## Fossil Crustacea from the Cretaceous Konservat-Lagerstätten of Lebanon

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We present a revision of the fossil crustaceans (Crustacea: Decapoda, Isopoda, Lophogastrida, Stomatopoda, Cirripedia) from the Late Cretaceous Konservat-Lagerstätten in Lebanon, Middle East. Although knowledge about these groups has increased during recent years, fossil crustaceans from Lebanon remain poorly studied and their importance widely underestimated. The main purpose of this study is to provide a new synthesis taking into account both the historical works and recent advances in crustacean studies. An overall review of the fossil crustacean faunas is presented and encompasses material from Cenomanian (Hakel, Hadjoula, En Nammoura) and Santonian (Sahel Alma) outcrops. The taxonomic treatment includes detailed descriptions of each species known to occur in the aforementioned Lagerstätten. All the diagnoses and descriptions are presented using standard criteria and common descriptive terminology. As much as was possible, we endeavoured to figure all the species recorded in the literature with photographs and reproductions of the historical illustrations. Thus *c.* 900 specimens have been studied. This revision also greatly improves our knowledge of fossil crustaceans by providing formal descriptions of thirteen new genera and twenty new species. The present review is due to be published in a monograph (collection *Mémoires du Muséum*) by the end of 2016.

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## Redescription of *Amiskwia sagittiformis* from the Burgess Shale as a stem-group lophotrochozoan

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*Amiskwia sagittiformis*, with its pair of strong cephalic tentacles, paired lateral fins, rounded caudal fin, and streamlined body, is one of the most iconic fossils from the Burgess Shale. It has been compared to chaetognaths, nemertines, and more recently molluscs; its phylogenetic status, however, remains highly problematic. This study is based on twenty-one new specimens from the Royal Ontario Museum and incorporates the five original Walcott specimens. It is the first revision of *Amiskwia* since Conway Morris's seminal 1977 redescription. Specimens were studied using detailed stereomicroscopy, interference photography, SEM imagery, and elemental mapping. The epidermis is smooth, with the exception of small spicules (*c.* 20 µm thick and up to 0.8 mm in length) sparsely covering



the body. The gut includes an anterior helicoidally arranged section followed by a straight and partially phosphatized intestine. The head bears a pair of terminally attached, flexible tentacles and contains a ventrally oriented feeding apparatus with potential salivary glands – previously interpreted as cerebral ganglia and the anterior gut – with closely, regularly spaced comb-like structures. Other internal features include potential muscular, vascular, and nervous tissues. *Amiskwia* lacks defining features of any modern phylum; however, the presence of spicules suggests a connection with lophotrochozoans.

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## Cretaceous bearing formations effect on modelling dinosaur diversity

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Every environment contains a specific set of conditions that act on fossil remains, representing the combined influence of local agents (*e.g.*, landscape, precipitation, temperature). As habitats shift in response to macro-scale change, the nature and distribution of preservation regimes also vary, creating cascading effects through the diagenetic processes associated with particular environments. We outlined a new modelling approach to evaluate the impact of physical variables in biasing the fossil record, revealing whether potentially suitable environments for fossil vertebrate preservation made it into the lithosphere. We focused on the latest Cretaceous (Campanian and Maastrichtian) of western North America, an area yielding considerable data on dinosaur distribution and which has been the focus of a notable volume of research. A new high-resolution global atlas of palaeogeographic maps for regional-scale palaeogeographic interpretations has been used in conjunction with a HadCM3 coupled global climatic model run over these palaeogeographies. Palaeontological data have been harvested from databases (Paleobiology Database) and the literature. Habitat modelling and estimated variation in niche ranges gives a new glimpse into some main biogeographic events concerning dinosaur communities during what is considered a ‘high diversity window’ in the evolutionary history of dinosaurs and the lead-up to the K-Pg mass extinction.

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## Systematic review of Messinian crabs of Oran (Algeria)

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During the Messinian, the temporary closure of the Strait of Gibraltar caused several desiccation phases in the Mediterranean basin. The impact of this crisis on decapod crustaceans has yet to be studied. A first step toward this goal is to further our knowledge on pre-evaporitic decapods. Our study focuses on the diverse and well-preserved fauna of crabs from the early Messinian ‘yellow marls’ of Oran (Algeria) in the Les Planteurs and Ravin Blanc outcrops. We based this study on 55 specimens including type specimens and unpublished material. A micropalaeontological analysis revealed that both outcrops correspond to similar fully-marine environment. Our systematic revision allowed us to recognize seven species ascribed to five genera, listed here in decreasing order of abundance: *Lobocarcinus*, *Geryon*, *Maja*, *Calappa*, *Hyas* – from the most common to the rarest. Among those we describe two new species: *Lobocarcinus* nov. sp. which was previously confused with the more recent (Pleistocene) *L. sismondai*, and a second species of *Geryon* sp. only known from Ravin Blanc. Since *Lobocarcinus* are abundant



in the Mediterranean area from the Miocene to the Pleistocene and the other species are ascribed to genera with extant representatives, this fauna from Oran provides an interesting comparison point between environments before and after the Messinian crisis.

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### Carbon isotope stratigraphy, biostratigraphy and correlation of the Lower Cambrian Shackleton Limestone, Transantarctic Mountains, Antarctica

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During the early Cambrian, East Antarctica and Australia were sutured together forming East Gondwana, sharing a geological and palaeontological history. New fossils and stable carbon isotope data from the Shackleton Limestone of East Antarctica is a piece in the puzzle of the Lower Cambrian biostratigraphy of East Gondwana that has remained poorly resolved since its discovery. The shared presence of *Dailyatia odyseiei* Evans and Rowell, 1990 between the Shackleton Limestone and the Arrowie Basin of South Australia demonstrates that the Shackleton Limestone correlates to the new *Dailyatia odyseiei* biozone erected for South Australia, indicating a Cambrian Series 2 Stage 3 age for the Shackleton Limestone. All species described are also present in Series 2 Stage 3-4 sedimentary deposits of either the Stansbury or Arrowie Basins of South Australia. Helcionelloid molluscs and hyoliths also demonstrate a link to the Bastion Formation, North-East Greenland. Shared taxa with the lower Cambrian glacial erratics from the South Shetland Islands shows these fossils were sourced from rocks at least coeval to the Shackleton Limestone, but not from outcrops described herein. Correlations to the Xinji Formation of North China are also discussed. Difficulties arise in interpreting isotopic data, as clear excursions do not always exist with fossil data and vice versa. Nevertheless, correlations to secular isotope excursions are hypothesized and highlight the requirement for multiple lines of stratigraphic data for stratigraphic correlation.

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### Investigating the molluscan fauna of the Shackleton Limestone (Transantarctic Mountains, Antarctica) with linear and outline morphometrics

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The molluscan fauna of the lower Cambrian (Series 2 Stage 3-4) Shackleton Limestone contains an abundance of helcionelloid steinkerns. The fauna of the Shackleton Limestone allows identification of a strong biogeographic link between East Antarctica



and South Australia, and the Bastion Formation of North-East Greenland. Amongst the helcionelloids, bilaterally compressed, incomplete internal moulds likely belonging to the stenothecids are common. The loss of the basal-most part of the steinkern results in the loss of the taxonomically important parietal train, leaving only the simple apical portion. The lack of informative morphology of this molluscan fauna mounts a challenge for phylogenetic analysis and landmark-based morphometrics due to a lack of characters and homologous points. We employ a morphometric approach to understanding the relationships of these fossils, which quantifies the morphology and compares them to similar material from coeval sedimentary deposits in order to identify overall patterns of similarity and identify putative phylogenetic relationships. This is achieved by studying the angle created between the comarginal ribs of the specimens as well as by conducting an elliptical Fourier analysis (EFA). This work is relevant to theoretical discussion on species delimitation in the fossil record and the nature of the species concept in its palaeontological application.

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### Global diversity patterns of Lepidosauria from the Triassic–Oligocene: what can they tell us about the long-term evolutionary history of the clade?

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Lepidosauria (which includes lizards, snakes and the tuatara) is a successful extant clade that originated at least 240 million years ago, and is represented by a wide variety of fossil forms. Long-term patterns of diversity have yet to be comprehensively assessed, particularly for terrestrial taxa. Here I examine terrestrial lepidosaur diversity, from the Triassic to Palaeogene (252–23 Ma), on genus-level occurrences (1,973 specimens representing 458 genera) from the Paleobiology Database. Shareholder quorum subsampling (SQS) was used to produce a sampling-corrected taxic richness curve. At a quorum >0.5, there is a decline in diversity across the Triassic/Jurassic and Jurassic/Cretaceous boundaries. A major peak in diversity occurs in the Campanian, dipping sharply before the K-Pg mass extinction. A subsequent Paleocene rise likely represents recovery following this. Diversity peaks again in the early Eocene, followed by a decline in the late Eocene, and another recovery into the Oligocene; this may be associated with the Grande Coupure event. Data are highly skewed, with 45% of specimens originating from North America, a clear indication of sampling bias. It is important therefore to examine diversity at smaller scales, e.g. continent-level or lower, in order to better understand the possible differential effects of extinction events on multiple continents.

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### A history of sea serpents: reassessing the early fossil record of Lampridiformes (Teleostei: Acanthomorpha)

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Lampridiformes is a morphologically distinctive clade of marine pelagic spiny-rayed fishes, including iconic species such as the homeothermic opah (*Lampris guttatus*) and the giant elongated oarfish (*Regalecus glesne*). A relatively high number of lampridiform relatives





are known in the fossil record, as early as the Late Cretaceous (~95 Ma). However, the phylogenetic position of most of these fossil taxa is poorly constrained. In order to better understand their early evolution, we reviewed several Palaeogene fossil taxa. For example, *Whitehippus* (Eocene of England) is redescribed with CT-scan data. In contrast with previous interpretations, we show that this taxon is one of the oldest anatomically modern Lampridiformes. On the other hand, the very strange *Bajaichthys* from the Eocene of Italy, while described as an elongated lampridiform (Taeniosomi), belongs in fact to Zeiformes (dories). Finally, we present a preliminary phylogenetic analysis of Lampridiformes including Palaeogene taxa alongside modern diversity. A collection of deep-bodied, so-called 'veliferoid' fossil taxa are placed at varying positions in the tree, helping to break down the sequence of acquisition of modern lampridiform's characters states. The oldest crown-Lampridiformes are found in the earliest Palaeocene, suggesting that the diversification of the group took place rapidly after the K-Pg extinction event.

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### Architecture of the Laureacean inflorescence *Mauldinia* revisited

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Abundant inflorescence fragments of *Mauldinia* have been collected from the Cenomanian of Saint-Laurent-la-Vernède and Saint-André-d'Olérargues, southeast France. The slender axis bears tiny, caduceus, spirally arranged, lateral units, each borne at the axilla of one persistent subtending bract. Lateral units have a bilateral symmetry, a marked dorsi-ventral flattening, a slight concavity, and a ventral position of flowers. Besides their small sizes, they can bear up to nine sessile flowers and fruits, which leave circular scars. Each lateral unit is a contracted inflorescence with sutures of pieces that are difficult to distinguish. The rough bilobed shape was previously interpreted as fused bracts, cladodes or bracteoles. According to our research, it derives from the compression of a determinate inflorescence of double cyme with acropetal maturation. The dorsal surface of the lateral unit shows tiny folds that we interpret as bracts. This cymose organization of lateral unit occurs in living Lauraceae; however, such a compressed unit with this shape is unknown in any living families. The whole inflorescence corresponds to a 'dichasium spike'. It resembles catkins due to its small size, which suggests that they may have been pendant as in birch. This original architectural model illustrates the already diversified inflorescences of early angiosperms from the Cenomanian.

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### Systematic reassessment of the earliest mammalian fauna (Saint-Nicolas-de-Port, Upper Triassic, France)

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The locality of Saint-Nicolas-de-Port (Upper Triassic, France) yielded the most important collection of earliest mammaliaforms. This collection includes more than three quarters of the available material for Triassic mammaliaforms, with representatives of all groups (morganucodonts, 'symmetrodonts', and haramiyids). However, despite twelve publications between 1978 and 1999, most of this material remains undescribed. After description of around 500 molariform and premolariform teeth, 18 species and three



indeterminate taxa are identified. Among morganucodonts, several genera known in other sites are recognized (*Morganucodon*, *Paceyodon*, *Paikasigudodon*). Two new species are described (*Megazostrodon chenali* sp. nov. et *Rosierodon anceps* gen. et sp. nov.). Upper and lower molariforms of *Brachyzostrodon* are associated for the first time. Among 'symmetrodonts', one new species of *Kuehneotherium*, *K. stanislavi* sp. nov., and a new genus of Kuehneotheriidae, *Fluctuodon necmergor* gen. et sp. nov., are described. *Woutersia* is revised. The hitherto unknown upper molariforms of *Delsatia* are identified. Among haramiyids, the description of the material referred to *Thomasia* demonstrates the need for an exhaustive revision of this genus. *Theroteinus* is revised, with the erection of a new species, *T. rosieriensis* sp. nov. This study raised several issues on the systematics of earliest mammaliaforms, especially on definition of key taxa.

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### Erymid fauna (Crustacea: Decapoda: Erymidae) in french Early Cretaceous deposits

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Erymid lobsters (Crustacea, Decapoda, Erymidae) are relatively common and abundant in Jurassic rocks (c. 70 species) but are far less common in the Early Cretaceous with only around 20 species listed in Europe, North America, South America, Australia, Antarctic, Japan and Madagascar. Here we present a study of the twelve species of erymid lobsters from the Early Cretaceous of France. Based on new observations, the concepts of some erymid genera are updated and new diagnoses are proposed for *Eryma* Meyer, 1840, *Enoploclytia* McCoy, 1849, *Palaeastacus* Bell, 1850, *Pustulina* Quenstedt, 1857 and *Stenodactylina* Beurlen, 1928, including carapace groove pattern, morphology of first pereopods and also a complex new structure – the post-orbital area – located in front of the cephalic region. The new genus *Tethysastacus* is erected on the basis of its very simple groove pattern compared to previous genera and includes *Tethysastacus tithonius* (Van Straelen, 1936) n. comb. (Valanginian, France) as type species. Four new species from France are also described: *Eryma vocontii* n. sp. (Albian) which extends the stratigraphic range of *Eryma* to the Albian, *Pustulina occitana* n. sp. (Berriasian), *Pustulina colosseae* n. sp. (Hauterivian) and *Enoploclytia augustobonae* n. sp. (Barremian) which is the oldest known *Enoploclytia* representative.

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### The ecological and phylogenetic significance of gill arch and gill raker morphology from computed tomography (CT) scanning

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Pachycormids are a modestly diverse clade of Mesozoic fishes thought to show a range of trophic ecologies. Claims about pachycormid feeding ecology have largely been made based on external anatomy (e.g. jaw and tooth structure), but there is some evidence for additional specializations of the gill arches and associated rakers. In order to further investigate the relevance of these undersampled traits, we used CT scanning to examine *in situ* gill skeletons of pachycormids with very different oral dentitions: the tooth-bearing *Pachycormus* (Early Jurassic), the fang-bearing *Hypsocormus*, and edentulous



*Martillichthys* (both Late Jurassic). We find that raker morphology differs considerably between these genera. Based on revised phylogenetic analyses incorporating our new anatomical observations, we find that taxa with broadly similar raker morphologies are closely related, with the most conspicuous example being the presence of long, elaborate rakers in the putatively suspension-feeding edentulous pachycormids. This suggests that raker morphology provides both phylogenetic and ecological information, and that key divergences in pachycormid evolution that appear to be ecologically driven are associated with apomorphic gill raker morphologies. Inclusion of additional characters observed via CT may further improve understanding of pachycormids relationships to both one another and other early crown neopterygians.

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### Intrinsic and extrinsic ecological determinants of extinction at the End-Triassic mass extinction

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We assess the ecological effect of the End-Triassic mass extinction on marine communities along with the functional patterns of recovery into the Early Jurassic. Using the Bambach ecospace model, we show that, although taxonomic extinction was severe, extinction amongst functional groups was less so, with only two modes of life apparently disappearing at the end of the Triassic. We assess how intrinsic and extrinsic ecological factors influence extinction intensity. Extinction was highest in the tropics, and Panthalassan taxa suffered higher extinction rates than taxa residing in the Tethys Ocean. Reef taxa suffered the highest levels of extinction, whilst those inhabiting the continental shelf were the least affected. An erect benthic or pelagic mode of life appears to have been most susceptible to extinction whilst suspension feeders, particularly those with presumed symbiotic relationships, suffered higher extinction rates than taxa displaying other feeding strategies. Non-motile taxa appear to have suffered higher levels of extinction than motile taxa. The results show that both intrinsic and extrinsic ecological factors have a bearing on whether taxa are more or less likely to survive a mass extinction event and that determinants of extinction at major biotic crises differ from those during periods of background extinction.

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### Testing terrestrial tetrapod diversity change across the Carboniferous–Permian Boundary

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The Carboniferous and Permian (359–252 Ma) witnessed the establishment of the first terrestrial tetrapod ecosystems against a backdrop of major environmental change, including the collapse of the tropical rainforest biome at the end of the Carboniferous. However, there is disagreement surrounding the patterns of tetrapod diversity change during this interval, stemming from the ongoing debate on the importance of spatial and temporal sampling biases in the fossil record. To investigate early tetrapod diversity across



the Carboniferous–Permian boundary, a new global dataset (>400 species from 520 unique localities) has been created within the framework of the Paleobiology Database. Raw data suggest a major increase in global and alpha taxic diversity from the late Carboniferous to early Permian, punctuated by lower diversity in the earliest Permian (Asselian–Sakmarian). This is distinct from previous datasets, which showed continuous diversity increases through this interval. However, these estimates do not account for temporal variations in sampling. We estimated sampling using formation counts and locality numbers, and used a residuals approach to model diversity changes: provisional results support a period of reduced diversity in the earliest Permian, following the rainforest collapse. Ongoing work is estimating diversity using additional approaches including SQS and TRiPs.

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### Geochemistry of early Middle Triassic sedimentary sequences from Winterswijk (the Netherlands): reconstructing the palaeoenvironmental conditions and taphonomic preservation of a sauropterygian assemblage

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The Winterswijkse Steengroeve quarry complex in the east of the Netherlands exposes a ~40 m thick sedimentary sequence comprising intertidal and shallow marine strata. The overall transgressive sequence consists of primary and reworked carbonates of a microbial origin. These early to middle Anisian strata were deposited in and alongside the northeastern margin of the epicontinental Muschelkalk Sea. Numerous beds within the succession preserve a shallow marine palaeofauna through a relative abundance of skeletal material from sauropterygians, fishes and crustaceans. Improved insight into the trophic relations within this habitat can help elucidate the mode and pacing of ecological recovery after the Permo–Triassic mass extinction event. Biogeochemical proxies may provide crucial information on such ecological interrelations, but untangling the primary biological signal from secondary diagenesis has proven to be complex. Here we present a detailed lithostratigraphical description accompanied by natural gamma-ray analysis and stable carbon and oxygen isotope data of the sediment matrix from the Winterswijkse Steengroeve locality. These stratigraphic records and geochemical analyses provide important information regarding the sedimentary and diagenetic conditions and will aid correlation. This contextual information on preservation and palaeoenvironment is a prerequisite towards understanding the trophic relations during the biotic recovery after the Permo–Triassic mass extinction.

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### Myriapod transcriptomics and the timing of terrestrialization

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Phylogenomic analyses of Myriapoda based on novel Illumina transcriptomes have reinforced myriapod monophyly and a sister group relationship with Pancrustacea, strengthened a centipede–millipede clade as an alternative to the traditional Progoneata,



and retrieved ordinal-level topologies that are mostly compatible with morphological hypotheses. For the most complete taxonomic sample (including most orders of Diplopoda and nearly all families of Chilopoda), ten supermatrices explored the effect of several potential phylogenetic biases at different levels of gene occupancy per taxon. The morphologically-supported scheme of centipede relationships is recovered in matrices that maximize gene number but at the expense of lesser gene occupancy, whereas more complete matrices using fewer genes produce more morphologically anomalous groupings. Coding calibration fossils in a morphological matrix designed around extant species in the transcriptomic sample facilitates internally-consistent node calibration as well as total evidence dating. The first *Illumina* transcriptomes for Pauropoda and both symphylian families allows the Edafopoda versus Dignatha controversy to be tested. Divergence estimates for total-group Chilopoda and Diplopoda in the Cambrian substantially pre-date palaeontological evidence for these groups, which are first known from crown-group fossils in the Přidolí-Lochkovian. The myriapod stem group remains one of the enigmas of the arthropod fossil record.

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### The Pleistocene rise and current threat of the reef coral *Acropora*

**Kilian Eichenseer and Wolfgang Kiessling**

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Staghorn corals of the genus *Acropora* are dominant reef-builders in modern Indo-Pacific reefs and have been prevailing in Caribbean reefs until the 20th century. The fossil record of *Acropora* dates back to the Paleocene, yet throughout most of the Cenozoic, *Acropora* is a minor component of fossil reefs and only became widely abundant during the Pleistocene. To demonstrate the veracity of this trend we investigated spatial and temporal fluctuations of *Acropora* abundance and diversity in the Cenozoic fossil record and today. Neither climatic data predicting weathering intensity nor experiments on the dissolvability of different coral genera indicate a taphonomical bias against *Acropora* in the fossil record. To explain the apparent mismatch between the evolutionary rise of *Acropora* and its ascent to ecological dominance in reefs, glacioeustatic sea-level fluctuations have been evoked. The fast growth and easy asexual reproduction by breaking off branches allowed staghorn corals to keep up with rapid sea-level rise. In contrast to its geologically recent success, *Acropora* is particularly vulnerable to anthropogenic stressors. Fossil abundance of coral genera appears to be unrelated to their ability to cope with the recent disturbances.

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### Body size evolution in major amniote clades during the late Palaeozoic–Early Mesozoic

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Basal therapsids, archosauromorphs and parareptiles were characteristic elements of terrestrial faunas during the Palaeozoic to Mesozoic transition. Late Permian and Early Triassic ecosystems were dominated by Therapsida. These ecosystems were subsequently replaced by archosauromorph-dominated ecosystems in the later part of the Triassic. The parareptiles flourished mainly during the middle Permian, hit a diversity peak right after the end-Permian mass extinction event but went extinct at the end of the Triassic. Here we



present preliminary results of our analyses of body size evolution during the Late Permian–Early Jurassic in these major amniote clades. Using phylogenetic comparative methods different models of continuous character evolution were fitted against available body size data. The changes in body size among archosauromorphs are best explained by an early burst (EB) model. Parareptiles follow an Ornstein–Uhlenbeck (OU) model. Models that allowed for rate variation along different branches did not outperform a simple Brownian motion (BM) model in both cases. Body size evolution in Therapsida is best explained by an OU model (closely followed by EB). A heterogeneous rate model was favoured over a homogeneous rate BM model. Major rate increases are found among Late Permian dicynodonts and Early–Middle Triassic therocephalians.

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### Assessing the burrowing capacity in trilobites using finite element analysis

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An infaunal ethology has been confirmed for some trilobites such as the Cambrian *Agraulos* or the Ordovician *Asaphus* due to *in situ* preservation. However, burrowing behaviour is inferred (most of the time) for the functional morphology of trilobite taxa and a total lack of direct evidence is found. This is the case for some Cambrian and Ordovician trilobites such as *Monkaspis*, *Neseuretus* or *Megistaspis*. *Monkaspis* and *Megistaspis* had some morphological features such as a dagger-shaped body, smooth surface, wedge-shaped cephalon and the blade-shaped space in front of the glabella that seemingly allowed them an infaunal burrowing behaviour. However, in the case of *Neseuretus*, *Asaphus* and *Agraulus* they do not have such a mosaic of morphological features. Given this disagreement between the shape and the putative behaviour, we assess their capacity, from a biomechanical point of view, to make burrows using final element analysis (FEA). The stress distributions and the displacements obtained from the FEA models show a correlation between the areas with lower stresses and lower displacements in the librigenae. These results point out a structural behaviour in the cranidia capable of withstanding the forces produced during burrowing.

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### Secular variation of *Bathynotus kueichouensis* (Cambrian Series 2 Stage 4) from the Wuliu-Zengjiayan section of the Kaili Formation, South China

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Geographic variation is important in taxonomy, but temporal variation enjoys less attention, mainly because of the lack of sample size. Taxa close to extinctions suffer environmental stresses due to abiotic factors such as fewer food resources and isostatic or chemical changes. A secular study of the morphology below an extinction level allowed us to recognize morphological patterns prior to the extinction event. The cosmopolitan *Bathynotus kueichouensis* disappears a few metres below the Cambrian Series 2–3 border. Here we present a preliminary study to assess the morphological variation using geometric morphometric methods throughout the stratigraphic record of this taxon from a single section. The preliminary results suggest a variation in the size of the palpebral lobe, being



larger in the early specimens and becoming increasingly smaller towards the top of the section. A possible interpretation of this is environmental changes from deeper water to shallower waters toward the top of the stratigraphic record of *B. kueichouensis*. Further work is necessary and more taxa need to be included in this study to assess whether morphological patterns can be recognized prior to an extinction. Thus, causes of the secular variation of *B. kueichouensis* remain open.

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## High ectoparasitic pressure in early vertebrates inferred from the analysis of their squamation patterns

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Parasitic evidence is difficult to ascertain in the fossil record due to the soft-bodied nature of parasites. Only a few cases of exceptionally preserved fossils show traces or skeletal pathologies that can be putatively linked to a parasitic origin. Interestingly, several authors have proposed that some aspects of the squamation of schooling sharks have evolved in response to ectoparasitic pressure, providing an alternative approach for addressing this issue. Here we characterise the squamation pattern of extant schooling sharks, measuring different scale variables in eight body areas of 70 specimens, in order to establish a comparative framework for predicting high ectoparasitic pressures in extinct vertebrates. Our results show that species under strong ectoparasitic pressure have optimized some aspects of their squamations (reduction in the scale density and increase in crown angle) avoiding the settlement of ectoparasites. Similar patterns are here described in the thelodont *Lanarkia horrida*, suggesting that ectoparasitism could be an important pressure selection in the early stages of the evolution of the group, and that social interactions could be present in vertebrates as early as Silurian times.

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## Evolution and functional morphology of Cretaceous pelagic microcrinoids

**Andrew S. Gale**

University of Portsmouth, UK

The Roveacrinida are tiny pelagic microcrinoids which were abundant, even locally rock-forming, in Cretaceous oceans, but are often missed or ignored by palaeontologists. They underwent two main periods of phylogenetic radiation (Albian, Lower Campanian) both of which generated diverse and unusual morphologies which are interpreted as adaptations for weight reduction (skeletal thinning and voids), protection (short arms which cover soft tissues and elongated spines) and vertical migration in the upper water column (stabilizing spines, asymmetrical processes to cause rotation). The record of the latter radiation (Campanian) is very well represented by diverse taxa, and phylogenetic analysis demonstrates the presence of iterative morphological trends. Roveacrinida remained abundant and moderately diverse up to the K-Pg boundary event, which evidently brought about their extinction.



## Evaluation of several cladistic methodologies and their impact on a palaeontological dataset: the case of Diplodocidae (Dinosauria: Sauropoda)

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In order to assess reliable phylogenetic relationships between different taxa using cladistics, a good dataset by itself is not sufficient. The methodology with which the matrix of characters is treated plays a key role in the recovery of evolutionary lineages. The aim of this study is to discover the best methodologies to analyse the matrix of a particular clade: the Diplodocidae. Twelve analyses were performed, confronting different types of characters (discrete or continuous), weighting procedures (*a priori* weighting versus implied weighting) and ways to implement uncertain ratios or ranges in continuous characters. The results obtained were evaluated with the aid of different stratigraphic indexes to determine which methodology performed better by placing the most ancient taxa in a more basal position in the phylogenetic tree compared to more recent ones. In conclusion, the methodologies that perform better are the ones based on discrete characters scores, whereas the adoption of implied weighting does not seem to have a great influence. The use of uncertain character measures can lead to unresolved phylogenetic trees, which is probably due to the implementation of the algorithms used in the phylogenetic analysis.

## <sup>34</sup>S/<sup>32</sup>S of vertebrate apatite: a new tracer of past living environment

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In ecological studies, the sulfur isotope composition ( $\delta^{34}\text{S}$  values) of soft tissues allows the determination of both past and present-day living environments of organisms. However, technical limitations have so far prevented reliable sulfur isotope analyses of minerals having low sulfur content, such as bioapatite, the crystalline component of skeletal tissues. The development of 'purge-and-trap' technology in elemental analysers has recently demonstrated new possibilities to solve some of those technical difficulties. We have used a VarioPYROcube elemental analyser (EA) equipped with 'purge-and-trap' technology, interfaced in continuous flow mode to an Isoprime 100 isotope ratio mass spectrometer, to measure the sulfur isotope compositions of bioapatite samples. Our results demonstrate the capacity of this analytical setup to measure the  $\delta^{34}\text{S}_{\text{V-CDT}}$  values of low-S bioapatite samples (0.14 to 1.19 wt%) with a good analytical precision ( $1\sigma = 0.5$ ;  $n = 14$ ). Our results also show that the  $\delta^{34}\text{S}_{\text{V-CDT}}$  values of modern and fossil vertebrate bioapatites allow discrimination between marine environments and freshwater or terrestrial ones. Sulfur isotope analysis of bioapatite has great potential to track the living environment of extinct vertebrates for which only fossilized bones or teeth have been preserved.





## Oceanic island vegetation buried by recurrent Holocene explosive eruptions: preliminary results from Faial Island (Azores, Portugal)

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On volcanic islands, the interaction between explosive volcanic events and the vegetation creates ideal taphonomical settings for plants and soils to be buried and preserved. In the Azores Islands the palaeobotanical record is linked with the volcanic activity. Although plant macrofossils have been known since the 19th century, palaeovegetation diversity and palaeoecology of Azores Islands is still poorly known. Efforts to define a pre-colonization vegetation are based mainly on historical descriptions, on the surviving native vegetation, and on fossil pollen analysis from lake or bog cores. Here we present the preliminary results from a palaeobotanical survey on Faial Island. The island has a record of 12 sub-plinian and phreatomagmatic trachyte eruptions younger than 16 ka BP. Several sites with unaltered trunks, charcoallified trunks in ignimbrite deposits and leaf fossils preserved in tuffs, associated with palaeosols, were recognized during fieldwork. Other outcrops expose palaeosols preserved within sequences of pumice fall deposits. We propose that the combination of macrofossils and pollen assemblages from palaeosols buried by deposits of the same volcanic event sampled at different elevations will contribute to the reconstruction of Faial Island's past vegetation. Moreover, the vegetation resilience between eruptions can be tested. Extant neocological studies of Azores vegetation will gain significantly from this palaeobotanical perspective.

## The fossil record of the other end of the size range – tiny predatory arthropods

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A predator is a fascinating type of organism. Part of this fascination is perhaps caused by the feeling of being in danger when thinking of or looking at a predator. This is likely also the reason why a majority of the public like large or super-sized predators. Luckily, the fossil record has a rich variety of such forms available. Groups such as eurypterids, *Anomalocaris*, *Dunkleosteus*, *Liopleurodon* or *Tyrannosaurus* can be easily recognized by the non-specialist. Yet, these super-sized predators are nothing less than the tip of the iceberg. Many more medium-sized predators have been identified in the fossil record, each being a few centimetres in size and eating smaller prey whilst most likely being themselves eaten by the larger predators. We can even scale further down. Many modern-day predators are less than 5 mm in size and represent an important part of the modern food web. It might seem more unlikely that such small-sized predators can be identified in the fossil record. However, we will present examples of such tiny fossil predators from among the arthropods, from various eras throughout the Phanerozoic and in numerous different preservation types.



*Journal of Paleontological Techniques*: a free, open-access journal exchanging knowledge between technicians, preparators and researchers

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*The Journal of Paleontological Techniques* (JPT) was established in 2006 in the Museu da Lourinhã (ML), Portugal, to provide a platform for preparators of the ML to share ideas and knowledge with their peers. It has grown to be an open-access, free journal, publishing mostly on the collection, preparation, conservation and exhibition of natural history objects, such as holotypes of extant species, fossils and historical museum specimens. These natural history objects provide a wealth of information on past and present biodiversity. Because collection and/or conservation techniques might alter the objects in ways that could negatively influence the outcomes of future research, a detailed report of the methodologies used from acquisition to conservation of specimens is crucial. Despite the importance of such reports, until recently, no specific, scientific publications existed for museum technicians and scientists to share knowledge. *The Journal of Paleontological Techniques* publishes a wide variety of articles, ranging from excavation reports and papers on preparation techniques to new methodologies in collection management and scientific study, among others. Manuscripts are subjected to peer-review to ensure high scientific standards. Papers are published as single-paper volumes upon final approval of the proofs, and are available in PDF format under a CC-BY licence. The editorial board currently consists of an international group of early-stage scientists. Most editors have a palaeontological background; however, all have a unique expertise within that field (e.g. microscopy, photogrammetry, phylogeny, morphometrics, preparation and microbiology). JPT welcomes your submissions!

## Skeletal structure and function in the stemless crinoids *Marsupites* and *Uintacrinus*

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*Marsupites* and *Uintacrinus* were unusual articulate crinoids with an enlarged, globose calyx and five long, branched arms, but no stem, holdfast or other attachment structures. They lived during the Late Cretaceous ‘golden age’ of crinoid diversity, reaching near-global distribution with up to five species and subspecies stretching across the Boreal, Tethyan and Austral realms. They are also known for their exceptional preservation in Lagerstätten such as the Niobrara Chalk, Kansas, USA. The stratigraphic ranges of the two genera overlap, relatively briefly, for 200 ka in the Santonian–Campanian. They remain somewhat enigmatic, with alternative life habits suggested: from a benthic reclining ‘snowshoe’ to an actively swimming ‘hemipelagic dredger’. It appears, however, that they may have shared a unique calyx structure. Here we present analyses of skeletal structure, including plate size, density and organization, with implications for the life habits and evolutionary relationships of these aberrant Cretaceous taxa.



## Exploring the unrealised potential of the brachiopod collections at the Natural History Museum, London

**Zoe Hughes, Chris Hughes, Richard J. Twitchett and Kenneth G. Johnson**

*Natural History Museum, London, UK*

The NHM, London's brachiopod collections have enormous, unrealised, scientific potential. Well-preserved brachiopods are an archive of palaeoenvironmental information, and geochemical analyses of their shells provide proxy data for a range of parameters such as temperature. They are common, robust, and widespread, and are model organisms for size-change studies. There are ~1,000 drawers of Mesozoic and Cenozoic brachiopods in our collections, which provide a potential of several orders of magnitude increase in published occurrences from that critical time interval. One key problem in realising this potential is the current curatorial state of the collections. The absolute numbers of specimens are unknown (as many individuals might be registered under one number); others are in old, unacceptable containers, lack critical locality or stratigraphical information, or are in too poor a state to be easily digitized. As a first step in realising the full potential of our brachiopod collections we are conducting a collections survey to enhance their potential utility and to identify those that have most scientific potential and which should be prioritized for digitization. Preliminary results indicate that there are c. 400,000 Mesozoic–Cenozoic specimens of which 20% are assigned to the best stratigraphic and geographic resolution.

## Reconstruction of the motion and hindfoot posture of *Rhoetosaurus brownei* Longman, 1926 (Sauropoda, Gravisauria)

**Andréas Jannel, Olga Panagiotopoulou, Anthony Romilio, Jay P. Nair and Steven W. Salisbury**

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The Middle Jurassic (Late Bathonian–Middle Callovian) basal sauropod *Rhoetosaurus brownei* is the largest known pre-Cretaceous terrestrial Australian vertebrate. Represented as a near-complete right hind limb, key aspects of the palaeobiology of *Rhoetosaurus* remain unresolved. The current study combines three-dimensional modelling and photogrammetry to reconstruct the range of motion (ROM) of the foot of *Rhoetosaurus* to elicit pedal flexibility and posture. Our findings show that *Rhoetosaurus* had a high degree of digit mobility at all the metatarsophalangeal joints (total excursion angle >80°) and in the sagittal, transverse and frontal planes at the distal-most interphalangeal joints (excursion angle >100°). The position of the autopodial articular surfaces suggests that the metarsophalangeal joints were permanently elevated in life, an indicator of skeletal digitigrady. This joint may have been ventrally connected with the plantar aspect of the foot by a compliant fibrous pad, consistent with sauropod track data, and therefore likely to have been functional plantigrade, as has been previously suggested. These results provide new insights into the simulated ROM and posture of the hind foot of *Rhoetosaurus*; we recognize that additional parameters (including loading regimes and ichnological data) provide future modelling aspects to further our understanding of *Rhoetosaurus* pedal biomechanics.



## Dessine-moi une courbe de diversité des conodontes

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Conodonts underwent a decline in terms of diversity and disparity across the Silurian Period, sharply contrasting with their outstanding diversification in the Ordovician. Abiotic factors have been invoked as the main controls over Silurian conodont turnover at the regional scale, but the mechanism of this purported control is unclear. In order to formulate testable hypotheses concerning conodont diversity, a measure of turnover and an understanding of its spatial scale are required. The Silurian (uppermost Telychian through Ludfordian) succession of Gotland, Sweden, provides an unparalleled opportunity to quantify local (sample and habitat) and regional components of conodont diversity, thanks to four decades of exhaustive sampling by the late Lennart Jeppsson. A succession of coeval assemblages derived from a range of environments allows us to quantify community turnover and track environmental niches of individual species across an interval of *c.* 10 million years, and ultimately offers a chance to translate local ecological processes into macroevolutionary patterns.

## A new key Smithian (Early Triassic) quantitative ammonoid biochronology from the western USA basin

**Romain Jattiot<sup>1,2</sup>, Hugo Bucher<sup>1</sup>, Arnaud Brayard<sup>2</sup>, Morgane Brosse<sup>1</sup>, Jim Jenks<sup>3</sup> and Kevin Bylund<sup>3</sup>**

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Since the pioneering work of Silberling and Tozer (1968), the western USA basin has been known to include an excellent record of Smithian ammonoids. The Smithian is a crucial time interval, recording the first global, major diversification–extinction cycle after the Permian–Triassic boundary mass extinction. Our intensive sampling of the lower portion of the Thaynes Group in the Palomino Ridge area (northeastern Nevada) yielded abundant and well-preserved Smithian ammonoid faunas. Based on new data from Palomino Ridge and previous data from neighbouring localities in Utah, we present the first quantitative Smithian ammonoid biochronological scheme for the western USA basin. The biochronological sequence comprises five unitary association zones that can be correlated with other localities from the Northern Indian Margin. Three unitary association zones (UAZ1, UAZ2 and UAZ3) are defined for the early Smithian, one (UAZ4) spans the entire middle Smithian and one (UAZ5) comes into the first part of the Late Smithian. Finally, a provisional UAZ6 could represent the second part of the Late Smithian. This zonation stands in contrast to the 14 Smithian unitary association zones previously established in the Northern Indian Margin. The latter is shaped by much higher turnover rates, especially during the middle Smithian.



## Reconstructing the internal anatomy and lifestyle of a Jurassic crustacean from the La Voulte Lagerstätte

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The La Voulte Konservat-Lagerstätte is a renowned site from the Callovian (Jurassic). Its exceptionally fine-detailed preservation – in three-dimensional sideritic nodules – yields various fossils, including crustaceans. X-ray microtomography was applied to an exceptionally preserved specimen of a polychelidan lobster to investigate its external and internal anatomy. Polychelidans are fascinating crustaceans that were known from their fossils before their extant counterparts were discovered in the deep sea. They differ from other crustaceans by having four or five pairs of claws. Although recent palaeontological studies have clarified the systematics and phylogeny of the group, the biology of extant polychelidans and their anatomy are poorly documented. Numerous aspects of the evolutionary history of the group remain obscure, in particular how and when polychelidans colonized the deep sea and became restricted there. The revealed key parts of the external and internal anatomy – mouthparts, digestive tract and reproductive organs – of *Voulteryon parvulus* (Eryonidae) compared with dissected specimens clearly identify this specimen as a female with mature ovaries. This set of new observations offers new insight into the feeding and reproductive habits of these Mesozoic animals. Contrary to other Jurassic polychelidan lobsters, *V. parvulus* spawned, and probably inhabited, relatively deep-water environments, as do extant polychelidans.

## Development origin of the synsacral in jawed vertebrates: implications for vertebral development and fusion

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The synsacral is a structure incorporating multiple elements of two or more anterior vertebrae of the axial skeleton, forming immediately posterior to the cranium. It has been convergently acquired in the fossil group 'Placodermi', in Chondrichthyes (Holocephali, Batoidea), and to varying degrees in certain mammalian taxa. Examination of early developmental stages indicates that in the Batoidea and the 'Placodermi', individual vertebrae developed normally and only later become incorporated into the synsacral, implying regular somite segmentation and vertebral development. Here we show that in the holocephalan *Callorhynchus milii*, uniform and regular vertebral segmentation also occurs, with anterior individual vertebra developing separately with subsequent fusion into a synsacral. Vertebral elements forming directly behind the synsacral continue to be incorporated into the synsacral through growth. This appears to be a common pattern through the Vertebrata. Our observations on synsacral development in three major groups of early jawed vertebrates also indicate that fusion involves heterotopic cartilage and perichondral bone/mineralized cartilage developing outside the regular skeleton. We suggest that chondrichthyans have potential as ideal extant models for identifying the genes involved in these processes and to better understand the evolution of regionalization in vertebrates.



## Anti-predation strategy, growth rate and extinction amongst Pliocene scallops of the US eastern seaboard

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*Placopecten*, *Chesapecten* and *Carolinapecten* are scallop (pectinid bivalve) genera occurring in the Pliocene of the US eastern seaboard. The first, present in the area today, is a smooth, streamlined form, adept at escaping predators by swimming ('flight' strategy). The other two, which are extinct, are plicate ('ribbed') forms. Plication facilitates a 'resistance' strategy towards predators which is benefited by large size and high shell thickness – maximally so if these states are achieved early in life. Oxygen isotope profiles show that early ontogenetic extensional growth in Pliocene *Placopecten* was at the same moderate rate as in modern *Placopecten*. By contrast, in *Chesapecten* it was as fast as in the fastest-growing modern scallop (c. 80 mm per annum), and accompanied by development of an unusually thick shell, while in *Carolinapecten* it was substantially faster still (>140 mm per annum). Rapid growth in *Chesapecten* and *Carolinapecten* was probably enabled by high primary productivity, for which there is evidence from carbon isotope data, sediment composition and the associated biota. The extinction of *Chesapecten* and *Carolinapecten*, and the survival of *Placopecten*, can be attributed to a decline in primary productivity which prevented a maximally effective 'resistance' strategy towards predators but had no deleterious impact on a 'flight' strategy.

## Palaeoneuroanatomy of *Phuwiangosaurus sirindhornae* from the Sao Khua Formation in Thailand

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Mahasarakham University, Thailand

A very well-preserved and nearly complete braincase of *Phuwiangosaurus sirindhornae* has been discovered in the Early Cretaceous red beds of the Sao Khua Formation in Kalasin province, northeastern Thailand. It has been studied using computed tomographic techniques to generate three-dimensional models. The internal structure and endocast were compared with other sauropods. The endosseous labyrinth shows a close affinity to that of *Camarasaurus*.

## Evolution of animal behaviour in the Ediacaran–Cambrian transition

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The transition from the Ediacaran to the Cambrian (~541 million years ago) marks a fundamental leap in the evolution of life: the evolution of complex animal behaviour,



the decline in the microbial mats that characterised the Neoproterozoic, and a drastic change in the chemistry of the sediment–water interface. Disturbance is well known as a controlling factor in structuring modern communities. By combining detailed petrographic analysis with data on sedimentology, burrow densities, and ichnodiversity of the basal Cambrian stratotype we are able to place the evolution of animal behaviour recorded in these successions into an improved palaeoenvironmental context. Additionally, Ediacaran–Cambrian ichnofabrics are found to be comparable to experimentally produced ones created by simple ecdysozoans and lophotrochozoans collected from the dysoxic sediments of the Bonne Bay fjords of western Newfoundland. Using multivariate statistical analyses, it is possible to identify and quantify any correlation between palaeoenvironmental, ichnological and matground characteristics. This will create improved understanding of the interplay between biological and abiological processes during the evolution of complex animal behaviour in a palaeoenvironmental context.

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### Molecular evidence for a delayed emergence of modern squamates in the Middle to Late Jurassic

**\*Catherine Klein, Matthew A. Wills and Nicholas R. Longrich**

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Squamates (snakes, lizards and amphisbaenians) diverged from rhynchocephalians near the Permo–Triassic boundary. Their fossil record remains depauperate until the Cretaceous, producing extensive ghost ranges on phylogenies. Consequently, little is known of early squamate evolution. The oldest definitive fossils of crown squamates are Jurassic in age. On the basis of previous molecular clock models it has been estimated that this crown group originated near the Triassic–Jurassic boundary. Here we apply relaxed molecular clock models to existing trees and reveal that crown squamates may have originated later. Ten outgroup taxa and up to 44 calibration points are used, as multiple outgroup taxa and numerous calibration points are key to having a well-informed clock. The results suggest that basal divergences within squamates may have occurred in the Middle to Late Jurassic. This is consistent with the emerging pattern of vertebrates undergoing Mid-to-Late Jurassic radiations, observed so far in mammals, dinosaurs and pterosaurs. It also supports the suggestion that the Jurassic was an important period of diversification and evolutionary innovation.

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### Arumberiamorph structures discovered in modern microbial mats

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During the study of modern halotolerant microbial mats in salterns near the village of Kervael, western France we observed fanning-out and curved series of macroscopic ridges on the surface on a newly formed biofilm. The structure resembles the late Ediacaran fossil *Arumberia* which is widely distributed in Australia, Avalonia, Baltica, Siberia and



India, and it is always confined to intertidal delta-plain settings subject to fluctuating salinity conditions and periodic desiccation. Although the origin of the structure observed in modern microbial mats remains enigmatic, wrinkled and rugose variants of microbial biofilms exhibit, in general, increased levels of resistance to several environmental stresses. By analogy, the fossil *Arumberia* could be interpreted as a microbial mat morphotype developed in response to environmental perturbations in terminal Ediacaran shallow marine basins. If environmental conditions are likely to be responsible for the formation of *Arumberia*, it is then not that a specific biological community has survived since the Ediacaran – it is that the biological response of microbial communities that manifested itself quite commonly in certain terminal Ediacaran and early Cambrian environments can still be found today.

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### Palaeozoic acritarch diversity

**David M. Kröck<sup>1</sup>, Hendrik Nowak<sup>2</sup>, Claude Monnet<sup>1</sup> and Thomas Servais<sup>1</sup>**

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Most Palaeozoic acritarchs are thought to represent part of the marine phytoplankton and therefore may constitute a significant element at the base of the marine trophic chain during the Cambrian explosion and the subsequent Great Ordovician Biodiversification Event. It has been argued that a higher concentration of phytoplankton in the early Palaeozoic oceans triggered these major evolutionary events and had an important impact on metazoan diversification. The expanding and increasingly diverse phytoplankton could have served as food for the developing zooplankton, but also for various clades of suspension feeders and detritus-feeding organisms. Acritarch diversity remained high from the Ordovician to the Devonian. However, during the Devonian–Carboniferous boundary interval acritarch biodiversity significantly decreased, although a collapse of the marine food web is not observed in the fossil record. Here we present a new research project, based on a PhD research programme, to analyse the phytoplankton dynamics during the entire Palaeozoic. Similar to a prior study on Cambrian acritarch diversity (Nowak *et al.* 2016), we propose to reconstruct taxonomic diversity and disparity trends that can be compared with the biodiversity of marine invertebrates during the Palaeozoic. We will attempt to compile a complete database and calculate various diversity indices at global and regional scales.

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### RNames – a new stratigraphical database and a tool for occurrence-based palaeobiological analyses

**Björn Kröger and Kari Lintulaakso**

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RNames (<<http://rnames.luomus.fi/>>) is an open-access relational database linking stratigraphic units with others that are considered to be time-equivalent or time-overlapping. RNames is also a tool to correlate amongst stratigraphic units. The structure of the database allows for a wide range of queries and applications. Currently three algorithms are available, which calculate a set of correlation tables with Ordovician stratigraphic units, time binned into high-resolution chronostratigraphic slices (Global Stages; Stage Slices; and Time Slices). The ease of availability of differently binned stratigraphic units and the potential to create new schemes is one of the main advantages





and aims of RNames. Different time-binned stratigraphic units can be matched with other databases and allow for simultaneous up-to-date analyses of stratigraphically constrained estimates in various schemes. We exemplify these new possibilities with our compiled Ordovician data (+ 4,000 stratigraphic units, + 24,000 stratigraphic opinions, nearly 400 references) and analyse fossil collections of the Paleobiology Database based on the three different binning schemes. The presented diversity curves are the first sub-stage level global marine diversity curves for the Ordovician. A comparison among the curves reveals that differences in time slicing have a major effect on the shape of the curve.

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## Modelling the pattern of preservation of vetulicolians from the Cambrian Chengjiang Biota

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Vetulicolians are an enigmatic fossil group characterised by a bursiform anterior body (normally bearing five pairs of lateral pouches) and a segmented/annulated posterior body that, at least superficially, resembles that of arthropods. This unusual bodyplan and lack of information about anatomical structures within the anterior body make the interpretation of these animals problematic, with proposed affinities varying from unusual arthropods, stem-group deuterostomes, relatives of the tunicates, or chordates. Here we evaluate patterns of preservation across specimens and between localities, and quantify morphological characteristics for vetulicolians from the Chengjiang biota, to investigate how specific characters may be preserved or lost/decayed in the preservation sequence. This approach may elucidate their true taxonomic affinities.

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## Cambrian origin of mitrates (Echinodermata, Stylophora): new evidence from the Furongian of Korea and South China

**Bertrand Lefebvre<sup>1</sup>, Guiying Chen<sup>2</sup>, Seung-Bae Lee<sup>3</sup>, Fleur Noailles<sup>4</sup>, Samuel Zamora<sup>5</sup> and Xuejian Zhu<sup>6</sup>**

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Stylophorans are a clade of Palaeozoic echinoderms (middle Cambrian-Pennsylvanian) with a single feeding arm (aulacophore) and a flattened, fundamentally asymmetrical body (theca). In recent years, the traditional subdivision of the class Stylophora into the two orders Cornuta and Mitrata was questioned by several phylogenetic analyses, suggesting that (monophyletic) mitrates may derive from (paraphyletic) cornutes. Until recently, however, tackling phylogenetic relationships within stylophorans was seriously hampered by their limited Cambrian fossil record (especially in the Furongian) and apparently rapid diversification in Early Ordovician times. In the early 2000s, abundant, exquisitely



preserved stylophorans were collected in the Furongian of Guangxi Zhuang Autonomous Region, South China (Sandu Formation, Jiangshanian) and Korea (Dongjeom Formation, Stage 10). The careful examination of this material shows that it contains the oldest known undisputable remains of the three main clades of mitrates (lagynocystids, mitrocystitids and peltocystids) and, more importantly, that the morphology of these stylophorans shows a mixture of cothurnocystid (cornute-like) and more advanced (mitrate-like) features. These results not only confirm the paraphyly of cornutes, but they also suggest that the diversification of mitrates began in the Furongian. Consequently, their apparent rapid radiation in Early Ordovician times was largely the consequence of a poor late Cambrian fossil record.

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### A new solutan (Echinodermata, Blastozoa) from the Guzhangian (Cambrian Series 3) Weeks Formation of Utah, USA: evolutionary and palaeogeographic implications

**Bertrand Lefebvre<sup>1</sup> and Rudy Lerosey-Aubril<sup>2</sup>**

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A new solutan echinoderm is described from the upper part of the Weeks Formation (Guzhangian). The Cambrian (Series 3) succession of the central House Range in western Utah (USA) documents the early diversification of the class Soluta, which is characterised by a major ecological transition from sessile, 'pelmatozoan' primitive taxa (*Coleicarpus*, Wheeler Formation) to more and more vagile, temporarily attached (*Castericystis*, Marjum Formation) to mostly unattached, 'homalozoan' derived forms (new solutan, Weeks Formation). Although the fossil record of solutans remains patchy, the currently available data strongly speak to a Laurentian origin for this class in middle Cambrian times. The morphology of the Weeks solutan is remarkably intermediate between those of *Castericystis* and *Minervaeystis*. Its twisted, flattened dististele possibly represents an adaptation for a more efficient crawling atop soft substrates. This morphological feature also questions the phylogenetic relationships between syringocrinid and dendrocystitid solutans, and the possible evolution of the latter from basal *Minervaeystis*-like syringocrinids by paedomorphosis.

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### Exceptional late Cambrian fossils from McKay Group (British Columbia, Canada)

**Rudy Lerosey-Aubril<sup>1</sup>, Stacey Gibb<sup>1</sup>, John R. Paterson<sup>2</sup> and Brian D. E. Chatterton<sup>2</sup>**

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Documentation of non-biomineralizing animals that lived in the Furongian is essential for a comprehensive understanding of the diversification dynamics of early metazoans. Here we report new occurrences of exceptional preservation in Furongian strata of the McKay Group near Cranbrook, British Columbia, Canada. This locality has already yielded trilobites with phosphatized guts, all of the same species from the same interval. Two new horizons with soft-tissue preservation are documented; one has yielded a trilobite with an exquisitely-preserved gut belonging to a different species, the other a ctenophore and an aglaspigid arthropod. The ctenophore represents the first Furongian record of the



phylum and the first occurrence of Burgess Shale-type preservation in the late Cambrian of Laurentia. The aglaspidid is atypical in having twelve trunk tergites and a narrow 'tailspine'. The bearing of these features on the evolution of aglaspidid trunk tagmosis and the composition of aglaspidid exoskeleton will be discussed. The trilobite reveals previously unknown gut features, possibly related to enhanced capabilities for food processing. The fact that exceptional preservation is both stratigraphically more widespread and taxonomically more diverse in these deposits than previously realised offers promising perspectives for the study of the *c.* 600-m-thick unexplored part of the section.

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## New exceptionally-preserved arthropods from the middle Cambrian of Utah and Nevada, USA

**Rudy Lerosey-Aubril<sup>1</sup>, Andries Weug<sup>2</sup> and Jake Skabelund<sup>2</sup>**

<sup>1</sup>*University of New England, Australia*

<sup>2</sup>*Independent*

The Great Basin region of the western United States is home to nine Cambrian Konservat-Lagerstätten. None of them competes with the celebrated Burgess Shale (middle Cambrian, Canada) regarding the abundance of exceptionally-preserved fossils, but with time some have yielded rather diverse biotas. Still, new discoveries of exceptional material in these deposits remain important, for most of the non-biomineralizing taxa are known from a few incomplete specimens. Here we present exceptionally-preserved arthropods recently discovered in middle Cambrian strata of the Great Basin region. A specimen from the Pioche Formation (Nevada), apparently preserving nervous structures, represents the first occurrence of *Alalcomenaeus* (Megacheira) in this region. The Wheeler Formation (Utah) has yielded a large new taxon, characterised by hook-shaped pleurae and possibly related to *Sanctacaris*. The other fossils were recovered from the Marjum Formation (Utah). This includes a new arthropod displaying cephalic appendages with two antenniform branches, a median eye, and phosphatized digestive glands. Similarly phosphatized guts are described in specimens of *Modocia* (Trilobita) – these are the first examples of preservation of internal organs via phosphatization in this Konservat-Lagerstätte. An agnostid displaying cephalic appendages and a well-preserved specimen of *Naraoia*, the fifth to be found in these deposits, are also documented.

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## Filamentous fossils within the Ediacaran macrobiota: reproduction, construction and palaeoecology

**Alex Liu**

*University of Cambridge, UK*

Late Ediacaran (~580–560 Ma) fossil assemblages from Newfoundland, Canada, reveal abundant, previously undescribed macroscopic filamentous fossils within benthic deep-marine palaeocommunities. Filamentous structures occur in densities of hundreds per square metre, and exhibit a range of morphologies. Some filaments of centimetres to decimetres in length are observed to attach frondose organisms to the substrate, and represent a novel body plan within that group. Other filaments, of a few millimetres to several metres in length, traverse bedding surfaces, can bifurcate, and seemingly connect individual macro-organisms, potentially providing fossil evidence for a recently hypothesized stolon-like reproductive strategy within some Ediacaran taxa. Similar filamentous



impressions from the Ediacara Member of South Australia, and the Charnian Supergroup of Charnwood Forest (UK), demonstrate filamentous structures to be a widespread and prominent component of global Ediacaran macrofossil assemblages. Study of the spatial relationships between filamentous structures and contemporaneous macrofossil taxa offers a new avenue via which to investigate aspects of Ediacaran palaeoecology. Importantly, the close association of certain macrofossil taxa with filamentous impressions offers novel means by which to constrain their phylogenetic positions.

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### High diversity of small dinosaurs preceding the Cretaceous-Palaeogene (K-Pg) mass extinction

**Nicholas R. Longrich**

*University of Bath, UK*

Dinosaurs dominated on land for almost 150 million years, before disappearing at the end of the Cretaceous, 66 million years ago. Based on the best-known late Maastrichtian dinosaur assemblage, the Lancian fauna of western North America, it has been assumed that Maastrichtian dinosaur faunas were low in diversity and dominated by large species. However, small dinosaurs rarely preserve and tend to receive less attention, suggesting that these patterns may result from biases in preservation and study. A study of small dinosaurs from North America shows that a diverse fauna of small dinosaurs thrived alongside giants such as *T. rex* and *Triceratops*. New species of small Dromaeosauridae, Troodontidae, Caenagnathidae, Alvarezsauridae and Ornithischia are documented here. Total diversity includes 38 species ranging from 2 to 50,000 kg, occupying carnivorous, herbivorous, insectivorous and piscivorous roles; most (60 %) weighed  $\geq 1,000$  kg and many (40 %) weighed  $\geq 100$  kg. Hatchling *Tyrannosaurus*, *Nanotyrannus*, *Triceratops* and *Edmontosaurus* are present, emphasizing the role of juveniles in the food chain. Lancian dinosaurs exploited a remarkable range of niches, to a greater degree than almost any other fauna. These patterns are consistent with a catastrophic extinction of dinosaurs at the K-Pg boundary, driven by the Chicxulub impact.

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### A molecular palaeobiological investigation into arthropod terrestrialization

**Jesus Lozano-Fernandez<sup>1</sup>, Robert Carton<sup>2</sup>, Alastair R. Tanner<sup>1</sup>, Mark N. Puttick<sup>1</sup>, Mark Blaxter<sup>3</sup>, Jakob Vinther<sup>1</sup>, Jørgen Olesen<sup>4</sup>, Gonzalo Giribet<sup>5</sup>, Gregory D. Edgecombe<sup>6</sup> and Davide Pisani<sup>1</sup>**

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Animals have marine origins and only a few phyla contain fully terrestrial lineages. The process through which animals adapted to life on land is referred to as terrestrialization, and is an extreme case of adaptation. Arthropoda represent the largest majority of terrestrial biodiversity and have an extensive fossil record that suggests they were the first terrestrial animals. Arthropods colonized the land multiple times independently, allowing rigorous comparison of the alternative solutions adopted by the different groups to the same adaptive challenge. In this study we implemented a molecular palaeobiological approach,



merging molecular and fossil evidence, to elucidate the deepest history of the terrestrial arthropods. We focused on the three, independent, Palaeozoic arthropod terrestrialization events (Myriapoda, Hexapoda and Arachnida) and showed that a marine route to the colonization of land is the most likely scenario. Molecular clock analyses confirmed an origin for the three terrestrial lineages bracketed between the Cambrian and Silurian. While molecular divergence times for Arachnida are consistent with the fossil record, Myriapoda and Hexapoda are inferred to have colonized land earlier. An estimated origin of myriapods by the early Cambrian substantially predates trace or body fossil evidence, and raises the possibility of independent terrestrialization events in crown-group myriapods.

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## Two new enigmatic worms from the Chengjiang biota

**Xiaoya Ma<sup>1,2</sup>**

<sup>1</sup>*Yunnan University, China*

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

The fossilization of vermiform animals is relatively rare due to their soft bodies, which is why they only occur in some exceptionally preserved fossil assemblages, such as the early Cambrian Chengjiang Lagerstätte. Despite the great diversity of vermiform species recovered from the Chengjiang Lagerstätte, almost all of them are assigned to Priapulida or its close relatives, which were once dominant members of the benthic fauna in Cambrian marine communities. However, there is still little known about the early evolution of other vermiform phyla and their lifestyles. This study reports and describes two new non-priapulid vermiform taxa from the Chengjiang Lagerstätte. The fossils are very rare, as only one specimen has been discovered for each species in over 30 years of collecting. However, the specimens show distinct features that distinguish them from other reported fossil worms. For example, one of the species shows a close resemblance to acanthocephalans. Although the taxonomic and phylogenetic position of both new worms remains enigmatic, they expand both the biodiversity and ecological diversity of known early Cambrian ecosystems.

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## A case of mass mortality of large trilobites in the Fezouata Shale (Lower Ordovician, Morocco): evidence for benthic hypoxic episodes?

**\*Emmanuel L. O. Martin<sup>1</sup> and Rudy Lerosey-Aubril<sup>2</sup>**

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The discovery of the Fezouata biota (Early Ordovician, Morocco) represents a major breakthrough in our understanding of the early Palaeozoic diversification of animals. Yet, little is known of the environmental and early diagenetic contexts that facilitated its preservation. A taphonomic approach to the preserved assemblages might prove informative in this regard, as illustrated herein with the study of a cluster of large trilobites. The monospecific assemblage comprises 92 remains of *Platypeltoides magrebiensis*, the only fossils found on a bedding surface c. 25 m<sup>2</sup> in size. They display various degrees of articulation, 39.3 % of them representing fully (FA) or partially (PA) articulated exoskeletons. Width frequency distribution is normal and restricted (4.5–11.5 cm), with no obvious difference between FA or PA specimens and isolated sclerites; this suggests a biologically-induced size-sorting. Limited to null transport is also indicated by the absence of preferential horizontal and dorsum orientations. No clear preferential facing direction



of FA specimens is observed, but these specimens are predominantly (75 %) dorsum-down. The absence of body flexure, the preservation on a single plane, and this preferential dorsum-down orientation suggest that the 20 FA individuals died before burial. This census-assemblage documents a mass mortality event, probably resulting from an episode of benthic hypoxia.

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### Virtual visits to past environments in learning programmes for university students

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Direct contact with nature has an important impact on people's desire to study and protect the environment. Likewise, learning programmes about palaeoenvironmental research can be supplemented by virtual visits to geological contexts rich in ancient records. Personal visits create emotions, and combining them with scientific instructions is a powerful teaching strategy. Therefore, we have started to build an international course on past environments aiming to illustrate steps in the history of nature, with the contribution of leading experts on different topics. The course will include 16 lecture units of c. 700 slides with a focus on terrestrial palaeoenvironments. Outstanding features and transformations of natural systems will be shown by telling stories of key sites and particular geological contexts. The learning programme is intended to be: attractive for students, simulating a walk through nature; up to date and scientifically correct, including artistic reconstructions of the highest fidelity; and have a special focus on lesser-known and less conventional topics from around the world. The project is still a work in progress and open to contributions from the palaeontological community. The combination of different experts from various research fields in palaeontology promises to lead to a highly interesting and innovative teaching programme for an international audience.

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### Deep life in deep time: the palaeobiology of the subsurface

**Sean McMahon<sup>1</sup>, John Parnell<sup>2</sup> and Ashleigh van Smeerdijk Hood<sup>1</sup>**

<sup>1</sup>*Yale University, USA*

<sup>2</sup>*University of Aberdeen, UK*

Palaeobiology is traditionally concerned with the history of life on Earth. In recent decades, however, samples from mines and boreholes have revealed that our planet's biosphere extends several kilometres downwards below the seafloor and land surface. Deep pores and fractures host vast numbers of bacteria, archaea, fungi and microinvertebrates; 'life in Earth' may exceed 20% of the planet's biomass (McMahon and Parnell 2014). Although the contemporary deep biosphere is the subject of major research efforts, scant attention has been paid to its shifting size, activity and interaction with biogeochemical cycles throughout Earth's history. We contend that palaeobiologists should therefore turn their attention to the subsurface. The fossil record of deep life includes mineralized cellular remains, borings, and isotopic anomalies, but is drastically undersampled. Here we present: new heavy-metal isotopic evidence from Devonian, Permian and Triassic reduction spheroids consistent with a subsurface bacterial origin; a new estimate for



the present continental subsurface biomass, based on the latest cell counts and models of crustal groundwater distribution, with implications for biomass distribution through Earth's history; and preliminary results from a new model of  $H_2$  production by mineral radioactivity, an important subsurface energy source.

## Phylogeny and origin of Giraffidae based on characters of the bony labyrinth

**Bastien Mennecart<sup>1</sup>, Maria Rios Ibanez<sup>3</sup>, Gertrud E. Rössner<sup>2</sup> and Loïc Costeur<sup>1</sup>**

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The living family Giraffidae with its two genera *Giraffa* and *Okapia* has a long evolutionary history spanning most of the last 15 Ma. The family is known from a plethora of fossil taxa across the whole Old World from Eurasia to Africa. Giraffes are the only ruminants to bear two to five epiphyseal permanent cranial appendages, the ossicones. A further characteristic of the family is the presence of a bilobed lower canine which is widely used to diagnose extinct members. Despite this apparent wealth of data, little is known as to the origin of Giraffidae. A number of taxa bearing ossicone-like cranial appendages, such as the Palaeomerycidae and their North American relatives the Dromomerycinae, or branched or flattened cranial appendages such as the Climacoceratidae, have been variously related to giraffids, but without any consensus. We ran a preliminary cladistics analysis based on the bony labyrinth of Giraffidae and the above-mentioned problematic fossil taxa. It showed that the bony labyrinth is a powerful structure for the phylogeny of ruminants. Some morphological characteristics (cochlear morphology and orientation of the vestibular aqueduct) are unique to Giraffidae among the ruminants and give insights into the phylogeny and origin of this iconic group.

## Plesiosaur remains from the Lower Jurassic part of the Kap Stewart Formation, Jameson Land, East Greenland – evidence of the earliest marine incursion

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Two dorsal vertebrae and one dorsal rib were collected at a mountain ridge in the Kap Stewart Formation at Carlsberg Fjord, near Lepidopteris Elv, at Jameson Land, East Greenland, during the 2012 and 2016 Geocenter Møns Klint Dinosaur Expeditions. The Kap Stewart Formation is Rhaetian to Sinemurian in age, and the bones were found in the middle of the Formation, corresponding to the Hettangian part of the Formation. The collected bones show clear plesiosaur affinities: amphicoelous centra, paired ventral nutritive foramina in the centrum, unfused neurocentral sutures and single headed ribs. The diameter of the centra is 2 cm indicating a small-sized individual. Plesiosaurs are exclusively marine animals and this find represents the first undoubtedly marine vertebrate, in contrast to previous records of hybodont sharks and turtles in the synrift Mesozoic



deposits in Greenland, and witnesses the earliest stages of the opening of the North Atlantic at 44° palaeolatitude.

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### The fish and the Fishclay – an old story revealed

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The famous K-Pg boundary strata at the UNESCO World Heritage Site, Stevns Klint, eastern Denmark is composed of a thin clay layer called the Fishclay. Despite the name, to date only one partly-articulated fish skeleton is known to have been recovered from the Fishclay; however, scales and singular skeletal elements are quite common. The specimen in question consists of a partially-preserved articulated skeleton of a probable Berycoid fish. Unfortunately, the head and tail with the prime diagnostic characters are missing, preventing a more specific identification. This study traces the origins of the Fishclay name and boundary strata from the very first description of Stevns Klint in 1759 by Abilgaard to the first occurrence of the name Fishclay in 1849 by Forchhammer. Interestingly, the same paper that introduced the name Fishclay also very briefly mentioned the existence of a partially preserved articulated skeleton of a small fish, the fish skeleton that has proven to be the only one known to exist from the Fishclay!

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### Tiering and competition in Mistaken Point Ediacaran communities

**\*Emily G. Mitchell<sup>1</sup> and Charlotte G. Kenchington<sup>2</sup>**

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Bedding-plane assemblages of Ediacaran fossils at Mistaken Point, Newfoundland (~565 Ma), are among the oldest known examples of macroscopic communities. These immobile organisms are preserved *in situ*, allowing spatial analyses to shed light on organism ecology. Competition for vertical space has been suggested to be the primary community structuring mechanism resulting in different taxa occupying different parts of the water column, known as tiering. The community structure of the four most diverse Mistaken Point communities ('D', 'E', 'G' and Lower Mistaken Point (LMP) surfaces) was examined using a combination of spatial analyses incorporating morphological variables and tiering metrics. Spatial analyses offer a way to identify inter- and intra-specific segregation, enabling resolution of the magnitude and type of competition. Tiering was quantified in terms of the overlap of specimen height. We found that tiering overlap decreases from the D to G to E to LMP surfaces but instances of large-scale spatial segregation become more frequent, suggesting an increase in the extent of resource competition. Additionally, specimens with larger discs are more strongly segregated than tall specimens despite occupying different vertical tiers. These findings suggest that competition for laterally-distributed resources played a major or even dominant role in structuring these ancient communities.





## Early Cretaceous vertebrates from the Xinlong Formation of Guangxi, southern China

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The vertebrate assemblage from the Early Cretaceous non-marine Xinlong Formation of the Napai Basin, in the southwestern part of Guangxi Zhuang Autonomous Region (southern China), includes chondrichthyans, actinopterygians, turtles, crocodilians and dinosaurs. This assemblage shows many similarities to those from non-marine formations of the Khorat Group of northeastern Thailand. It also seems to be particularly close to that from the Khok Kruat Formation, considered as Aptian in age, as shown especially by sharks and turtles and by the presence of iguanodontians. An Aptian age is therefore proposed for the Xinlong Formation. Stable isotopes suggest that this part of South China experienced subtropical arid conditions during the deposition of the Xinlong Formation. In its composition, the vertebrate fauna from the Xinlong Formation seems to be more similar to coeval faunas from Southeast Asia than to assemblages from northern China. Although this may partly reflect different depositional and taphonomic environments, it seems likely that, during Early Cretaceous time, southern China and Southeast Asia were part of a distinct zoogeographical province, different from that corresponding to northern China. This may be the result of both climatic differences and geographical barriers such as mountain chains.

## Biostratigraphy and geometric morphometrics of conchostracans (Crustacea, Branchiopoda) from the Late Triassic fissure deposits of Cromhall Quarry

**Jacob Morton<sup>1</sup>, David I. Whiteside<sup>1</sup>, Manja Hethke<sup>2</sup>, Michael J. Benton<sup>1</sup>**

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The enigmatic fissure deposits of southeast England and southern Wales are famous for their unique assemblage of Late Triassic vertebrates, although their age is contentious. While recent studies of palynomorphs have dated some as Rhaetian, their conchostracan (Crustacea, Branchiopoda) assemblages have not been described or used in biostratigraphy. We find that species determination of British Late Triassic conchostracans requires detailed observations of both shape and ornamentation. We provide evidence that *brodieana* is a subspecies of *Euestheria minuta*, the traditional view, rather than a distinct species. Finally, we find no distinction between conchostracans from bedded Rhaetian deposits of the UK and specimens collected from the fissure deposits of Cromhall Quarry, Gloucestershire, supporting a late Rhaetian age for these deposits.



## Hyaloliths are Palaeozoic lophophorates

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Hyaloliths – orthothecids and hyolithids – are abundant and globally distributed Palaeozoic ‘shelly’ fossils. The phylogenetic position of this group has remained unresolved, largely because of the idiosyncratic hyolith scleritome (operculum, conical shell, and paired ‘helens’ in hyolithids) and poorly understood soft anatomy. Since they were first described over 175 years ago, hyaloliths have most often been regarded as *incertae sedis*, allied with molluscs or assigned their own phylum. Here we reinterpret hyaloliths based mostly on abundant new specimens of the hyolithid *Haplophrentis* from the Burgess Shale (Stanley Glacier and Marble Canyon) showing exceptionally preserved soft tissues. Soft tissue characters include an extendable, gullwing-shaped, tentacle-bearing organ surrounding a central mouth, which we interpret as a lophophore, and a U-shaped digestive tract that ends in a dorsolateral anus. In combination with opposing bilateral sclerites and a ventrally elongated visceral cavity, these features indicate an affinity with the lophophorates (brachiopods, phoronids and tommotids), substantially increasing the early disparity of this prominent group. We interpret *Haplophrentis* as a semi-sessile epibenthic suspension feeder that used its ‘helens’ to elevate its tubular body above the sea floor. This study reconfirms the importance of Burgess Shale-type deposits in illuminating the evolutionary history of long-problematic taxa known only from skeletal remains.

## Biogeography of the Late Ordovician blastozoan echinoderms

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The diversity of blastozoan echinoderms echoes the major trends of the Great Ordovician Biodiversification Event, starting with a gradual increase and then flourishing dramatically in the Sandbian. Their major diversification is strongly related to an increase in longevity and cosmopolitanism. An exhaustive database of temporal, environmental and geographical occurrences of blastozoans at the species level has been compiled in order to consider the impact of several environmental factors on the Ordovician blastozoan biogeographic evolution. Ten associations of diverse blastozoans are identified since the mid Ordovician. The composition of the Baltican and Laurentian associations remains stable through the Ordovician, with main tropical and poleward migrations in the Sandbian and the early Katian, respectively. The peri-Gondwanan margin hosted two diversity hotspots during the Darriwilian at the origin of later coastal migrations. During the Katian, the palaeobiogeographical distribution of blastozoans results from the inheritance of a relatively strong provincialism (maintained until the Dapingian), and large-scale migrations along the peri-Gondwanan margins and across the Palaeo–Tethys ocean to reach the shallow water environments of the subpolar peri-Gondwana. Reconstructed oceanic currents support few of the shortest migration paths and therefore suggest that blastozoans larvae acquired survival abilities to wait before settlement.



## New Eocene Coleoid (Cephalopoda) Diversity from Statolith Remains

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New coleoid cephalopods are described from statolith remains from the Middle Eocene (Middle Lutetian) of the Paris Basin. Fifteen fossil statoliths are identified and assigned to the Sepiidae (*Sepia boletzkyi* sp. nov.,? *Sepia pira* sp. nov.), Loliginidae (*Loligo clarkei* sp. nov.), and Ommastrephidae (genus indet.) families. The sediments containing these fossils indicate permanent aquatic settings in the infralittoral domain. These sediments range in age from 46 to 43 Ma. Analysis of the fossil record of statoliths (from findings described here, together with a review of previously published data) indicates marked biases in our knowledge. Fossil statoliths are known from as far back as the Early Jurassic (199.3–190.8 Ma) but surprisingly, to the best of our knowledge, no record occurs in the Cretaceous. This is a 'knowledge bias' and clearly calls for further studies. Finally, we attempt to compare findings described here with fossils previously used to constrain divergence and/or diversification ages of some coleoid subclades in molecular phylogenies. This comparison clearly indicates that the new data reported here will challenge some estimated divergence times of coleoid cephalopod subclades.

## In Barrande's footsteps: re-evaluation of four enigmatic Cambro–Ordovician echinoderms from Bohemia (Czech Republic)

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The eight volumes of Barrande's *Système Silurien du centre de la Bohême* (1852–1902) represent a milestone for Palaeozoic biostratigraphy and palaeontology in the Czech Republic. In volume VII, Barrande (1887) described 26 new genera and 80 new species of Cambro–Ordovician 'cystidean' echinoderms. These taxa are now assigned to eight distinct classes: cinctans, coronoids, diploporitans, eocrinoids, edrioasteroids, rhombiferans, solutans and stylophorans. The morphology and taxonomic classification of four enigmatic 'cystidean' taxa are here re-evaluated, based on observations of Barrande's original material stored in the collections of the Palaeontological Department of the National Museum, Prague. Three specimens described as *Lapillocystites fragilis* Barrande, 1887 represent slightly disarticulated thecae of the edrioasteroid *Stromatocystites pentangularis* Pompeckj, 1896. Two specimens classified as *Cystidea concomitans* Barrande, 1887 are newly interpreted as slightly disarticulated supracentral integument of the cinctan *Trochocystites bohemicus* Barrande, 1887. *Anomalocystites ensifer* Barrande, 1887 was correctly identified as a mitrate stylophoran by Ubaghs (1968), who assigned it to a new genus of uncertain systematic affinities (*Spermacystis* Ubaghs, 1968). Re-examination of Barrande's original material suggests that *A. ensifer* and *Cystidea abscondita* Barrande, 1887 both correspond to kirkocystid mitrates (*Anatifopsis* spp.).



## New vertebrate coprolites from the Late Triassic Huai Hin Lat Formation of Thailand

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A thousand vertebrate coprolites were found from seven outcrops of the Huai Hin Lat Formation (Carnian–Norian age) in Chaiyaphum Province, northeastern Thailand. The coprolites were deposited in a lacustrine environment. Most of them are very well preserved. They were described on the basis of their morphology and eight ichnotaxa were recognized, including *Eucoprus* ichnosp., *Eucoprus cylindricus*, *Dicynodontocopros maximus*, *Sauropocopros bucklandi*, *Liassicopros hawkinsi*, *Heteropolacopros texaniensis*, *Bibliocopros* ichnosp. and *Hyronocopros amphibolar*. Two new ichnotaxa were found from this study and named *Hyronocopros khonsanensis* and *Rhopalocopros chaiyaphumensis*. The occurrence of *Bibliocopros* and *Hyronocopros* extends their stratigraphic distribution from the Late Pennsylvanian and Permian strata of north-central New Mexico to the Late Triassic strata of Thailand.

## When did the Isthmus of Panama form?

**Aaron O'Dea**

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Some recent studies suggest that the Isthmus of Panama formed many millions of years earlier than the widely recognized age of 3 Ma, a result that if true would revolutionize our understanding of environmental, ecological, and evolutionary change across the Americas. Fossil, rock and molecular records provide a cohesive narrative of gradually emerging land and constricting seaways, with formation of the Isthmus of Panama *sensu stricto* around 2.8 Ma. No clear evidence exists for an isthmus in place before that time.

## Alteration development on Carboniferous fossil remains (Ningxia, northwest China): the calcium–sulfur–iron triangle

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Conservation of fossil items in palaeontological collections represents a serious issue, especially when samples contain pyrite. Alteration arises when fossils are exposed to the atmosphere, which promotes oxidation. At worst, this process can result in the complete destruction of specimens. Experiments were carried out on fossils from the Upper Carboniferous Xiaheyan locality (Ningxia, China), from which a rich entomofauna is currently being investigated. Using SEM, XRD and Raman spectroscopy, we compared the initial composition and state of preservation of newly excavated fossiliferous or non-fossiliferous samples with those of ancient collection specimens and artificially-aged specimens. The obtained data show that a sequence of reactions, involving exogenous calcium from nearby calcite layers and endogenous iron and sulfur from framboidal pyrite located inside the fossils, takes place. One of the observed outcomes is a crystallization



of gypsum (calcium sulfate) inside pre-existing cavities or at the exposed surface. The mechanical pressure produced by the growth of such crystals can result in severe fragmentation of the fossils. To help avoid this issue, preventative artificial ageing was attempted. Our experiments suggest that the chemical composition of the fossil itself has a role in the degradation mechanism.

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### New insights into the ontogeny, morphology and phylogenetic affinities of machaeridians based on articulated *Plumulites*

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Machaeridians were long considered a palaeontological mystery, with their imbricating scleritome composed of alternating inner and outer shell plates having no counterparts in modern fauna. The discovery of an exceptionally preserved specimen with parapodia and chaetae from the Early Ordovician Fezouata shales confirmed that machaeridians are armoured annelid worms, with each segment bearing paired shell plates. However, the exact position of machaeridians among annelids remains poorly constrained due to the absence of unequivocal apomorphies linking machaeridians to extant polychaete clades. We report over one hundred articulated scleritomes of *Plumulites* cf. *tafaenensis* from the Tafilalt Biota from the Upper Ordovician of Morocco. Individuals range in body length from ~10 to 84 mm, allowing an unprecedented insight into the development of the machaeridian scleritome from juveniles to adults. This material confirms that machaeridians added successive shell plates, and therefore segments, during ontogeny, adding another key character that supports an annelid affinity for machaeridians. In addition to this material, we report new specimens of *Plumulites bengtsoni* from Fezouata that preserve new details of non-mineralized tissues. These specimens provide key evidence for the affinities of these long problematic fossils and phylogenetic analyses place them firmly in the annelid crown group in the aphroditacean total group.

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### Diversity, ecology and biogeography of Laurentian Radiodonta

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Our understanding of large pelagic predators such as *Anomalocaris*, *Hurdia*, *Peytoia* and *Caryosyntrips* has increased greatly in recent years. These stem group arthropods are well known from several Cambrian soft-bodied deposits, with much recent focus on taxa from the Emu Bay Shale (Australia), Chengjiang Biota (China) and Burgess Shale (Canada). Radiodonta are also an important component of Cambrian soft-bodied faunas from the Great Basin (Utah, Nevada and California, USA) and Kinzers Formation (Pennsylvania, USA). These were described over a long period of time (1979–2008) and



these discoveries were not always integrated with the studies of the last 5–10 years on radiodontan systematics and ecology. We re-examined all previously described Great Basin and Kinzers radiodontans, along with recently collected new specimens. This expands the known diversity of Radiodonta in Laurentia. Further, new morphological features are identified for *Hurdia*, *Caryosyntrips* and *Anomalocaris*, and new species are recognized. Interpretation of their functional morphology suggests taxa from the Great Basin and the Kinzers possessed a range of ecologies, mirroring what is seen from the Burgess Shale. Finally, the temporal distribution of Radiodonta in Laurentia supports the previously identified overall trend that Anomalocarididae dominate in older sites whereas Hurdidae dominate in younger ones.

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### Panderiidae, Hemibarrandiidae, Nileidae (Trilobita): so far, yet so close

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Panderiidae was originally erected as a subfamily of Illaenidae (Bruton, 1968), but its status and affinity were soon questioned. The Illaenina revision by Lane and Thomas (1983) suggested that Panderiidae could not even be related to this suborder, but subsequent authors maintained the panderiids inside Illaenina. In turn, Nileidae was assigned by Chatterton and Fortey (1988) to Asaphina, as a member of the superfamily Cyclopygoidea. Since then, this view has been largely consensual. Nonetheless, Whittington (2003) considered that Nileidae should be allied with Illaenidae rather than with Asaphina. In between Panderiidae and Nileidae, the Hemibarrandiidae is a low-diversity group from the high-latitude peri-Gondwana realm recently revised by Mergl and Kozák (2016). Although consensually assigned to *Panderia* Volborth, the species *Nilaeus beaumonti* Rouault represents a new genus allied to Hemibarrandiidae members. The detailed morphological study of *N. beaumonti* has allowed its generic reassessment and led to the recognition of a close relationship between these taxa and members of the Nileidae, with whom they share important characters. The previous assignment of Panderiidae and Hemibarrandiidae to Illaenina is rejected, the separation of the discussed taxa at order level is not justified, but there are still many unsolved questions related to these enigmatic groups.

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### British Silurian Myodocope ostracods

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The Silurian myodocope ostracods from Britain comprise six families, twelve genera and twenty-two species, plus three species in open nomenclature. New material includes representatives of the families Bolbozoidae, Entomozoidae, Cypridinidae and Seminovidae n. fam. Fine biostratigraphic control allows the development of a myodocope biozonation for the Wenlock and Ludlow series. Seven myodocope biozones are established, from the early Homerian (Wenlock) to the late Ludfordian (Ludlow) stages. This biozonation allows inter-continental correlation of Silurian successions in Europe, in Arctic Russia and Central Asia.



## New remains of Mosasauroidae (Squamata) from the Late Cretaceous of Aude (France)

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Mosasaur remains (Squamata) were collected from the Santonian of Aude (southern France), near the bridge of the village of Sougraigne. The identification of these bones shows the presence of two different genera of similar size. The cranial bones, some vertebrae, two scapulae and a phalanx are assigned to a Plioplatecarpinae *Platecarpus* cf. *tympanicus*, while the pelvic bones and a femur? are instead referred to a Tylosaurinae. Two phylogenetic analyses confirmed the affiliation of the Plioplatecarpinae to this clade and a relationship close to the species *P. tympanicus*. Only the presence of the zygosphenes–zygantrum complex on the dorsal vertebrae could differentiate it from the species *P. tympanicus*. The range of the genus *Platecarpus* from the Santonian was hitherto limited to the United States: the material from Sougraigne allows us to expand it to France. Some taphonomic marks observed on some bones can be attributed to the teeth of sharks (like *Squalicorax*), teleosts or even mosasaurs.

## Palaeoenvironmental changes in the Polish Basin as recorded by plant carbon isotopes and fossil charcoal

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New carbon isotope and charcoal abundance data from the Polish Basin offer a new insight into Early Jurassic palaeoenvironments. Following extreme climatic changes and a mass-extinction at the Triassic–Jurassic boundary (~201 Ma), the Early Jurassic (~201–174 Ma) saw continued environmental changes in both the marine and terrestrial realms. Sedimentary cores recovered from the Polish Basin have allowed us to produce new records of changes in atmospheric and wildfire activity changes using carbon isotope stratigraphy and analyses of fossil charcoal abundance. Negative carbon isotope excursions are recorded in fossil plant material at the Triassic–Jurassic boundary and during the Toarcian, indicating releases of isotopically light carbon into the ocean-atmosphere reservoir during the Early Jurassic. Initial analyses of fossil charcoal abundance appear to indicate increases in wildfire activity in the Polish Basin, which seem to coincide with negative carbon isotope excursions. Previous studies from other sites show a peak in fossil charcoal abundance at the Triassic–Jurassic boundary, coincident with negative carbon isotope excursions. Our new data allow us to recognize environmental changes and their effects on a local scale within the Polish Basin, as well as to assess these changes on a wider scale by comparison to other Early Jurassic sites around the world.



## Uncertain-tree: discriminating among competing approaches to the phylogenetic analysis of phenotype data

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Morphological data provide the only insight into classifying the majority of life's history, but choosing an appropriate method for the analysis of morphological cladistic matrices remains debated. Traditionally, parsimony methods have been favoured but recent studies have shown that these approaches are not as accurate as the Bayesian implementation of the Mk model. Here we expand on these findings in several ways: we assess the impact of tree shape, maximum-likelihood estimation using the Mk model, and analyse both binary and multistate characters. We find that all methods struggle to correctly resolve deep clades within asymmetric trees, and based on small character matrices. The Bayesian Mk model is the most accurate method for estimating topology, but with lower precision than other methods. Equal weights parsimony is more accurate than implied weights parsimony, and maximum likelihood estimation using the Mk model is the least accurate method. We conclude that the Bayesian implementation of the Mk model should be the default method for phylogenetic estimation from phenotype datasets, and we explore the implications of our simulations in reanalysing several empirical morphological character matrices. A consequence of our finding is that high levels of precision or the ability to classify species or groups with much confidence should not be expected when using small datasets. It may now be necessary to depart from the traditional parsimony paradigms of constructing cladistic matrices, towards datasets constructed explicitly for Bayesian methods.

## Survival of the smallest? Trends in brachiopod size across the end-Triassic mass extinction

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Many taxonomic groups have been shown to physically respond to changes in environment, such as brachiopods that are known to display body size changes in response to climatic events. Environmental changes just before the Triassic–Jurassic boundary caused a mass extinction, and this study investigated the impact of this event on brachiopod body size. Using the Natural History Museum, London collections, the study was undertaken at the generic level for groups within the Rhynchonellida. The three principal axes were measured on specimens that, where possible, were recorded to ammonite zone stratigraphic resolution. Body volume was calculated using the Novack-Gottshall (2008) method. These data were used to investigate the significance of any changes in mean size and to undertake a time series analysis. Only two of the genera measured are recorded in both the Triassic and Jurassic, *i.e.* *Rhynchonella* and *Calcirhynchia*. There is a significant drop in body volume between the Rhaetian and the Hettangian, with many genera being smaller in the early Jurassic. The next step in the study is to consider the effect of facies differences in specimens from varying localities, and to increase sample sizes.





## Evaluating bite marks and predation of fossil jawless fish during the rise of jawed vertebrates

**\*Emma Randle and Robert Sansom**

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Vertebrate assemblages were generally dominated by jawless fish (ostracoderms) during the Silurian, but towards the end of the Devonian, jawed vertebrates dominated. Theories accounting for this faunal shift range from predation or competitive displacement by jawed vertebrates to limited dispersal capabilities of ostracoderms resulting in elevated sensitivity to large-scale climatic fluctuations. Differences in feeding ecologies between ostracoderms and jawed vertebrates (generally interpreted as filter feeders and predators respectively) rule out competitive displacement. Here we present direct evidence for the predation of heterostracan ostracoderms from the fossil record. We found puncture marks on more than 25 heterostracan specimens that are consistent with interpretation as bite marks; for example, the marks exhibit: regular geometric shape; complementary traces on both sides of the animal; a distinct pattern; and evidence of sublethal (repair) attacks. Occurrences of these attacks dramatically rise during the Emsian, which coincides with an increase in gnathostome diversity. We use the distribution of jawed vertebrates and occurrences of heterostracan bite marks through space and time to test hypotheses relating to increasing predation, possible faunal interactions, and the evolutionary history of vertebrates.

## The new rudist phylogeny (Bivalvia, Hippuritida)

**Valentin Rineau and Loïc Villier**

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Rudists (order Hippuritida) are heterodont bivalves close to the Megalodontidae. They appeared in the Upper Jurassic and spread all around the Tethys in warm shallow seas, only to become completely eradicated at the Cretaceous–Palaeogene boundary. This group developed completely original morphologies, probably due to a shell uncoiling, which make them recognizable at first glance. A strong development of the myocardial apparatus, the loss of a ligament and the presence of canals in the shell are some examples of morphological events which occur in rudists. Here we present a new phylogeny based on representatives of each family – from Diceratidae to Hippuritidae – to resolve the early nodes of the rudist phylogeny. We point out the weaknesses of the unique previous phylogeny, on the formalization of homology hypotheses, and we propose a completely new set of morphological descriptors, and therefore characters, based on comparative anatomy with a decomposition of traditional ‘morphological wholes’ (e.g. hinge) into independent characters (e.g. anterior tooth, central tooth socket). We show that the previous unique character ‘pallial canals’ can be decomposed to point to four different origins. The results are presented in three-taxon analysis, a cladistic method that uses a new formalization of homologies directly in trees, and without matrix.



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## Discriminating between melanosomes from different tissues using geometry and trace element chemistry: a tool for interpreting fossil vertebrate soft tissues

\***Valentina Rossi and Maria E. McNamara**

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Melanosomes are important components of integumentary tissues in modern vertebrates and have been reported from various vertebrate and invertebrate fossils ranging in age from the upper Palaeozoic to the Cenozoic. Much previous work on fossil melanin has focused on reconstructions of integumentary colour in fossils. Modern vertebrates, however, also possess melanin in internal tissues; the impact of these internal melanosomes on interpretation of fossil soft tissues – and fossil colour – has not been assessed. Here we present the first systematic analysis of the anatomical distribution and abundance of melanosomes in different vertebrate taxa. The abundance of melanin in tissues of extant amphibians, reptiles, birds and mammals was assessed using histological sections. Melanin extracts from these tissues were analysed using scanning electron microscopy and synchrotron X-ray fluorescence. Our results reveal that melanosomes are abundant in internal organs of extant vertebrates. These internal melanosomes always differ in trace element chemistry, and, in some taxa, in geometry, to melanosomes from the skin. These findings can be applied to fossils to allow integumentary and non-integumentary melanosomes to be discriminated, thus allowing more accurate interpretations of internal anatomy and integumentary colour in fossils.

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## Primitive contour feathers in paravian dinosaurs and the evolution of avian plumage

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Identifying fossil feather morphology is challenging. Here, comparisons between phylogenetically distant dinosaur taxa allow for better understanding of feather morphology and insight into their function and evolution. An *Anchiornis* specimen possesses disarticulated contour feathers revealing a novel feather type – a ‘shaggy’, open-vaned, bifurcated feather with long barbs attached to a short rachis. Comparisons between *Psittacosaurus*, *Sinosauropteryx* and *Anchiornis* suggest a range of plausible contour feather morphologies for *Sinosauropteryx* with a ‘tuft’ morphology of multiple barbs connected basally but lacking a rachis tentatively preferred. Comparison with *Confuciusornis* supports *Anchiornis* flight feathers being at least partially open-vaned. Open-vaned contour and flight feathers in *Anchiornis* suggest that differentiated barbicels may be relatively derived characters. ‘Shaggy’ contour feathers would have influenced *Anchiornis* thermoregulatory and water repellence abilities, and along with open-vaned flight feathers, would have decreased aerodynamic efficiency. Simplified, open-vaned *Caudipteryx* forelimb feathers support secondary flightlessness and imply that other potentially secondarily flightless theropods, like large dromaeosaurs, had simplified feathers and were ‘shaggy’ in appearance. The results have implications for many non-avian dinosaur depictions and the function and evolution of feathers.



## Testing adaptive radiation scenarios in marine fishes by combining phylogenomic and paleobiological data

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Adaptive radiation scenarios have been invoked to explain the diversity of some of the best studied groups of organisms (e.g. rift lake cichlids, Hawaiian silversword alliance, passerine birds). Under the most traditional adaptive radiation model, numerous lineages start diverging within a brief period of time from an ancestral adaptive type, with each new lineage filling an available ecological niche; subsequently this rapid initial morphological evolution is replaced by relative stasis due to most available niches having already been filled. A number of recent studies, based on molecular phylogenies, questioned the generality of this model and found little evidence of an early burst of morphological diversification in most studies. For most of these clades, however, it is not known if inclusion of the palaeodiversity would have modified the results. I will compare the results of our study of several major groups of marine teleosts, such as tetraodontiforms (puffers, triggerfishes and allies), acanthuroids (surgeonfishes, luvar) and sparoids (seabreams, emperors and allies). All of these groups possess a rich fossil record, which to date has rarely been used in evolutionary studies. I will show how the results based on extant taxa and those based on extant plus extinct species differ, and how inclusion of fossil data can alter the conclusion of studies based on molecular phylogenies.

## Take the fish taxi! Phylogeny and palaeobiogeography of the Margaritiferidae

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Today, eleven species of Margaritiferidae occur scattered over Eurasia, North America and northern Africa. Margaritiferidae likely originate from the extinct Silesunionidae. Although identification of fossil remains is problematic, numerous Mesozoic and Cenozoic fossils can be assigned with some confidence to the Margaritiferidae. Results of molecular phylogenetic analysis of all extant species, based on two mitochondrial and three nuclear markers, were processed with BEAST to infer divergence times. Assuming mean substitution rates, the Margaritiferidae are calculated to have originated in the Miocene. Using fossils for calibration, the results indicate substitution rates ten times lower than usual and four levels of intercontinental relationships. This is difficult to explain as Margaritiferidae occur exclusively in fresh water; their parasitic larvae usually attach to the gills of amphidromous host fish and thus it is unlikely that land bridges promote propagation. It is further unlikely that mussel larvae survive travel in saline waters. We propose that Margaritiferidae spread during phases of high freshwater runoff or seasonal freshwater layering. This model has broader implications for the phylogeography of the Unionida, which all depend on the 'fish taxi' for propagation.



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## Are rudist bivalves cockles? How *Pachyrisma grande* Morris and Lycett, 1850 may jumble Mesozoic bivalve phylogeny

**Simon Schneider**

CASP, UK

*Pachyrisma grande* and the family Pachyrismatidae are considered the most likely ancestors of the Hippuritida. The Hippuritida (*vulgo* ‘rudists’) are one of the most diverse bivalve groups of the Mesozoic with approximately 200 genera and 2,000 species. The origins of *Pachyrisma* are considered to lie in the Megalodontidae, a group of large-sized Triassic lagoonal bivalves, predominantly occurring in the Tethyan realm. Re-study of *Pachyrisma grande* has revealed several characters that were previously unknown or misinterpreted. These include the presence of radial external ornament on the posterior slope, a posterior lateral tooth PI, a pitted pallial line, the absence of a lunule and the shape and position of the nymph. These features support *Pachyrisma* as the closest known ancestor of the Hippuritida, but not as a descendent of the Megalodontidae. The cardioid hinge and the lack of a lunule suggest an origin close to *Protocardia* in the Cardioidea. The proposed evolutionary relationships have several broader implications for bivalve systematics. Megalodontidae probably went extinct at the Triassic–Jurassic boundary, early cardioid evolution requires revision, Hippuritida are probably descended from Cardioidea *via* the Pachyrismatidae, and Cardioidea are thus paraphyletic with regard to Hippuritida.

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## An unexpected gastropod: a possible representative of the predominantly Mesozoic family Spinilomatidae (Mollusca: Caenogastropoda) found in the Middle Danian (Early Paleocene) coralline limestone of Faxø Quarry, Denmark

**K. Ingemann Schnetler<sup>1</sup> and Jesper Milàn<sup>2,3</sup>**

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The coralline limestone of the Middle Danian (Early Paleocene) Faxø Formation of Faxø Quarry, Denmark has yielded a very diverse mollusc fauna, with more than 220 described species of gastropods alone. A new specimen is identified as a possible representative of the family Spinilomatidae. The specimen is preserved as an impression in the consolidated limestone. By making a silicone mould of the impression, a high-quality cast of the specimen was retrieved, enabling identification. Previously, the family Spinilomatidae was known only from the Mesozoic of Europe and India and from the Late Paleocene of California. This extends the biogeographical range of the subfamily to Europe and highlights the status of Faxø Quarry as an important fossil locality.

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## What are ‘opossum-like’ fossils? New phylogenetic hypothesis based on CT-scanning and new features on petrosal anatomy

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Herpetotheriids are considered a key taxon in the evolutionary history of Marsupialiformes and particularly in the origin of opossums. Herpetotheriids include fossil marsupialiformes



whose dentition is said to be 'opossum-like'. However, the concept of 'opossum-like' falsely combines herpetotheriids and peradectids, with no phylogenetic basis. Rather, this concept is based on the general, and largely plesiomorphic, morphological resemblance of herpetotheriids to extant opossums. New data on internal aspects of the skull of herpetotheriids revealed by X-ray microtomography (CT-scanning) allow a better understanding of the phylogenetic affinities of 'opossum-like' marsupialiformes. The present study describes and compares 3D models of the petrosal bone of *Peratherium elegans*, *Peratherium cuvieri* and *Amphiperatherium minutum*. A cladistic analysis of osteological characters (including the ear region) in 23 extant and fossil metatherians (including the four herpetotheriids of this study) confirms the highly informative nature of this bone for phylogenetic reconstructions. The results indicate that *P. cuvieri*, *P. elegans* and *A. minutum* form a monophyletic group, but the other herpetotheriid of the analysis, *Herpetotherium cf. fugax*, is not part of this clade. This casts into doubt the monophyly of herpetotherids and the relationships of peradectids and herpetotheriids with the crown clade Marsupialia.

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***Paracestracion danieli* sp. nov., a new species of bullhead shark from Eichstätt, Germany (Chondrichthyes: Heterodontiformes)**

**\*Tiffany Slater<sup>1</sup>, Kate Ashbrook<sup>1</sup> and Jürgen Kriwet<sup>2</sup>**

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A new species of bullhead shark (Chondrichthyes: Heterodontiformes) is reported from the Kimmeridgian of Eichstätt, Germany. This subadult specimen is compared to the holotype *Paracestracion falcifer* (AS-VI-505) and to the related extant juveniles *Heterodontus japonicus*, *Heterodontus zebra*, *Heterodontus philippi* and two adult *Heterodontus japonicus*. *Paracestracion danieli* sp. nov. differs in its tooth morphology, number of tooth families, and position of the anterior fin spine, coracoid and puboischiadic bar. Additionally, seven distance measurements are used to investigate differences in body shape throughout ontogeny and between species. Measurements include total body length, length of coracoid and puboischiadic bar and the distance between each of the first and second dorsal fins, the second dorsal fin and caudal fin, the pectoral and pelvic fins, and the pelvic fins and anal fin. Principal components analysis of these data reveals a strong divergence between *Paracestracion danieli* sp. nov., *Paracestracion falcifer* and *Heterodontus*; most of the variation relates to the distance between the pectoral and pelvic fins and the distance between the posterior dorsal and caudal fins (PC1=78.9%; PC2=15.9%). This investigation reveals a greater species diversity of the extinct genus *Paracestracion* than previously thought.

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**Phanerozoic survivors: actinopterygian evolution through the Permo–Triassic and Triassic–Jurassic extinction events**

**\*Fiann Smithwick**

University of Bristol, UK

Actinopterygians (ray-finned fishes) successfully passed through four of the big five mass extinction events of the Phanerozoic, but the effects of most of these extinction events on the group are poorly understood. It has so far been assumed that the Permo–Triassic mass



extinction (PTME) and end-Triassic extinction (ETE) had little impact on actinopterygians, despite devastating many other vertebrate groups. Here, we test this assumption using two independent morphometric techniques, geometric and functional, plus diversity estimates, to assess the effects of these two extinction events on the group. The PTME sees small but insignificant changes in both disparity measures while diversity actually increases. Relatively low levels of disparity in the Early Triassic are followed by increases from the Middle to Late Triassic, with a particular expansion of functionspace coinciding with the radiation of neopterygians and the evolution of novel feeding adaptations. Through the ETE, a drop in diversity occurs alongside small shifts in geometric and functional disparity, followed by expansions into novel areas of ecospace. Little evidence is observed for major perturbations in actinopterygian evolution through either extinction event, suggesting that the PTME and ETE did not have the severe negative impacts on the group observed for other major clades.

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### Exceptional preservation of the basal body of conodont elements from the Dienerian (Early Triassic) of Oman: implications for systematics and functional morphology

**Louise Souquet and Nicolas Goudemand**

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Conodonts are extinct marine jawless vertebrates, most recently assigned to stem cyclostomes based on phylogenetic analyses. This interpretation is supported by a functional model that suggests that conodonts fed using a pulley-like mechanism, similar to crown cyclostomes (Goudemand *et al.* 2011). The feeding apparatus of conodonts usually consists of 15 teeth-like elements constructed from two tissues: an enamel-like crown and a dentine-like basal body. The basal body tissues are rarely preserved, and has never been reported from grasping S and M elements of Triassic conodonts. Goudemand *et al.*'s functional model (2011) was based on Early Triassic conodonts and assumed that the basal body did not hinder the movement of the element around a presumed 'lingual cartilage'. Here we report for the first time elements of neospathodid conodonts from Dienerian rocks of Oman where the basal body is partly preserved. Specimens recovered to date support the functional model. As new material is recovered, we hope to find more such specimens to assess these observations.

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### Photogrammetry: preserving for future generations an important fossil site in Maine-et-Loire (France)

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'La Tranchée des Malécots' is a disused road-stone quarry in the south of the Armorican Massif in Chateaufonds-sur-Layon (Maine et Loire, France). This important site is situated next to abandoned Carboniferous coal mines of the same name and provides a unique window into the Namurian (326.4–315 Ma) flora of the region. The geology of the site was first recorded by Carpentier in 1932 and is attributed to the 'Sillon houiller de la Basse-Loire' structural unit. The site consists of bedded 'pierres carrées' (= square stones) volcanoclastic ash deposits interspersed with layers rich in plant remains. These rocks are



heavily jointed and thus prone to freeze-thaw weathering. The palaeoflora is dominated by large (1–9 m) lycoposid trunks and branches (*Lepidodendron*; *Lepidodendropsis*), *in situ* rhizomes (*Stigmaria*), leaves (*Lepidophylloides*), and numerous unidentified plant remains. Fossils are preserved as carbonized compressions or as three-dimensional moulds. In the 80 years since the discovery of the site, weathering and vegetational growth have taken their toll on the sections. Here we present the results of preliminary attempts to conserve the remaining fossils for future generations using photogrammetry: a digital technique that produces realistic three-dimensional models using minimum equipment and with little overall cost.

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## Trophic dynamics in the Burgess Shale: re-evaluating the community ecology of the Greater Phyllopod Bed through biovolumetrics and taphonomy

\***Richard Stockey<sup>1</sup>** and **Martin R. Smith<sup>2</sup>**

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<sup>2</sup>*Durham University, UK*

Our understanding of Cambrian ecology stems primarily from exceptionally preserved deposits such as the Burgess Shale. To date, community reconstructions have focused on abundance data to understand the structure of Cambrian ecosystems. Biomass, however, is increasingly used to quantify ecological dominance within modern environments. Moreover, the archetypal Burgess Shale ‘community’ occurring in the Greater Phyllopod Bed may represent a composite assemblage of transported fauna and organisms living *in situ*. Previous community studies therefore provide a potentially biased description of early metazoan ecosystems. Here we supplement existing population data with new surveys of body size variation and species associations to model the relative ecological roles of taxa from the Greater Phyllopod Bed. Biomass estimates indicate that scavenging marine worms dominated the burial environment, contradicting previous hypotheses that deposit-feeding arthropods were the ecological nexus. Our approach further reveals at least two distinct communities preserved in the Greater Phyllopod Bed: an *in situ* trophic web dominated by the priapulidomorph *Ottoia* and morphologically similar problematica, plus laterally and vertically transported death assemblages. We present a new, dynamic model of Burgess Shale palaeoecology, separating components of external food webs from the indigenous scavenging fauna of the low-oxygen burial environment.

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## Early and middle Cambrian palaeoscolecid (Cycloneuralia) of southern Scandinavia

**Michael Streng, Jan Ove R. Ebbestad and Vivianne Berg-Madsen**

*Uppsala University, Sweden*

A previously undocumented diversity of Cambrian palaeoscolecids is presented from localities in Sweden, Norway, and Denmark. The material includes isolated sclerites as well as the first macroscopic specimens reported from the palaeocontinent Baltica. The sclerites are all of early middle Cambrian age and have been assigned to at least four new species of *Hadimopanella*. The two recovered macroscopic specimens are of late early Cambrian and of early middle Cambrian age, respectively. The early Cambrian specimen is described as *Maotianshania?* sp. and represents the first record of the family Maotianshaniidae outside China. The middle Cambrian specimen is almost complete and represents a new species of



*Wronascolex*. It is characterised by a previously undocumented distribution of sclerites, which change in size and ornamentation from the anterior to the posterior end of the annulated trunk. This distribution pattern can explain the high variability of species of the sclerite-based genus *Hadimopanella* as well as the occurrence of rare morphotypes of *Hadimopanella* in otherwise rich samples. Evaluation of the available data on the ontogeny of palaeoscoleids regarding the relationship between body and sclerite size suggests that sclerite size might be species-specific and should be considered when comparing taxa with morphological similar sclerites.

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## Reconstructed life cycle of a Proterozoic holozoan

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Phosphatic nodules from the c. 1 Ga non-marine Torridonian Sequence of northwest Scotland preserve populations of multicellular cell balls (stereoblasts), some of which are surrounded by a distinctive jacket of elongate cells. These complex multicellular forms co-occur with naked stereoblasts and unicellular, multinucleate cells that form a syncytium (coenobium). These microfossils are described in a companion poster by Wacey *et al.* Exceptional preservation of individual specimens at successive stages of differentiation has enabled us to hypothesize a reconstructed life cycle. Endoreduplication and karyokinesis in a single cell form a distinctive coenobium. As the original cell wall degrades, individual nuclei cellularize, forming a naked stereoblast. Cell differentiation occurs when some of the parenchymatous cells of the stereoblast begin to elongate, forming sausage-shaped cells. These elongate cells then migrate to the surface, thicken their walls, and form a surficial layer that is one cell in thickness. Our hypothetical life cycle parallels that seen today in the free-living, saprophytic ichthyosporean, *Creolimax fragrantissima*, but with the addition of the distinctive outer layer which probably functioned as a cyst wall. This fossil adds to growing evidence that suggests that multicellularity in metazoans evolved via the co-option of developmental pathways that had evolved previously in ancestral unicellular holozoan protists.

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## Dentures and a gummy sauropod

**Suravech Suteethorn**

*Mahasarakham University, Thailand*

Series of sauropod tooth rows lacking jawbone (dentures) are reported from the Early Cretaceous Sao Khua Formation at the Phu Kum Khao locality in Kalasin Province, Northeastern Thailand. The set of lower teeth SM K4-346 and -347 is composed of 23 entire teeth and fragments from several others. Teeth from the extremities of the denture have the smallest size, whereas the largest teeth are in the middle of the row. The crowns are slightly wider labiolingually at mid-length. Teeth are separated from each other and show a peculiar twist, as in SM K4-347-8 to -12. The apex of the eighth tooth shows slight rotation, the ninth and tenth point downwards and the twelfth is completely rotated. This condition confirms that there was no jawbone. It is not clear, however, how such





an unusual phenomenon like a jawbone-less denture could be preserved. The discovery of isolated dentures might be linked to the presence of a thick gum which would keep the position of teeth *in situ* after the body decays.

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## Alpha diversity and palaeoecology of the Cretaceous in the Alpstein, Switzerland

**Amane Tajika and Christian Klug**

*University of Zurich, Switzerland*

The Alpstein massif (northeastern Switzerland) has been of great interest for geologists for several decades because of its excellent outcrops. Although rich and relatively high diverse associations of fossils have been reported, there has been no comprehensive overview of the macrofossil associations. Here, we report the fossil assemblages and discuss palaeoecological changes from the Barremian to Cenomanian of the Alpstein. Examined units include the Tierwis Formation consisting of the Altmann and Drusberg Members (latest Hauterivian–late Barremian), the Schrattenkalk Formation (late Barremian–Aptian), the Garschella Formation (Aptian–earliest Cenomanian) and the Seewen Formation (Cenomanian). We sampled macrofossils from highly fossiliferous layers of the Tierwis area of the Alpstein and analysed palaeoecological changes using ecospace utilization approaches. All fossils were classified based on ecological parameters of tiering, motility and feeding mechanism and were subsequently plotted into the three-dimensional ecospace. The results of the palaeoecological analyses demonstrated dynamic changes in ecospace utilization through time. Comparison of the results of our palaeoecological analyses and regional sea level fluctuations suggests that the two phenomena are linked.

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## New microgastropod assemblages from the lower Miocene of the Mesohellenic Basin

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The lower Miocene (Aquitanian) microgastropods of Greece are poorly documented. The present study focuses on well-preserved material from a section in the Mesohellenic Basin in the Grevena area which has not been described previously. Palaeobiogeographically, the basin belongs to the rather homogeneous Proto-Mediterranean-Atlantic Region (which includes France, the entire Mediterranean, and central Iran). The Mesohellenic Basin is a piggy-back basin that was active from the end of the Eocene until the Middle Miocene and contains abundant marine fossils. Previous studies of the Oligocene and lower Miocene focused mostly on larger-sized species. In the present study, systematic analysis of the fossil content of the section has yielded interesting results that inform the fossil molluscan record of the Hellenic area. About 60 species of microgastropods were identified, most of which are recorded for the first time from the Lower Miocene of Greece, and including potential new species. The faunal composition suggests affinities with early Miocene faunas from Italy and Austria, and the ecological characteristics of the fauna indicate a shallow marine oligohaline to euhaline environment.



## Body size change of marine benthic macroinvertebrates in response to environmental stressors during the Pliensbachian–Toarcian Extinction Event (Early Jurassic)

\***Hannah Tilley<sup>1</sup>, Richard J. Twitchett<sup>2</sup>, Jonathan A. Todd<sup>2</sup> and Silvia Danise<sup>3,4</sup>**

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The Pliensbachian–Toarcian (~183 Ma) was an interval of global warming and associated environmental changes which altered terrestrial and marine ecosystems worldwide. In the aftermath of this hothouse extinction interval, temporary body size decrease (the Lilliput effect) has been documented in some marine benthic macroinvertebrates. This may have conferred a selective advantage in the presence of shifting environmental factors. In this study we recorded body size of 39 Pliensbachian–Toarcian marine macroinvertebrate species from the Cleveland Basin, North Yorkshire. Analyses showed that surficial, filter-feeding functional groups had a greater proportion of surviving taxa in the aftermath of the extinction interval than other functional groups. Significant decrease in the body size of the common filter-feeder *Pseudomytiloides dubius* after the extinction interval is consistent with the Lilliput effect. Each of the measured geochemical proxies of environmental change had a significant relationship with at least one of the species or functional groups.  $\delta^{98/95}\text{Mo}$  (‰) showed the greatest number of significant correlations with individual species, whereas  $\delta^{13}\text{C}_{\text{org}}$  (‰) displayed more significant correlations with functional groups. Significant relationships between geochemical proxies and sizes of individual species or functional groups support previous evidence that ecological change was probably driven by environmental shifts during this past warming event.

## Palaeoecological reconstruction of the community of the Kalana Lagerstätte

**Oive Tinn<sup>1</sup>, Leho Ainsaar<sup>1</sup>, Philippe Gerrienne<sup>2</sup>, Stefi Guiton<sup>1</sup>, Kalle Kirsimäe<sup>1</sup>, Viirika Mastik<sup>1</sup> and Tõnu Meidla<sup>1</sup>**

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<sup>2</sup>University of Liège, Belgium

The Kalana Lagerstätte (Aeronian, Silurian) in Central Estonia has revealed a number of exceptionally preserved fossils, both auto- and heterotrophs. The most abundant fossil group in the Lagerstätte is non-calcified algae; the fauna is diverse and includes benthic, nektonic and planktonic animals. The excellent preservation of some fossils, notably some specimens of crinoids, suggests that they were buried *in situ*. However, shelly fossils, including brachiopods and gastropods, are common in storm-accumulated coquina lenses. Ten ostracod taxa have been identified to date. Cuticle remains of the eurypterid *Eurypterus tetragonophthalmus*, occasional accumulations of shells of leperditids and rare trilobite remains have been reported. Tabulate corals, small rugosan corals and conulariids are quite common; less common fossils include bryozoans, sponges, orthoconic and coiled nautiloids, and a single recently discovered agnathan.



## Storm deposits as graves for the Fezouata Biota (Lower Ordovician, Morocco)

**Romain Vaucher, Bernard Pittet, Hélène Hormière, Emmanuel L. O. Martin and Bertrand Lefebvre**

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The Great Ordovician Biodiversification Event (GOBE) is one of the most important radiations of the Phanerozoic Eon. The GOBE is characterised by an exponential diversification of classes within phyla that appeared during the Cambrian. Palaeontologists have recognized a major gap in the record of soft-bodied faunas spanning the late Cambrian – Middle Ordovician time interval. The recent discovery of a late Tremadocian Konservat-Lagerstätte in the Fezouata Shale (Anti-Atlas, Morocco) that yielded thousands of exceptionally well-preserved fossils (EPF) is thus of prime importance for understanding the rise of animal life. In the Zagora area, Lower Ordovician deposits consist in c. 900m of siltstones and sandstones deposited in an epicontinental sea dominated by storms and waves, at the periphery of Gondwana. Both the Fezouata Shale and the overlying Zini Fm characterise the Early Ordovician in this area. EPF are almost exclusively found on surface beds of argillaceous siltstones directly overlain by fine-grained sandstones (distal storm deposits). Since EPF are only found in this manner and never in the finest sediments devoid of storm deposits, their fast burying by storm deposits appears to be a pre-requisite to initiate the exceptional preservation of soft tissues and organisms.

## A closer look at a possible stem group holozoan from the 1 Ga Torridon Group of northwest Scotland

**David Wacey<sup>1</sup>, Paul K. Strother<sup>2</sup>, Martin D. Brasier<sup>3,†</sup> and Charles H. Wellman<sup>4</sup>**

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Phosphatic nodules within the non-marine Torridonian Sequence of Scotland have long been known to harbour microfossils, but up until recently their diversity, ecology and systematic relations were not assessed. Of particular interest are populations of multicellular cell balls, the mature form of which consists of an inner, spheroidal mass of tightly-packed cells that is tightly enclosed by elongate, sausage-shaped, thick-walled cells forming a surficial layer that is one cell in thickness. Exceptional preservation in different populations shows individual specimens at successive stages of differentiation enabling the reconstruction of a potential life-cycle for the organism (see companion poster by Strother *et al.*). Here we present correlated morphological and geochemical data from specimens at different stages in the life cycle using light microscopy, nanoSIMS ion mapping, plus 2D and 3D electron microscopy. These data provide insights into the mechanism of exceptional preservation of these organisms, the nature of the internal contents of the cells, and permit three-dimensional reconstruction of the detailed morphology of selected specimens.



## Complexity of crustacean feeding apparatuses: new insights from the Rhynie Chert

**Philipp Wagner, Joachim T. Haug and Carolin Haug**

LMU Munich, Germany

The famous Early Devonian Rhynie Chert provides deep insights into a 400 million-year-old non-marine habitat. The exceptional preservation of the *in situ* silicified fossils from this Lagerstätte allows detailed studies on floral and faunal elements. The floral elements are abundant and diverse. Fossil faunal elements are less abundant; these include several species of arthropods, inhabiting both terrestrial and aquatic habitats. Aquatic arthropods are represented mainly by entomostracan crustaceans, e.g., *Lepidocaris rhyniensis*, *Ebullitiocaris oviformis* and *Castracollis wilsonae*. These species represent some of the earliest known non-marine crustaceans. Preservation of details in these fossils ranges down to the optical resolution properties of visible light, i.e., 200 nm. This allows extremely fine individual structures such as setules and spinules to be identified and compared to their modern day counterparts. Here we present new insights into the morphology of these early crustaceans, focusing on mouthpart morphology and organization, using a wide range of documentation methods that include fluorescence microscopy, high-resolution macrophotography and optical tomography. Morphology and organization of the feeding apparatuses provide vital insights into the ecology of these crustaceans and allow conclusions about food uptake and possibly life history traits.

## Anatomy and affinities of a new 535-million-year-old medusozoan from the Kuanchuanpu Formation, South China

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The early Cambrian Kuanchuanpu Formation from South China (Ningqiang, Shaanxi Province) yields abundant small shelly fossils (SSF) that include embryonic stages of medusozoans. Their exceptional preservation in calcium phosphate allows very detailed reconstruction of their internal anatomy using X-ray microtomography. Although these fossils reveal unknown aspects of the early evolution of cnidarians, important issues remain unresolved such as the development cycle of these early medusozoans, their taxonomy and their relationship to modern cnidarian groups. Here we describe *Sinaster petalon* gen. et sp. nov., a new species of medusozoan characterised by a pentamerous symmetry and a smooth periderm which contrasts with the stellate external ornament of co-occurring forms such as *Olivoooides*. X-ray microtomography reveals fine details of its internal anatomy such as coronal muscles, perradial and adradial frenula, interradial septa, accessory septa, gonad-lamellae, tentacle buds and perradial pockets. The insertion of the gonad lamellae of *S. petalon* gen. et sp. nov. into the interradial septa is similar to that in extant cnidarians and fossil embryos from the early Cambrian Kuanchuanpu biota.



## A new Pleistocene interglacial fauna from Dalian, Northeast China, associated with Early Palaeolithic artefacts

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A wealth of fossil material from the Late Pleistocene *Mammuthus-Coelodonta* faunal complex have been recovered in Northeast China, but earlier Pleistocene fossils from this region have been meagre. In 2013, an interglacial fauna was discovered at Luotuoshan in Dalian, Liaoning Province, the first of its type in Northeast China. The mammalian assemblage from the upper unit of Luotuoshan bears strong resemblance to a typical Middle Pleistocene interglacial fauna, but with at least one fossiliferous horizon exceeding 780 ka in age. In particular, the presence of *Palaeoloxodon*, *Stephanorhinus*, *Pachycrocuta*, *Sinomegaceros*, *Trogontherium* and *Megantereon*, among other taxa, reflects outstanding similarities to the classic Zhoukoudian *Homo erectus* localities. An abundance of stone tools found alongside the animal remains, plus bones with butcher marks, clearly indicate early human activity in the area. The fauna and artefacts at Luotuoshan hold much interest for future research. Despite the absence of hominin remains from excavations to date, Luotuoshan has crucial implications for the origin and environmental background of the interglacial faunas found in classic Middle Pleistocene hominin sites, such as Mauer and Zhoukoudian, and the origins and nature of hominin interactions with the associated faunas.

## The Natural History Museum, London, rescue dig at Woodeaton Quarry, Oxfordshire – an update

David J. Ward, Simon Wills, Emma L. Bernard and Philippa Brewer

*Natural History Museum, London, UK*

Woodeaton Quarry exposes one of the most complete sections of the Middle and Late Bathonian (Middle Jurassic) in southern England. The exposure displays a continuous and accessible section from beneath the Taynton Stone to the Forest Marble. The quarry is being restored to become a nature reserve. Although some sections have been preserved, some exposures of the Rutland and White Limestone formations have been lost. Since 2013 a series of visits were made by the NHM, London, to log sections and gather representative macrofossils, micropalaeontological and microvertebrate samples. While doing so, a horizon rich in microvertebrate remains was discovered just below the Forest Marble. This assemblage has produced a mixture of marine (possibly reworked), aquatic/semiaquatic and terrestrial taxa. Vertebrate remains are typically fragmentary small postcranial elements along with isolated teeth and scales, showing little sign of transportation. Taxa include mammals (amphitheriids, amphilestids, docodonts, multituberculates, and haramyiids), dinosaurs (dromaeosaurs and possible thyreophorans), pterosaurs, fish, frogs, albanerpetontids, salamanders, lizards, crocodiles, turtles and sharks. Plant remains are common and the abundance of charophytes suggests deposition in freshwater. Recently, numerous egg shell fragments have been found, probably representing turtles, crocodiles and non-avian dinosaurs. This is currently the oldest fossil egg shell mixed assemblage known worldwide.



## Resolving the Bajocian radiation of dinoflagellates: new records from the Middle Jurassic of Europe

**\*Nickolas Wiggan<sup>1,2</sup>, James B. Riding<sup>2</sup> and Matthias Franz<sup>3</sup>**

<sup>1</sup>*University of Cambridge, UK*

<sup>2</sup>*British Geological Survey, UK*

<sup>3</sup>*Geological Survey of Baden-Württemberg, Germany*

Dinoflagellates underwent a major radiation during the Bajocian (Middle Jurassic, 170–168 Ma), during which *c.* 100 dinocyst species appeared. Despite this, Bajocian dinocysts have received relatively little study. Here we present the results of a high-resolution palynological and chemostratigraphical study of the European Bajocian. The Late Aalenian–Early Bajocian saw a major phase of archaeopyle (excystment aperture) experimentation, whilst the genus *Dissiliodinium* became extremely abundant. This may have been linked to an increase in bioproductivity, as indicated by a positive shift in our carbon isotope records. *Dissiliodinium* declined in abundance in the middle Bajocian as other cyst-forming dinoflagellates radiated dramatically, with the appearance of *c.* 60 new dinocyst species by the earliest Bathonian. The family Gonyaulacaceae expanded through this interval to become the dominant family of cyst-forming dinoflagellates; this dominance persists to the Recent. Our stratigraphic data suggest that the Bajocian radiation of dinocyst taxa through Europe was strongly influenced by third-order sea level cycles, with first appearances correlating with transgressive episodes. Other groups of pelagic organisms, including ammonites and fishes, were also radiating at this time, which suggests major innovations in pelagic ecosystems. Given these wider-scale changes, the Bajocian radiation may form part of the Mesozoic Marine Revolution.

## Heritability of species range size and Rapoport's rule in Early Jurassic ammonoids

**Axelle Zacaï<sup>1</sup>, Emmanuel Fara<sup>1</sup>, Arnaud Brayard<sup>1</sup>, Rémi Laffont<sup>1</sup>, Jean-Louis Dommergues<sup>1</sup> and Christian Meister<sup>2</sup>**

<sup>1</sup>*CNRS UMR 6282, Université de Bourgogne Franche Comté, France*

<sup>2</sup>*Natural History Museum of Geneva, Switzerland*

Geographic range size is a fundamental ecological and evolutionary feature of species that results from a complex interplay of intrinsic (*e.g.* dispersal ability, ecological tolerance) and extrinsic factors (*e.g.* environmental features, physical barriers). Using a dataset of 214 ammonite species from the early Pliensbachian of the western Tethys and adjacent areas, we tested for the heritability of species range size and for the existence of a Rapoport effect. Heritability of range size was analysed using Moran's I, and the correlation between range size and latitude was analysed using a generalized linear model that integrates phylogenetic relatedness. We found that species range size may be partly determined by phylogeny, but this heritability is modulated by environmental stability. Heritability may be labile through time in a single lineage and may differ among contemporaneous species of a same clade. Distribution of species range sizes follow Rapoport's rule only at high latitudes, whereas species at lower latitudes show larger average range sizes that do not increase with latitude. This result corresponds to the 'climatic variability hypothesis', with spatio-temporal homogeneous temperatures at low latitudes and a marked gradient of temperatures and seasonality at higher latitudes.



## The oldest mesophotic reefs? Devonian biostromes in the Holy Cross Mountains (Poland)

**Mikolaj Zapalski<sup>1</sup>, Tomasz Wrzosek<sup>2</sup>, Stanisław Skompski<sup>1</sup> and Błażej Berkowski<sup>3</sup>**

<sup>1</sup>University of Warsaw, Poland

<sup>2</sup>University of Silesia in Katowice, Poland

<sup>3</sup>Adam Mickiewicz University in Poznań, Poland

Mesophotic reefs are coral communities occurring in water depths of 30–150 m. At such depths light is attenuated, and thus corals occurring in such environments display adaptations for light harvesting, such as platy morphology. Such morphologies are used as a tool for recognition of photosymbiosis in fossil corals. The Givetian biostrome from Laskowa (Holy Cross Mountains, Poland) is dominated by platy corals. In these communities, the most frequently occurring tabulates are coenitids (*Roseoporella* and *Platyaxum*, rarely *Coenites*) and alveolitids. Their length-to-thickness ratios are typically 4–8:1, but up to 20:1, indicating striking lateral growth. Colonies are usually 15–25 cm long but can be up to 45 cm long. Nearly all tabulates in this biostrome display moderate levels of colony integration and very small diameters of corallites (< 1 mm). Additional faunal elements include pachyporid and auloporid tabulates, rugose corals, chaetetid sponges, brachiopods (atrypids, gypidulids and rhynchonellids) and crinoids. Another coenitid-dominated biostrome with alveolitids and heliolitids occurs in the Eifelian of Skąły, some 45 km west of Laskowa. Palaeogeography and sedimentology evidence deeper environments, while colony integration, small corallites and platy morphology confirm photosymbiosis in tabulates. These biostromes are possibly the oldest mesophotic reefs.

## On the difficulties of understanding elephantid systematics from isolated teeth

**\*Hanwen Zhang<sup>1</sup> and Adrian M. Lister<sup>2</sup>**

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

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

The Elephantidae has been the poster child for rapid evolutionary rate and phyletic morphological transitions in the established palaeontological literature. However, most of their scientifically scrutinized fossil record is restricted to isolated molars, due to the low preservation potential of craniomandibular materials and comparatively un-diagnostic postcrania. Whereas different criteria of dental morphology such as lamellar number, hypsodonty index and enamel figure shape are informative of elephantid evolution and palaeoecology, they have always been susceptible to a high degree of parallelism throughout the evolutionary history of the elephantids. Furthermore, a unique horizontal tooth replacement system, involving very large molars that are durable for long periods, creates considerable intraspecific variations in dental morphology as a result of differences in wear stages and positions in tooth rows. This catalogue of caveats obscures phylogenetic signals to an extent that a robust cladistic analysis of elephant phylogeny remains to be achieved. Understanding the nature of dental homoplasies and sources of metrical errors will be crucial towards a modern, quantitatively testable understanding of elephantid evolution.





# **The Palaeontological Association**

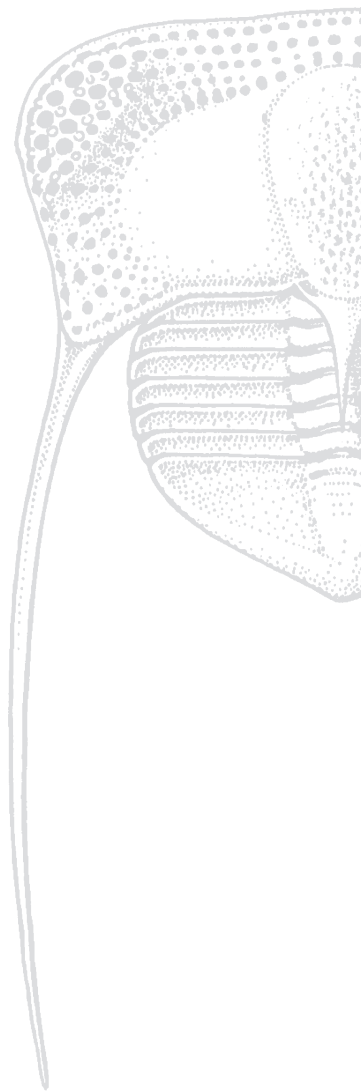
## **Annual General Meeting**

**16.15**

**Thursday**

**15th December**

**Papers**







## Annual Meeting 2016 and AGM

### Notification is given of the 60th Annual General Meeting

The AGM will be held during the Annual Meeting at Université Claude Bernard Lyon 1, France, on 15th December 2016, following the scientific sessions.

#### AGENDA

1. Apologies for absence
2. Minutes of the 59th AGM, Cardiff University
3. Trustees Annual Report for 2015
4. Accounts and Balance Sheet for 2015
5. Election of Council and vote of thanks to retiring members
6. Report on Council Awards
7. Annual address

#### DRAFT AGM MINUTES 2015

Minutes of the Annual General Meeting held on Wednesday, 15th December 2015 at Cardiff University, UK.

- 1. Apologies for absence.** Dr P. Winrow, Dr L. G. Herringshaw, Dr M. E. McNamara, Dr R. J. Butler.
- 2. Minutes.** Proposed by Dr C. T. S. Little and seconded by Dr M. D. Sutton, the minutes of the 2014 AGM were agreed a true record by unanimous vote.
- 3. Trustees Annual Report for 2014.** Proposed by Prof. G. D. Sevastopolu and seconded by Prof. J. C. W. Cope, the report was agreed by unanimous vote of the meeting.
- 4. Accounts and Balance Sheet for 2014.** Proposed by Dr C. J. Buttler and seconded by Prof. P. C. J. Donoghue, the accounts were agreed by unanimous vote of the meeting.
- 5. Election of Council and vote of thanks to retiring members.**
  - 5.1** Prof. D. A. T. Harper extended a vote of thanks to the following members of Council who were retiring from their positions this year: Dr M. D. Sutton and Dr J. Hellawell. Prof. Harper also thanked Dr T. J. Palmer for his service as Executive Officer and announced that Dr J. Hellawell would be replacing him as the Association's new Executive Officer from January 2016.
  - 5.2** The following members were elected to serve on Council: President: Prof. D. A. T. Harper; President Elect: Prof. M. P. Smith; Vice Presidents: Prof. E. J. Rayfield and Dr D. J. Ward; Treasurer: Dr P. Winrow; Secretary: Prof. R. J. Twitchett; Editor-in-Chief: Dr A. B. Smith; Editor Trustees: Prof. C. H. Wellman, Dr M. Ruta; Newsletter Editor: vacant; Book Review Editor: Dr T. J. Challands; Publicity Officer: Dr L. G. Herringshaw; Education Officer: Dr C. J. Buttler; Outreach Officer: Dr F. Gill; Internet Officer: Dr A. R. T. Spencer; Meetings Coordinator: Dr T. R. A. Vandenbroucke; Ordinary Members: Dr R. J. Butler, Dr C. T. S. Little, Dr M. E. McNamara, Dr M. Munt, and Dr I. Rahman.
  - 5.3** Prof. G. Cuny and colleagues will organize the Annual Meeting in 2016 at the Université Claude Bernard Lyon 1, France.

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

- 6.1 The Lapworth Medal was awarded to Prof. J. A. Clack FRS (University of Cambridge, UK).
  - 6.2 The President's Medal was awarded to Prof. G. E. Budd (Uppsala University, Sweden).
  - 6.3 The Hodson Award was presented to Dr R. B. J. Benson (University of Oxford, UK).
  - 6.4 The Mary Anning award was presented to Mr L. Koch (Ennepetal, Germany).
  - 6.5 Undergraduate Research Bursaries were awarded to: Mr G. A. Coleman, University of Bristol, supervised by Prof. M. J. Benton, *Dissecting the rise of the archosaurs*; Mr W. Jessop, University of Oxford, supervised by Dr A. C. Daley, *Were co-existing archaeocyathids partitioning suspended food matter by having different pore sizes, in order to reduce competition for resources?*; Mr L. E. Meade, University of Birmingham, supervised by Dr R. J. Butler, *3D photogrammetric imaging and re-analysis of a unique Late Carboniferous footprint assemblage from Shropshire*; Ms N. Meyer, University of St. Andrews, supervised by Dr A. Zerkle, *Multiple sulphur isotope studies of pyritised microbially induced sedimentary structures, Neoarchaeon Ghaap Group, South Africa*; Mr C. Nedza, University of Leicester, supervised by Prof. M. A. Purnell, *3D textural analysis of tooth wear in insectivores, and its application to fossil mammals*; Ms K. Norden, University of Bristol, supervised by Dr J. Vinther, *Effects of diagenetic processes on melanosome morphology in iridescent feathers*; Mr J. O'Shea, University of Bristol, supervised by Dr I. Rahman, *Testing functional hypotheses in Cambrian cinctan echinoderms using computational fluid dynamics*; Mr G. Samarawickrama, Plymouth University, supervised by Dr U. Balthasar, *Shell thickness distribution in Ordovician and Silurian rhynchonelliformean brachiopods*.
  - 6.6 Research Grants were awarded to: Dr J. F. Hoyal Cuthill (University of Cambridge), *Resolving the evolutionary relationships of the Ediacaran biota with new quantitative methods*; Dr B. Metcalfe (VU University Amsterdam), *The Lilliput effect: growth rate or longevity?*; Dr J. Ortega-Hernández (University of Cambridge), *The origins of aerial breathing in terrestrial ecosystems: insights from virtual fossil reconstruction*.
  - 6.7 Under the Small Grants Scheme, the following awards were announced: Sylvester-Bradley Awards to Ms C. M. Bullar (University of Bristol), *Braincase anatomy, phylogeny and the success of Neoceratopsia*; Mr D. J. Marshall (University of Bristol), *Insights into chelicerate evolution through comparative cuticular analysis*; Mr S. Pates (University of Oxford), *Diversity and ecology of the anomalocaridids of the Great Basin, USA*; The Callomon Award to Mr N. F. Adams (Royal Holloway, University of London), *Early Pleistocene Palaeontology of Westbury Cave, Somerset*; Stan Wood Awards to Ms C. Colleary (Virginia Tech), *Biomolecule preservation through time: mapping bone degradation in fossil Proboscideans from different depositional environments*; Mr M. Marzola (Copenhagen University), *The Late Triassic amphibian and reptilian fauna of the Jameson Land Basin (East Greenland) and its comparison with coeval European faunas*; and The Whittington Award to Dr M. R. Smith (Durham University), *Vetulicolian affinities reconsidered through the lens of ecdysozoan anterior organization*.
  - 6.8 The President's Award was presented to Mr J. W. Oyston (University of Bath).
  - 6.9 The Council Poster Prize was presented to Mr C. Nedza (University of Leicester).
  - 6.10 The 2015 best paper prizes were awarded to Prof. S. M. Holland and Prof. M. E. Patzkowsky for their paper entitled "The stratigraphy of mass extinction" (*Palaeontology*) and to Prof. L. E. Popov and colleagues for "Himalayan Cambrian brachiopods" (*Papers in Palaeontology*).
- 7. Annual Address.** The Annual Address entitled "Computer modelling and simulation of extinct organisms: its utility and limitations for reconstructing the evolution of locomotor behaviour" was given by Prof. J. R. Hutchinson (The Royal Veterinary College).



## Trustees Annual Report 2015

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

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.

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

**1.2 Grants-in-aid for meetings and workshops:** The Association provided funds to support the following meetings and workshops: 'Evolution and Development of Vertebrate Dentition: a Festschrift in honour of Moya Meredith Smith' (Dr Z. Johanson, Natural History Museum, London); 5th Polar Marine Diatom Workshop (Dr M. A. Barcena, University of Salamanca); 'Rooted in deep time: palaeontological contributions to systematics', 2015 Systematic Association Biennial Meeting Symposium (Dr R. B. J. Benson, University of Oxford); 'Rise of Animal Life: Cambrian and Ordovician biodiversification events' (Prof. K. El Hariri, Cadi-Ayyad University); 63rd SVPCA Meeting (Dr G. J. Dyke, University of Southampton); 'Co-evolution of life and the planet: broad-scale controls on biodiversity', GSA Annual Meeting Topical Symposium T149 (Prof. R. J. Twitchett, Natural History Museum, London); and 'Experimental solutions to deep time problems in palaeontology', IGCP591 closing meeting (Dr T. R. A. Vandenbroucke, Ghent University).

**1.3 Public meetings:** Four public meetings were held in 2015, and the Association extends its thanks to the organizers and host institutions of these meetings.

**59th Annual Meeting.** The Association's Annual Meeting is its flagship meeting and this year was held on 14th – 17th December at Cardiff University and Amgueddfa Cymru – National Museum Wales, UK. Dr C. J. Buttlar, Dr L. Cherns and Dr L. M. E. McCobb, with local support from colleagues and PhD students, organized the meeting, which included a symposium on 'Palaeobiotic interactions' and comprised a programme of internationally recognized speakers. There were 274 attendees. The Annual Address was entitled 'Computer modelling and simulation of extinct organisms: its utility and limitations for reconstructing the evolution of locomotor behaviour' and was given by Prof. J. R. Hutchinson (The Royal Veterinary College). The President's Prize for best oral presentation by an early-career researcher was made to Mr J. W. Oyston (University of Bath). The Council Poster Prize for best poster presentation by an early-career researcher was presented to Mr C. Nedza (University of Leicester).



*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 2015 meeting was organized by Mr J. N. Keating and a team of other students, and was held at the University of Bristol in April.

*Lyell Meeting.* The Association was one of the joint co-organizers of this annual meeting. The 2015 Lyell Meeting was held in March at Burlington House, London, on the topic of 'Mud, glorious mud, and why it is important for the fossil record' organized by Dr A. L. Coe (The Open University) and Prof. A. R. Lord (Senckenberg Research Institute).

*British Science Festival.* This is an annual forum for presentations to the public and general scientists. The Association sponsored its 2014 President's Prize winner, Mr D. J. Button (University of Bristol), to give a public talk on 'Dinosaur Behaviour: Recreating Lost Worlds' at the 2015 Festival in Bradford, which drew a large audience.

**1.4 Publications:** Publication of the journals *Palaeontology* and *Papers in Palaeontology* is managed by Wiley. During 2015, the following volumes were published: *Palaeontology* volume 58, comprising six issues; and *Papers in Palaeontology* volume 1, comprising four issues. The Association is grateful to Amgueddfa Cymru – National Museum Wales and The Lapworth Museum of Geology (University of Birmingham) for providing storage facilities for publication back-stock and archives. Council thanks Mr N. Stroud for assistance with the typesetting and production of the *Palaeontology Newsletter*.

**1.5 Research Grants:** Eleven applications for Palaeontological Association Research Grants were received. Three were recommended for funding in 2015, totalling £15,084, and were awarded to: Dr J. F. Hoyal Cuthill, University of Cambridge, 'Resolving the evolutionary relationships of the Ediacaran biota with new quantitative methods'; Dr B. Metcalfe, VU University Amsterdam, 'The Lilliput effect: growth rate or longevity?'; and Dr J. Ortega-Hernández, University of Cambridge, 'The origins of aerial breathing in terrestrial ecosystems: insights from virtual fossil reconstruction'.

**1.6 Small Grants Scheme:** The scheme received 19 applications. Seven were recommended for funding in 2016, totalling £9,491. Small grants were awarded as follows: Dr M. R. Smith (Durham University) received the Whittington Award; Mr N. F. Adams (Royal Holloway, University of London) received the Callomon Award; Ms C. Colleary (Virginia Tech) and Mr M. Marzola (Copenhagen University) received Stan Wood awards; Ms C. M. Bullar (University of Bristol), Mr D. J. Marshall (University of Bristol) and Mr S. Pates (University of Oxford) received Sylvester-Bradley awards.

**1.7 Undergraduate Research Bursary Scheme:** The scheme attracted ten applications. Eight were recommended for funding in 2015, totalling £11,600, as follows: Mr G. A. Coleman, University of Bristol, supervised by Prof. M. J. Benton; Mr W. Jessop, University of Oxford, supervised by Dr A. C. Daley; Mr L. E. Meade, University of Birmingham, supervised by Dr R. J. Butler; Ms N. Meyer, University of St. Andrews, supervised by Dr A. L. Zerkle; Mr C. Nedza, University of Leicester, supervised by Prof. M. A. Purnell; Ms K. Norden, University of Bristol, supervised by Dr J. Vinther; Mr J. O'Shea, University of Bristol, supervised by Dr I. A. Rahman; and Mr G. Samarawickrama, Plymouth University, supervised by Dr U. Balthasar.

**1.8 Publicity, outreach and engagement:** The Association continues to promote palaeontology and its allied sciences to the national media, radio and television. The Association is a major financial supporter of the Lyme Regis Fossil Festival and the Yorkshire Fossil Festival (held in Scarborough



in 2015). At both festivals, the Association had displays and activities for the public, which were organized and staffed by members of Council, the Executive Officer and volunteers.

**1.9 Outreach and Engagement Grants:** The scheme received a total of eight applications in 2015. Three were recommended for funding, totalling £15,724, and were awarded to: Dr R. J. Butler (University of Birmingham), 'Gesture control technologies and palaeontology: exploring innovative outreach and education approaches using 3D fossil models'; Ms S. Butterworth (Emerald Ant CIC), 'The Iguanodon Restaurant – Inspiring Communities in Earth Sciences through Art'; Dr S. Montanari (University of Edinburgh), 'Fossils For Everyone: Palaeontology Outreach in Children's Hospitals'.

**1.10 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), and online outreach projects (Palaeontology [Online]). The Association Twitter account, @ThePalAss, had 2,119 followers at the end of 2015, an increase of 969 on the numbers at the end of 2014. Towards the end of 2015 the Association launched a re-designed website (<[www.palass.org](http://www.palass.org)>) with the aim of making our online assets easier to navigate and find for our membership and the wider general public.

**1.11 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. J. A. Clack (University of Cambridge). 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. G. E. Budd (Uppsala University). 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 R. B. J. Benson (University of Oxford). The Mary Anning award, for an outstanding contribution by an amateur palaeontologist, was made to Mr L. Koch (Ennepetal, Germany). Council also awards undergraduate prizes to outstanding students in university departments where palaeontology is taught beyond Level 1.

**1.12 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. A donation will be made to the Biodiversity Heritage Library in order to scan back issues of all of the Association's publications so that they become freely available online. A new website was launched at the 2015 Annual Meeting and development will continue through 2016. Volume 59 of *Palaeontology* and volume 2 of *Papers in Palaeontology* will be published. The 60th Annual Meeting will be held in December 2016 at the Université Claude Bernard Lyon 1, France. The 2016 Progressive Palaeontology conference will be held at the University of Oxford. In late 2015, Council decided to investigate whether incorporation would be beneficial to the Association and help further its aims and objectives. Subsequently, in early 2016, Council's proposal to convert to a Charitable Incorporated Organisation (CIO) was agreed by the membership at an Extraordinary General Meeting held on 16th March 2016. It is anticipated that the process of converting to a CIO will be completed in 2016.



## 2. Achievements and Performance

**2.1 Meetings support:** During 2015, the Association agreed to support a total of ten palaeontological meetings, symposia or workshops worldwide (in the UK, USA, Spain and Morocco). In addition, our Postgraduate Travel Grant scheme supported six postgraduate students to present their work at national and international conferences. The Association's support enabled the worldwide dissemination of research to the benefit of the global palaeontological community.

**2.2 Publications:** During 2015, 119 papers were submitted to *Palaeontology*. Of these, 88 (74%) were considered suitable by the Editorial Board and 74 (62%) were subsequently accepted following peer review. The average time from acceptance to production was reduced for the second year running, to 46 days for papers published in volume 59 of *Palaeontology* (some of which had been published online in 2014). The same interval for papers in volume 1 of *Papers in Palaeontology* was higher (at 76 days), but this was due in part to a small number of initial papers that were held before online publication in 2014. The Association also sponsored the online publication of 34 Dryad data records associated with papers in volumes 59 and 1.

**2.3 Support for research:** In 2015 the Association agreed to fund the research activities of 18 early-career researchers based in four countries (the UK, USA, The Netherlands, Portugal). Two of this year's Undergraduate Research Bursary awardees presented their work at the 2015 Annual Meeting. Apart from directly benefiting the career development of the individuals concerned, the Association's funds enabled more palaeontological research to be undertaken worldwide than would otherwise have been the case. Overall, fewer grants were funded in 2015 compared to the previous year. Compared to 2014, applications for Research Grants increased (from six to 11) and success rates consequently fell (from 50% to 27%). For the Small Grants Scheme, applications remained the same (19) but success rates fell (from 47% to 37%) as fewer were awarded. The number of applications to the Undergraduate Research Bursary Scheme fell substantially (from 20 to ten) compared to 2014, and success rates consequently increased (from 50% to 80%). Each grant is now assigned a unique identifying number which authors are encouraged to use when acknowledging the Association's financial support in order to better track the individual outputs associated with each award.

**2.4 Outreach, education and public engagement:** During 2015, the Association supported the two major UK fossil festivals, at Lyme Regis and Scarborough, which attracted respectively an estimated 12,000 and 4,000 members of the general public of all ages. Secondary school students were particular beneficiaries of the Association's outreach and education activities, with a dedicated event associated with the Lyme Regis Fossil Festival. During 2015, we awarded three Outreach and Engagement grants to fund diverse projects led by Dr R. J. Butler, Ms S. Butterworth and Dr S. Montanari. Continued use of social media, in particular the Association's Twitter account, has enabled the rapid and regular dissemination of research news, including of new publications, meetings and other information, to a growing audience.

## 3. Financial Review

**3.1 Reserves:** As of 31st December, The Association holds reserves of £737,043 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 £142,930 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 2016 totalled £879,973.





**3.2 Summary of expenditure:** Total charitable expenditure, through grants to support research, scientific meetings and workshops in 2015, was £340,324. Governance costs were £20,989. Total resources expended were £393,980. 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 governing document of the Palaeontological Association is the Constitution adopted on 27th February 1957, amended on subsequent occasions as recorded in the Council and AGM Minutes.

**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. The Trustees are elected by vote of the Membership at the Annual General Meeting, following guidelines laid down in the Constitution.

**4.3 Trustees:** The following members were elected at the AGM on 17th December 2014 to serve as trustees in 2015: *President:* Prof. D. A. T. Harper; *Vice Presidents:* Mr D. J. Ward and Dr M. D. Sutton; *Treasurer:* Mr P. Winrow; *Secretary:* Prof. R. J. Twitchett; *Editor-in-Chief:* Dr A. B. Smith; *Editor Trustees:* Dr M. Ruta, Prof. C. H. Wellman; *Newsletter Editor:* Dr J. Hellawell; *Book Review Editor:* Dr T. J. Challands; *Internet Officer:* Mr A. R. T. Spencer; *Publicity Officer:* Dr L. G. Herringshaw; *Education Officer:* Dr C. J. Buttler; *Outreach Officer:* Dr F. Gill; *Meetings Coordinator:* Dr T. R. A. Vandenbroucke; *Ordinary Members:* Dr R. J. Butler, Dr C. T. S. Little, Dr M. E. McNamara, Dr M. C. Munt, Dr I. A. Rahman. *The Executive Officer* Dr T. J. Palmer and the *Publications Officer* Dr S. L. Thomas serve on Council but are not Trustees. Dr M. D. Sutton and Prof. R. J. Twitchett represented the Association on the Joint Committee for Palaeontology.

**4.4 Membership:** Membership on 31st December 2015 totalled 1,086 (1,071 at end 2014). Of these, 592 were Ordinary Members, 164 Retired Members, 19 Honorary Members, 274 Student Members and 37 Institutional Members. There were 43 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 Association is in a sound financial position. Potential financial risks were discussed as part of a Council Away Day held in October 2015. Succession planning for the Executive Officer was considered by Council as part of the Annual Review of Officers during 2015 and was implemented later in the year. Following advertisement of a revised, full-time position and a thorough interview process led by the President, a new Executive Officer has been appointed for 2016 and the Association is confident of a smooth transition.

#### 5. Reference and Administration

**5.1 Name and Charity Number:** The Palaeontological Association is a Charity registered in England and Wales, Charity Number 276369.

**5.2 Address:** The contact address of the Association is The Palaeontological Association, c/o IGES Llandinam Building, Aberystwyth University, Aberystwyth, SY23 3DB, UK.

**5.3 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 was managed by Quilter Cheviot Investment Management, 1 Kingsway, London WC2B 6XD.

**REFERENCE AND ADMINISTRATIVE DETAILS****Principal address**

c/o IGES, Llandinam Building,  
Aberystwyth University,  
Aberystwyth  
SY23 3DB

**Trustees**

Prof. D.A.T. Harper	President	
Dr M.D. Sutton	Vice President	
Dr D.J. Ward	Vice President	
Prof. R.J. Twitchett	Secretary	
Dr P. Winrow	Treasurer	
Dr A.B. Smith	Editor-in-Chief	
Dr M. Ruta	Editor Trustee	
Prof. C.H. Wellman	Editor Trustee	
Dr A.R.T. Spencer	Internet Officer	
Dr J. Hellowell	Newsletter Editor	Resigned 31st December 2015
Dr T.J. Challands	Book Review Editor	
Dr L.G. Herringshaw	Publicity Officer	
Dr F.L. Gill	Outreach Officer	
Dr C.J. Buttler	Education Officer	
Dr T.R.A. Vandenbroucke	Meetings Coordinator	
Dr R.J. Butler	Ordinary Member	
Dr C.T.S. Little	Ordinary Member	
Dr M.E. McNamara	Ordinary Member	
Dr M. Munt	Ordinary Member	
Dr I.A. Rahman	Ordinary Member	

**Independent examiner**

Corfield Accountancy Limited  
Chartered Accountants  
Myrick House  
Hendomen  
Montgomery  
Powys  
SY15 6EZ

**Bankers**

NatWest  
Sheffield City Centre  
42 High Street  
Sheffield  
S1 2GE

Approved by order of the board of trustees on 6 June 2016 and signed on its behalf by:

Dr P. Winrow – Trustee



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

I report on the accounts for the year ended 31 December 2015 set out on the following eight pages.

### Respective responsibilities of trustees and examiner

The charity's trustees are responsible for the preparation of the accounts. The charity's trustees consider that an audit is not required for this year (under Section 144(2) of the Charities Act 2011 (the 2011 Act)) and that an independent examination is required. The charity's gross income exceeded £250,000 and I am qualified to undertake the examination by being a qualified member of ACA ACMA.

It is my responsibility:

- to examine the accounts under Section 145 of the 2011 Act
- to follow the procedures laid down in the General Directions given by the Charity Commission (under Section 145(5)(b) of the 2011 Act); and
- to state whether particular matters have come to my attention.

### Basis of the independent examiner's report

My examination was carried out in accordance with the General Directions given by the Charity Commission. An examination includes a review of the accounting records kept by the charity and a comparison of the accounts presented with those records. It also includes consideration of any unusual items or disclosures in the accounts, and seeking explanations from you as trustees concerning any such matters. The procedures undertaken do not provide all the evidence that would be required in an audit, and consequently no opinion is given as to whether the accounts present a 'true and fair view' and the report is limited to those matters set out in the statements below.

### Independent examiner's statement

In connection with my examination, no matter has come to my attention:

- (1) which gives me reasonable cause to believe that, in any material respect, the requirements
  - to keep accounting records in accordance with Section 130 of the 2011 Act; and
  - to prepare accounts which accord with the accounting records and to comply with the accounting requirements of the 2011 Act

have not been met; or

- (2) to which, in my opinion, attention should be drawn in order to enable a proper understanding of the accounts to be reached.

Miss M R Corfield  
ACA ACMA  
Corfield Accountancy Limited  
Chartered Accountants  
Myrick House  
Hendomen  
Montgomery  
Powys  
SY15 6EZ

Date: 6 June 2016



## THE PALAEOLOGICAL ASSOCIATION

# Statement of Financial Activities for the Year Ended 31 December 2015

	See Note	Unrestricted funds £	Designated funds £	31.12.15 Total funds £	31.12.14 Total funds £
<b>INCOME AND ENDOWMENTS FROM</b>					
Donations and legacies		50,627	32,896	83,523	86,061
<b>Charitable activities</b>	<b>3</b>				
Public Meetings		35,460	—	35,460	—
Publications		268,753	—	268,753	268,660
Investment income	<b>2</b>	<u>13,564</u>	<u>232</u>	<u>13,796</u>	<u>13,587</u>
<b>Total</b>		368,404	33,128	401,532	368,308
<b>EXPENDITURE ON</b>					
Raising funds	<b>4</b>	32,667	—	32,667	29,631
<b>Charitable activities</b>	<b>5</b>				
Public Meetings		72,736	—	72,736	47,141
Grants & Awards		38,950	13,995	52,945	60,173
Administration		45,441	—	45,441	40,821
Publications		169,202	—	169,202	188,918
Governance Costs		<u>20,989</u>	<u>—</u>	<u>20,989</u>	<u>20,115</u>
<b>Total</b>		379,985	13,995	393,980	386,799
Net gains/(losses) on investments		<u>4,647</u>	<u>—</u>	<u>4,647</u>	<u>31,354</u>
<b>NET INCOME/(EXPENDITURE)</b>		(6,934)	19,133	12,199	12,863
<b>RECONCILIATION OF FUNDS</b>					
<b>Total funds brought forward</b>		<u>743,977</u>	<u>123,797</u>	<u>867,774</u>	<u>854,911</u>
<b>TOTAL FUNDS CARRIED FORWARD</b>		<u>737,043</u>	<u>142,930</u>	<u>879,973</u>	<u>867,774</u>

**CONTINUING OPERATIONS**

All income and expenditure has arisen from continuing activities.



## THE PALAEOONTOLOGICAL ASSOCIATION

## Balance Sheet

### At 31 December 2015

	See Note	Unrestricted funds £	Designated funds £	31.12.15 Total funds £	31.12.14 Total funds £
<b>FIXED ASSETS</b>					
Investments	10	619,336	—	619,336	626,180
<b>CURRENT ASSETS</b>					
Debtors	11	142,252	—	142,252	132,249
Cash at bank and in hand		<u>13,673</u>	<u>142,930</u>	<u>156,603</u>	<u>174,448</u>
		155,925	142,930	298,855	306,697
<b>CREDITORS</b>					
Amounts falling due within one year	12	<u>(38,218)</u>	<u>—</u>	<u>(38,218)</u>	<u>(65,103)</u>
<b>NET CURRENT ASSETS</b>		<u>117,707</u>	<u>142,930</u>	<u>260,637</u>	<u>241,594</u>
<b>TOTAL ASSETS LESS CURRENT LIABILITIES</b>		<u>737,043</u>	<u>142,930</u>	<u>879,973</u>	<u>867,774</u>
<b>NET ASSETS</b>		<u>737,043</u>	<u>142,930</u>	<u>879,973</u>	<u>867,774</u>
<b>FUNDS</b>	13				
Unrestricted funds:					
<b>General fund</b>				737,043	743,977
<b>Designated funds:</b>					
Sylvester Bradley				31,451	36,815
Jones-Fenleigh				25,750	24,362
Hodson				6,293	8,172
Callomon				5,113	6,500
Whittington				14,549	17,415
Stan Wood				<u>59,774</u>	<u>30,533</u>
				<u>879,973</u>	<u>867,774</u>
<b>TOTAL FUNDS</b>				<u>879,973</u>	<u>867,774</u>

The financial statements were approved by the Board of Trustees on 6 June 2016 and were signed on its behalf by:

Dr P. Winrow – Trustee



## THE PALAEOLOGICAL ASSOCIATION

## Notes to the Financial Statements for the Year Ended 31 December 2015

### 1. ACCOUNTING POLICIES

#### Basis of preparing the financial statements

The financial statements of the charity, which is a public benefit entity under FRS 102, have been prepared in accordance with the Charities SORP (FRS 102) 'Accounting and Reporting by Charities: Statement of Recommended Practice applicable to charities preparing their accounts in accordance with the Financial Reporting Standard applicable in the UK and Republic of Ireland (FRS 102) (effective 1 January 2015)', Financial Reporting Standard 102 'The Financial Reporting Standard applicable in the UK and Republic of Ireland' and the Charities Act 2011. 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.

#### Reconciliation with previous Generally Accepted Accounting Practice

In preparing the accounts, the trustees have considered whether in applying the Charities SORP FRS 102 a reinstatement of comparative items was needed. No restatements were required. In accordance with the requirements of FRS 102 a reconciliation of opening balances and net income for the year is provided with the net income under previous GAAP adjusted for the presentation of investment gains/(losses) as a component of reported income.

#### Reconciliation of Reported Net Income:

Net income/(expenditure) as previously stated	(£18,491)
Adjustment for gains on investments now treated as a component of net income	<u>£31,354</u>
2014 Net income as restated:	<b>£12,863</b>

#### Financial reporting standard 102 – reduced disclosure exemptions

The charity has taken advantage of the following disclosure exemption in preparing these financial statements, as permitted by FRS 102 'The Financial Reporting Standard applicable in the UK and Republic of Ireland':

the requirements of Section 7 Statement of Cash Flows.

#### 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.



## THE PALAEOLOGICAL ASSOCIATION

**Notes to the Financial Statements – *continued*****1. ACCOUNTING POLICIES – continued****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 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.

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**

	31.12.15 Unrestricted funds £	31.12.14 Total funds £
Deposit account interest	3,827	3,773
Investment Income	<u>9,969</u>	<u>9,814</u>
	<u>13,796</u>	<u>13,587</u>



## THE PALAEOLOGICAL ASSOCIATION

### Notes to the Financial Statements – *continued*

#### 3. INCOME FROM CHARITABLE ACTIVITIES

	Public Meetings	Publications	31.12.15 Total activities	31.12.14 Total activities
	£	£	£	£
Scientific Meetings	35,460	—	35,460	—
Palaeontology	—	259,392	259,392	255,074
Special papers	—	4,287	4,287	8,378
Offprints	—	475	475	775
Newsletter	—	—	—	250
Field Guides	—	4,289	4,289	3,933
Distribution	—	310	310	250
	<u>35,460</u>	<u>268,753</u>	<u>304,213</u>	<u>268,660</u>

#### 4. RAISING FUNDS

	31.12.15 Unrestricted funds	31.12.14 Total funds
	£	£
<b>Voluntary Income Costs:</b>		
Administration	28,917	25,977
<b>Investment Management Costs:</b>		
Stockbroker Fees	<u>3,750</u>	<u>3,654</u>
	<u>32,667</u>	<u>29,631</u>

#### 5. CHARITABLE ACTIVITIES COSTS

	Direct costs	Support costs (See note 6)	Totals
	£	£	£
Public Meetings	72,736	—	72,736
Grants & Awards	52,945	—	52,945
Administration	45,441	—	45,441
Publications	169,202	—	169,202
Governance Costs	—	20,989	20,989
	<u>340,324</u>	<u>20,989</u>	<u>361,313</u>

#### 6. SUPPORT COSTS

	Governance costs
	£
Governance Costs	<u>20,989</u>

#### 7. TRUSTEES' REMUNERATION AND BENEFITS

There were no trustees' remuneration or other benefits for the year ended 31 December 2015 nor for the year ended 31 December 2014.

##### Trustees' expenses

The total travelling expenses reimbursed to 20 Members of Council was £12,153 (2014: £12,143)





## THE PALAEOLOGICAL ASSOCIATION

**Notes to the Financial Statements – *continued*****8. STAFF COSTS****Analysis of Staff Costs and Remuneration**

	<b>£ 2015</b>	<b>£ 2014</b>
Salaries	59,582	63,017
Social Security Costs	3,925	4,505
Pension Costs	<u>22,513</u>	<u>18,537</u>
<b>Total</b>	<b><u>86,020</u></b>	<b><u>86,059</u></b>

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

	31.12.15	31.12.14
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.

**9. 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.

<b>Investment Gains/Losses</b>	<b>31st December 2015</b>	<b>31st December 2014</b>
Realised Gain/(Loss)	(£292)	£2,607
Unrealised Gain/(Loss)	<u>£4,939</u>	<u>£28,747</u>
<b>Total per Statement of Financial Activities</b>	<b><u>£4,647</u></b>	<b><u>£31,354</u></b>

**10. FIXED ASSET INVESTMENTS**

Investments are initially recognised 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.

**11. DEBTORS: AMOUNTS FALLING DUE WITHIN ONE YEAR**

	<b>£ 2015</b>	<b>£ 2014</b>
Prepayments	1,261	1,587
Accrued Income-receivable within 1 year	<u>140,991</u>	<u>130,661</u>
	<u>142,252</u>	<u>132,248</u>



## THE PALAEOLOGICAL ASSOCIATION

### Notes to the Financial Statements – *continued*

#### 12. CREDITORS: AMOUNTS FALLING DUE WITHIN ONE YEAR

	31.12.15 £	31.12.14 £
Trade creditors	19,098	37,560
Taxation and social security	1,553	1,679
Other creditors	<u>17,567</u>	<u>25,864</u>
	<u>38,218</u>	<u>65,103</u>

#### 13. MOVEMENT IN FUNDS

	At 1.1.15 £	Net movement in funds £	Transfers between funds £	At 31.12.15 £
<b>Unrestricted funds</b>				
<b>General fund</b>	743,977	(6,934)	—	737,043
<b>Designated funds:</b>				
Sylvester Bradley	36,815	(5,364)	—	31,451
Jones-Fenleigh	24,362	1,388	—	25,750
Hodson	8,172	(1,879)	—	6,293
Callomon	6,500	(1,387)	—	5,113
Whittington	17,415	(2,866)	—	14,549
Stan Wood	<u>30,533</u>	<u>29,241</u>	—	<u>59,774</u>
	<u>867,774</u>	<u>12,199</u>	—	<u>879,973</u>
<b>TOTAL FUNDS</b>	<u>867,774</u>	<u>12,199</u>	—	<u>879,973</u>

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

	Incoming resources £	Resources expended £	Gains and losses £	Movement in funds £
<b>Unrestricted funds</b>				
<b>General fund</b>	368,404	(379,985)	4,647	(6,934)
<b>Designated funds:</b>				
Sylvester Bradley	170	(5,534)	—	(5,364)
Jones-Fenleigh	1,988	(600)	—	1,388
Hodson	15	(1,894)	—	(1,879)
Callomon	113	(1,500)	—	(1,387)
Whittington	134	(3,000)	—	(2,866)
Stan Wood	<u>30,708</u>	<u>(1,467)</u>	—	<u>29,241</u>
	<u>401,532</u>	<u>(393,980)</u>	<u>4,647</u>	<u>12,199</u>
<b>TOTAL FUNDS</b>	<u>401,532</u>	<u>(393,980)</u>	<u>4,647</u>	<u>12,199</u>

#### 14. RELATED PARTY DISCLOSURES

There were no related party transactions for the year ended 31st December 2015.

#### 15. FIRST YEAR ADOPTION

##### Transitional relief

The charity has not taken advantage of any Transitional Relief.



## Detailed Statement of Financial Activities for the Year Ended 31 December 2015

	31.12.15 Unrestricted funds £	31.12.14 Total funds £
<b>INCOME AND ENDOWMENTS</b>		
<b>Donations and legacies</b>		
Donations	34,175	32,220
Subscriptions	49,348	53,841
	<u>83,523</u>	<u>86,061</u>
<b>Investment income</b>		
Deposit account interest	3,827	3,773
Investment Income	9,969	9,814
	<u>13,796</u>	<u>13,587</u>
<b>Charitable activities</b>		
Palaeontology	259,392	255,074
Special papers	4,287	8,378
Offprints	475	775
Newsletter	—	250
Field Guides	4,289	3,933
Distribution	310	250
Scientific meetings	35,460	—
	<u>304,213</u>	<u>268,660</u>
<b>Total incoming resources</b>	<b>401,532</b>	<b>368,308</b>
<b>EXPENDITURE</b>		
<b>Raising donations and legacies</b>		
Administration	28,917	25,977
<b>Investment management costs</b>		
Stockbroker Fees	3,750	3,654
<b>Charitable activities</b>		
Palaeontology	51,996	62,935
Special Papers	—	3,994
Offprints	—	930
Field Guides	—	27
Newsletters	16,971	16,100
Distribution	—	1,035
Marketing	2,298	2,330
Publication Costs	69,079	64,464
Editorial Costs	28,858	37,103
Public Meetings	72,736	47,141
Grants & Awards	37,821	45,241
Research Grants	15,124	14,932
Administration	45,441	40,821
	<u>340,324</u>	<u>337,053</u>
<b>Support costs: Governance costs</b>		
Trustees' expenses	12,153	12,143
Accountancy and legal fees	574	550
Administration	8,262	7,422
	<u>20,989</u>	<u>20,115</u>
<b>Total resources expended</b>	<b>393,980</b>	<b>386,799</b>
<b>Net income/(expenditure) before gains and losses</b>	7,552	(18,491)
<b>Realised recognised gains and losses</b>		
Realised gains/(losses) on fixed asset investments	4,647	31,354
	<u>4,647</u>	<u>31,354</u>
<b>Net income</b>	<b><u>12,199</u></b>	<b><u>12,863</u></b>

**Palaeontological Association year ended 31st December 2015.**

Nominal	Holding	Cost (bought pre 2015) £	Value end 2014 £
£20,000	UK 4.5% Gilt 07/03/19 GBP 0.01	20,092.99	23,120.00
£18,000	UK 4.75% Stock 07/03/20 GBP 100	18,145.87	21,449.00
£64,176.46	COIF Charities Fixed Interest Fund	85,000.00	87,600.87
500	BG Group Ordinary 10p shares	3,977.95	4,325.00
1,425	BP Ord 25c shares	5,047.35	5,857.00
804	Royal Dutch Shell B shares	4,671.00	17,953.00
600	BHP Billiton \$0.5 shares	4,341.48	8,331.00
600	South32 Ltd (Di)		
437	IMI Ord 25p shares	4,267.00	5,519.00
1,728	Melrose Indust Ord 0.1p	5,562.00	4,965.00
420	Experian Ord 10C	3,444.95	4,570.00
300	Diageo Ord	5,826.00	5,546.00
400	Persimmon Ord 10p	4,516.00	6,312.00
400	Persimmon Ord 10p		
300	Unilever PLC Ord GBP 0.031111	4,326.21	7,884.00
170	AstroZeneca Ord 25c	8,145.00	7,744.00
650	Glaxo Smithkline Ordinary 25p shares	10,232.42	8,944.00
2,000	Tesco Ord GBP 0.05	6,225.78	3,780.00
460	Pearson Ordinary 25p shares	8,069.00	5,474.00
175	Carnival Plc Ord USD 1.66	3,996.49	5,108.00
2,150	BT Group Ordinary 5p shares	7,409.00	8,632.00
2,277	Vodafone Group Ord USD 0.11428571	3,434.00	5,070.00
700	National Grid Ord GBP 0.113953	3,648.26	6,427.00
2,250	Barclays 25p Ord shares	4,867.00	5,479.00
1,465	HSBC Holdings Ordinary 0.5 US Dollar shares	4,534.00	8,916.00
1,200	Great Portland Estates Ord	8,503.00	8,856.00
4,400	TR Property Ord 25p shares	7,560.85	12,518.00
1,500	Jupiter Ord 2p	6,066.00	5,474.00
4250	Fidelity EUR Value Ordinary 25P shares	4,059.07	6,906.00
650	RIT Capital Partners Ordinary £1 shares	4,903.90	9,081.00
670	Blackrock World Mining Ord 5P	4,019.09	2,079.00
3,900	Edinburgh Dragon Trust Ordinary £0.20 shares	4,478.10	10,652.00
1,225	Brown Advisory US Equity Value £B	14,789.62	22,148.00
425	Findlay Park Partners US Smaller Companies	6,158.47	21,620.00
2,825	Ishares S&P 500 GBP	20,319.63	37,622.00
120	GLG Japan Corealpha Equity I H Acc	11,330.79	18,661.00
150	GLG Japan Corealpha Equity I Acc		
65	Roche Hldgs Ag Genusscheine Nvp	7,226.55	11,321.00
6,600	Henderson Gbl Invs European Special Sits I Inc	7,037.91	9,893.00
6,600	Fund Partners Ltd Crux European Spl Situation		
26	Veritas Asset Mgmt Veritas Asian A GBP	8,182.27	9,453.00
900	JPMorgan Am UK Ltd Emerging Markets I Instl	5,043.10	5,196.00
2,499	Bluecrest Allblue Ord Npv GBP shares	3,020.28	4,653.00
300	Morgan Stanley	9,958.00	9,918.00
4,443	Aberdeen Investment Property Trust B	4,681.00	5,220.00
1,283.80	COIF Charities Investment Fund Acc Units	75,000.00	145,902.71
Total		442,117.38	626,179.58



### Schedule of Investments (Note 10 to the Accounts)

Proceeds (sold in 2015) £	Cost (bought in 2015) £	Gain realised during 2015 £	Value end 2015 £	Gain unrealised during 2015 £
			22,502.00	-618.00
			20,887.00	-562.00
			84,353.54	-3,247.33
			4,925.00	600.00
			5,045.00	-812.00
			12,406.00	-5,547.00
			4,560.00	-3,771.00
	700.26		315.00	-385.26
			3,765.00	-1,754.00
			5,027.00	62.00
			5,044.00	474.00
			5,570.00	24.00
			8,108.00	1,796.00
380.00	0.00	380.00		
			8,780.00	896.00
			7,848.00	104.00
			8,925.00	-19.00
2,986.46		-793.54		
4,304.72		-1,169.28		
			6,766.00	1,658.00
			10,142.00	1,510.00
			5,032.00	-38.00
			6,563.00	136.00
			4,925.00	-554.00
			7,855.00	-1,061.00
			9,936.00	1,080.00
			13,257.00	739.00
			6,776.00	1,302.00
			7,395.00	489.00
			10,927.00	1,846.00
			1,213.00	-866.00
			9,419.00	-1,233.00
			21,144.00	-1,004.00
			23,304.00	1,684.00
			39,070.00	1,448.00
22,501.01		3,840.01		
	22,838.31		21,653.00	-1,185.31
			12,181.00	860.00
7,140.00		-2,753.00		
	7,140.00		10,991.00	3,851.00
			10,272.00	819.00
			4,626.00	-570.00
4,856.54		203.54		
			8,850.00	-1,068.00
			5,526.00	306.00
			153,452.49	7,549.78
42,168.73	30,678.57	-292.27	619,336.03	4,938.88



## Nominations for Council

At the AGM, the following vacancies will occur on Council:

- Vice-President
- Secretary
- Newsletter Editor
- Publicity Officer
- Outreach Officer
- Education Officer
- Internet Officer
- Three Ordinary Members

Nominations received by the deadline are as follows:

- Vice President: Prof. Richard J. Twitchett
- Secretary: Dr Crispin T.S. Little
- Newsletter Editor: Dr Maria E. McNamara
- Publicity Officer: Dr Liam Herringshaw (2nd term)
- Outreach Officer: Dr Lucy McCobb
- Education Officer: Dr Caroline Buttler (2nd term)
- Internet Officer: Dr Alan R.T. Spencer (2nd term)
- Ordinary Members (three posts): Prof. Andy Gale; Dr Alexander Dunhill; Dr David Bond

No other nominations were received by the deadline.



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*Notes...*



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