

# Progressive Palaeontology 2021

# **Abstract Booklet**

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### Code of Conduct for Palaeontological Association Meetings

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

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

#### **Behavioural expectations**

It is the expectation of the Palaeontological Association that meeting attendees behave in a courteous, collegial and respectful fashion to each other, volunteers, exhibitors and meeting facility staff. Attendees should respect common sense rules for professional and personal interactions, public behaviour (including behaviour in public electronic communications), common courtesy, respect for private property and respect for intellectual property of presenters. Demeaning, abusive, discriminatory, harassing or threatening behaviour towards other attendees or towards meeting volunteers, exhibitors or facilities staff and security will not be tolerated, either in personal or electronic interactions.

#### Digital images and social media

Do not photograph a poster or record a talk without the author's express permission. While the default assumption is to allow open discussion of presentations on social media, attendees are expected to respect any request by an author to not disseminate the contents of their talk or poster.

#### **Reporting unacceptable behaviour**

If you are the subject of unacceptable behaviour or have witnessed any such behaviour, you can report it (anonymously if you choose to) via the <u>online reporting form</u>.

Anyone experiencing or witnessing behaviour that constitutes an immediate or serious threat to public safety, or a criminal act is expected to contact the appropriate law enforcement agency. Those witnessing a potential criminal act should also take actions necessary to maintain their own personal safety.

#### Dear Delegates

Welcome to Progressive Palaeontology, a postgraduate student conference of the Palaeontological Association (PalAss). PalAss is a charity that promotes the study of palaeontology and its allied sciences through publications, sponsorship of meetings and workshops, provision of web resources and a large annual programme of awards and grants.

Membership fees for students are just £20 a year. Members receive many benefits including the Association's newsletter, online access to the PalAss journals *Palaeontology* and *Papers in Palaeontology*, a discount on Field Guides and other books, and eligibility for Association awards and grant schemes including the Postgraduate Travel Fund.

Our flagship Annual Meeting is a major international conference in December with subsidized registration for students, and contributions to travel costs are made to a large percentage of student members who are presenting their work. The President's Prize and Council Poster Prize are awarded to the best presentations from early career researchers at the meeting each year, each with a certificate and cash prize.

The Association has a public engagement group that involves postgraduate student members as volunteers at outreach events. PalAss has members all over the globe and we welcome new members at <u>www.palass.org</u>. You can also find us on Facebook and Twitter (@ThePalAss).

Dr Jo Hellawell

Executive Officer The Palaeontological Association

# STUDENTS!

### Are you a student who works in or is interested in palaeontology?

The **Palaeontological Association** is an international organisation that exists to promote the study of palaeontology and its allied sciences.

Did you know we subsidise memberships for students? For **only £20 a year** we offer:

### Access to the latest palaeo science and news!

Online access to Association journals Palaeontology and Papers in Palaeontology, a discount on other publications (e.g. field guides) and we keep you up to date with the latest news in our Association newsletter.



### We can help fund your research and travel to conferences!



Grants of up to  $\pounds 1500$  are available to students to fund research projects. We also offer grants of up to  $\pounds 200$  to postgraduate student members for travel to any international meetings (even those not run by the Association).

### Want career guidance and mentorship?

The Association has established a mentoring scheme to assist you throughout your academic career. The scheme is open to all PhD student members.



### Want to get involved with science engagement?

The Association participates in many outreach activities (including fossil festivals and our own YouTube channel) and offers grants for public engagement. We support the increased participation of diverse voices in palaeontology!

### Don't forget our student conference ProgPal!

The Association helps support Progressive Palaeontology, an annual conference run by PhD students for PhD students. Meet your peer group, discuss your science and gain experience presenting!



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### We make attending the Annual Meeting cheaper!

The Association's flagship Annual Meeting is a major international conference in December with several hundred delegates. Registration is subsidised for students, and contributions to travel costs may be made for students giving a presentation. All students are eligible for our poster or presentation prizes!

# Become a member of the Palaeontological Association

For more details and to sign up go to: www.palass.org

A big thank you for sponsorship and support from:











### A message from your conference co-chairs

Hello delegates and welcome to ProgPal 2021! For the second year in a row, Progressive Palaeontology will be running entirely online, allowing you to peruse presentations at your own pace and interact with other attendees from around the world. Although we can't see you in person, we're so excited to hear about all of your work, and to find out what you've been up to over the past year or so. Whether you're back in the office or working from home, we've got lots of exciting content running throughout the three-day duration to keep you occupied!

We wouldn't have been able to run this conference on without the help of some wonderful people, including the ProgPal21 team (Lou Andrews, Sam Bright, Eryka Kritikos, Alice Leavey, Bethany Pittard, and Grace Varnham), PalAss Internet Officer and tech genius Russell Garwood, and our workshop hosts: Sebastian Groh, Philip Mannion, and Soledad De Esteban Trivigno.

ProgPal is one of our favourite events in the Palaeo calendar to attend each year, and so we hope that you'll be able to enjoy it as much as we do!

Have a great conference,

*Cecily & Miranta -* conference co-chairs and big fans of dinosaurs (see attached photos)





### Timetable

#### Thursday 17th June

🏂 Content launch	1am PDT / 4am EDT / <b>9am BST</b> / 4pm HKT
The Paleobiology Database workshop	2am PDT / 5am EDT / <b>10am BST</b> / 5pm HKT (2 hours)
Stepping out of Academia workshop	2am PDT / 5am EDT / <b>10am BST</b> / 5pm HKT (2-3 hours)
<i>G</i> Break/lunch	4am PDT / 7am EDT / <b>12pm BST</b> / 7pm HKT (1 hour)
Evolutionary History workshop	6am PDT/9am EDT/ <b>2pm BST</b> /9pm HKT (2 hours)
Cebreaker event	10am PDT / 1pm EDT / <b>6pm BST</b> / 1am HKT (2 hours)

#### Friday 18th June

💬 Presenter Q&A 1	1am PDT / 4am EDT / <b>9am BST</b> / 4pm HKT (1 hour)
🖲 Tea break	2am PDT / 5am EDT / <b>10am BST</b> / 5pm HKT
🌈 LGBTQ+ meetup	4am PDT / 7am EDT / <b>12pm BST</b> / 7pm HKT (1 hour)
💬 Presenter Q&A 2	6am PDT/9am EDT/ <b>2pm BST</b> /9pm HKT (1 hour)
🖱 Tea break	7am PDT / 10am EDT / <b>3pm BST</b> / 10pm HKT
💬 Presenter Q&A 3	9am PDT / 12pm EDT / <b>5pm BST</b> / 12am HKT (1 hour)
🚯 Quiz	11am PDT / 2pm EDT / <b>7pm BST</b> / 2am HKT

#### Saturday 19th June

💬 Presenter Q&A 4	2am PDT / 5am EDT / <b>10am BST</b> / 5pm HKT (1 hour)	
🖹 Tea break	3am PDT / 6am EDT / <b>11am BST</b> / 6pm HKT	
💬 Presenter Q&A 5	7am PDT / 10am EDT / <b>3pm BST</b> / 10pm HKT (1 hour)	

### **Q&A** sessions

Q&A 1 - Friday 9am BST	Q&A 2 - Friday 2pm BST	Q&A 3 - Friday 5pm BST
Ruby Barrett	Najat Al-Fudhaili	Wafa Alhalabi
Harry Blake	Maria Grace Burton	Sophia Anderson
Emily Carlisle	Vicky Coules	Emily Brown
Jana Čepičková	Matthew Dempsey	Madleen Grohganz
James Chester	Danijela Dimitrijevic	Robert Higgins
Thibault Durieux	Alejandro Giraldo	Niklas Hohmann
Patrycja Dworczak	Alice Maher	Ravi Kiran Koorapati
Joseph Flannery Sutherland	Adam Manning	Madison Lalica
Emily Green	Luke Meade	Rebecca Logie-Inions
Adhiyan Jeevathol	Sophie Mires	Sarah Losso
Isaac Kerr	Laura Mulvey	Kyle Marson
Isabella Leonhard	James Mulqueeney	Rosalba Lizbeth Nava-Rodríguez
Katherine Marriott	Romain Pintore	Meg Nibbelink
Case Vincent Miller	Jane Reeves	Kelly Pfeiler
Bouwe Reijenga	Lisa Schnetz	Justyna Slowiak
Elizabeth Steell	Bryan Shirley	Holly Smith
Carl van Gent	Matthew Staitis	Veronika Vesela
Grace Varnham	Christopher Stockey	
Amber Wagstaffe	Morgan Tobin	
	Chloe Walker-Trivett	

Q&A 4 - Saturday 10am BST	Q&A 5 - Saturday 3
Muhammad Aqqid Saparin	Matteo Battini
Harry Berks	Jack Cooper
Filippo Bertozzo	Jenna Davenport
Samuel Bulmer	Kamila Faizieva
Sofia Chambi-Trowell	Przemyslaw Gruszka
Yi-Yang Cho	Struan Henderson
Matthieu Chotard	Jess McCoy
Priya Gordon	Roisin Mooney
Eloise Hunt	Daniel Pérez Pinedo
Pei-Chen Kuo	Spencer Pevsner
Anna Lene Claussen	Panagiotis Sianis
Jack Lovegrove	Ana Laura Silva Paiva

James Rawson

William Rutter

Thomas Pavey William Richardson

Denis Theda

#### 3pm BST

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Michael Sprague

Stephanie Woodgate

Christian Voiculescu-Holvad

### Accessing the conference materials and platforms

#### **Research presentations**

Research presentations will be available to view for the full duration of the conference, from 9am BST on Thursday 17<sup>th</sup> to 5pm BST on Saturday 19<sup>th</sup> June. All presentations, including both posters and talks, will be available through the Palaeontological Association website (https://www.palass.org/meetings-events/progressive-palaeontology) If you are a PalAss member at the time of registration, you will need to log in to the website to access the presentations using your PalAss log-in details. If you are not a member at the time of registration, you will be sent temporary log-in details prior to the conference which will enable you to view all of the presentations.

#### **Live Events**

All of our live events (workshops and quiz night) will take place using Zoom. You will need to download the app in order to see the broadcasts: you can do so in advance by visiting their website (https://zoom.us), or automatically the first time you try to access a Zoom call. Prior to the live events we will email delegates with the zoom link for the activities they have signed up for.

### Discord 🥥

All communications, delegate interactions, Q&A sessions, announcements etc. will be done in the ProgPal 2021 Discord. Discord is a group-chatting platform that is organised by #channels that people use to talk about different subjects. You can either have it run on your internet browser or (preferably) you can install the Discord software on your computer (https://discord.com). Each presenter will have a separate text channel for their allotted Q&A session. For information on how to use Discord throughout the conference, see our guide which will be emailed to you separately.

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### Information about events

#### Workshops

We are offering three workshops at this year's ProgPal:

- O The Paleobiology Database
- Stepping out of Academia: why, when, and how?
- Preconstructing the evolutionary history of organisms

All attendees signed up to these events will receive information a few days before the start of the conference via email. The email will include any materials required for the workshop, and will also contain your zoom link to access the event. Please follow all instructions given to you, some of which may require you to take action before the workshop begins. We kindly ask that you aim to arrive in the Zoom session 5–10 minutes before the start of the workshop in case you encounter any issues. If you realise that you can no longer attend a workshop that has limited places, please contact us as soon as possible so that we can allocate your space to another delegate.

### Icebreaker 💭

The icebreaker event will take place on Discord, and will be an opportunity for you to chat with all other delegates across a series of themed channels. We will be starting up some games and activities throughout the evening to keep you all occupied! Keep an eye on our social media channels for some inspiration on refreshment ideas!

#### LGBTQ+ Lunch 🌈

On Friday lunchtime we will be meeting for an hour or so in an informal setting on Discord. Please send a direct message to either of the conference co-chairs (Miranta or Cecily) if you would like to be added to this channel.

### Quiz Night 🏇

In the absence of ProgPal's annual dinner, we will be holding a live-streamed quiz night. The quiz will be held via Zoom.

Quiz teams should be made up of no more than four delegates. Delegates can form their own teams, but we will also organise a pooling system to put new teams together. If you do not already have your team of up to four people, we will circulate a Google Form via email where you can submit yourself, and up to one other delegate, in order to connect with other attendees.

We will email out links to both the quiz (Zoom) and the answer submission sheet (Google Form). Please ensure that you have come up with a team name before the quiz starts, as this will help us with marking your answers. During the quiz, we recommend setting up a group chat for your team on a separate video or messaging platform. One person from each team should be nominated to fill in and submit the Google Form with your answers

### How to contact us

We will be using social media channels throughout the conference. These are:

- Twitter: @ProgPal2021 (#ProgPal21)
- Facebook: Progressive Palaeontology 2021

Please also feel free to email us at progpal2021@palass.org or to direct message us on Twitter or Discord (right-click on any committee member's name on the right-hand panel in the server).

### Abstracts

### **Full Talks**

#### Funny bones: an ecomorphological analysis of the bovid humerus

#### Sophia Anderson<sup>1</sup>, Kris Kovarovic<sup>1</sup>, W. Andrew Barr<sup>2</sup>

<sup>1</sup>Durham University, United Kingdom <sup>2</sup>George Washington University, United States of America

When seeking to understand early human evolution, it is fundamental to understand the ecology of the environment in which those early humans lived. Pleistocene Bovidae (Mammalia: Artiodactyla) communities of the Lake Victoria Basin, East Africa, provide an excellent opportunity to reconstruct the palaeoecology of the region during early Homo sapiens evolution. Many of the bovids occupying this area in the Pleistocene are still extant today, but several have since become extinct, and reconstructing their ecology is key to fully understanding the ancient ecosystem and how it differs from that of modern Africa. Here, we seek to develop the bovid distal humerus as an ecological proxy using 2D and 3D geometric morphometrics on extant bovid specimens. The humerus is particularly informative due to its extensive roles in weight-bearing and forelimb use. We focus on the distal humerus (the elbow articulation) as this section of bone is dense and frequently preserved in the bovid fossil record, and additionally there are many attachment and origin sites for muscles involved in lower forelimb movement concentrated at the distal humerus. 2D analysis has, so far, provided evidence of a consistent relationship between shape variations and body mass categories, as well as evidence that distal humerus shape may be effective in distinguishing broad phylogenetic and habitat preference categories. 3D analyses are ongoing, and we ultimately aim to utilize our findings to assess the ecology of Rusingoryx atopocranion - an unusual Pleistocene wildebeest relative with unique distal humerus morphology known to have been hunted by humans.

Past resilience and future vulnerability of planktic foraminiferal carbonate production: a question of the rate of environmental change

#### Ruby Barrett<sup>1</sup>, Monsuru Adebowale<sup>1</sup>, Heather Birch<sup>1</sup>, Jamie Wilson<sup>1</sup>, Daniela N. Schmidt<sup>1</sup>

<sup>1</sup>University of Bristol, United Kingdom

Anthropogenic climate change is warming our oceans. Consequently, marine organisms are already on the move. Plankton are expected to be vulnerable to warming, with their carbonate production projected to decline - altering ocean biogeochemistry. In the modern ocean planktic foraminifers are important carbonate producers, generating half of total open-ocean carbonate. Despite this importance, their response to climate change is

often quantified in short-term laboratory studies. Such studies are unable to account for factors which contribute to resilience, such as acclimation and adaption. To overcome this limitation, we utilise the geological record. Using a combined data and modelling approach we investigate how planktic foraminifers respond to warming during the Palaeocene-Eocene Thermal Maximum (PETM; ~56 Ma). The PETM is associated with high latitude warming up to 10°C, ocean acidification and reduced open-ocean productivity due to increased surface ocean stratification. We quantify regional change in foraminiferal abundance and size at an Atlantic, Pacific, and Southern Ocean site. To upscale these results, we apply a trait-based model for planktic foraminifers (ForamEcoGEniE) to the geological record for the first time. Our analysis evidences a poleward migration due to sea surface warming. However, against expectation, we observe no significant change in foraminiferal carbonate production. We postulate that this unexpected resilience is due to a relative slow rate of change during the PETM compared to the modern. To test this hypothesis, we apply ForamEcoGEnIE to low and high anthropogenic CO<sub>2</sub> emission trajectories. These experiments highlight the importance of tracking a low emissions pathway to sustain ocean biogeochemistry.

#### Form-function evolution: avian beaks and nests

#### Matteo Battini<sup>1</sup>, Michael J. Benton<sup>1</sup>, Sally E. Street<sup>2</sup>, Susan D. Healy<sup>3</sup>, Kevin N. Laland<sup>3</sup>, Catherine Sheard<sup>1</sup>

<sup>1</sup>University of Bristol, United Kingdom <sup>2</sup>Durham University, United Kingdom <sup>3</sup>University of St Andrews, United Kingdom

Birds are a popular and extensively studied group of feathered vertebrates that exhibit an impressive array of forms, including a vast diversity of beak shapes. Traditionally, the evolution of beak diversity in birds has been associated with differences in diet and foraging behaviour. Studies carried out at a global scale reflect this but also emphasize that the relationship between beak shape and ecology bears a strong phylogenetic signal. However, none of these studies have ever been able to perfectly explain macro-scale beak shape variation. Bird beaks have functions beyond food processing, such as song and object manipulation. In particular, beak shape may be co-evolving with nesting strategy, as some - but not all - nest-building strategies require material to be handled with the beak. Using data collected for 6,348 species, we tested the form-function link between avian morphology (beak and Bauplan) and species nesting structure and location. We find that these variables are correlated and that random forest models - machine learning algorithms - can predict species nesting strategy from beak and Bauplan morphology with ~62-86% and ~70-93% accuracy, respectively. This relationship has many implications for morphological constraints on reproductive behaviour, including the increased possibility of inferring the nesting behaviours of extinct taxa.

# The macroevolutionary impacts of major environmental changes on avian wing morphology and flight ability

#### Harry Berks<sup>1</sup>, Catherine Sheard<sup>1</sup>, Mike Benton<sup>1</sup>

<sup>1</sup>University of Bristol, United Kingdom

Flight is a key feature of birds and dictates much of their natural history. With high extant diversity and a rich evolutionary history, neornithines show a range in their flight ability and with it, their wing morphology. While ecological correlates of the extant distribution of wing morphologies are a subject of substantial research effort, far less is known about the drivers of macroevolutionary changes in wing morphologies over geological time scales and the response to large-scale environmental changes. By employing phylogenetic comparative methods on a global dataset of wing morphology, we investigate the macroevolutionary history of the neornithine wing. Our results found that uncertainty in avian phylogenetics, both topology and timings, is a key barrier to reliable results. We recover an increase in disparity and evolutionary rate of wing morphology around the K-Pg mass extinction, suggesting that birds evolved to fill flight-intensive niches left open by the extinction of pterosaurs and stem birds. We also find links between the high global temperatures of the early Eocene and increased evolutionary rates of wing morphological evolution and a reduction in flight ability with the cooling of the Earth through the Cenozoic. Taken together, these results suggest that migratory behaviour evolved in accordance with shifts in global temperatures across geologic timescales. Our results have implications for how birds adapt to environmental change and could therefore aid with conservation in the face of anthropogenic global warming.

#### Assessing conflict between early neornithischian tree topologies

#### Emily Brown<sup>1,2</sup>, Richard Butler<sup>2</sup>, Paul Barrett<sup>1</sup>, Susannah Maidment<sup>1</sup>

<sup>1</sup>Natural History Museum, United Kingdom <sup>2</sup>University of Birmingham, United Kingdom

The 'hypsilophodontids' are a group of small-medium bodied, bipedal neornithischians that lived between the Early Jurassic and the end-Cretaceous. The systematic placement of these taxa relative to each other and to major neornithischian clades remains highly disputed, with recent phylogenetic analyses recovering two conflicting placements for these taxa. This has impeded our understanding of important character changes throughout the evolutionary history of Neornithischia, but presents an opportunity to investigate the causes of conflict in the data matrices behind these conflicting topologies. Here, we compare and contrast three recent independent data matrices used to analyse neornithischian relationships, to understand how character and taxon sampling has influenced these conflicting results. We find that although the matrices investigated differ substantially in taxon completeness and stability, these factors do not influence the topologies observed. This suggests that future analyses can confidently include taxa with large amounts of missing data. We identify several characters that are disproportionately influential of tree topology and should be reassessed in future studies. Excluding characters

from several skeletal partitions prior to parsimony analysis can also significantly alter the resulting tree topology, and in some cases, recovers the 'hypsilophodontids' in the alternative hypothetical placement. The phylogenetic position of the 'hypsilophodontids' remains largely enigmatic, but our study highlights problems that should be addressed in future analyses.

#### The origin of placental mammals according to the fossil record

#### Emily Carlisle<sup>1</sup>, Daniele Silvestro<sup>2</sup>, Philip Donoghue<sup>1</sup>

<sup>1</sup>University of Bristol, United Kingdom <sup>2</sup>University of Fribourg, Switzerland

Recent molecular clock analyses have suggested that placental mammals originated in the mid to late Cretaceous, before the Cretaceous-Paleogene (K-Pg) mass extinction. However, there are no unequivocal fossils of placental mammals from the Cretaceous to support this. Definitive fossils of placental mammals only appear after the K-Pg boundary, at which point they rapidly radiate leading into the 'Age of Mammals'. Here we use the Bayesian Brownian Bridge model to estimate the age of origin of placental mammals based on the fossil record. The model uses fossil diversity through time to inform a random walk from the clade's present-day diversity back to the estimated origin of the clade within a Bayesian framework. This model works well with clades that have poor fossil records, such as the early placental mammals, and does not require a phylogeny, thereby mitigating the lingering uncertainty over the branching pattern at the root of the placental tree of life. Our results support a Cretaceous origin for placental mammals, in agreement with the molecular data, and demonstrate that the group was already present before the K-Pg mass extinction and experienced a radiation during the Paleogene. The Bayesian Brownian Bride model can therefore help to reconcile paleontological data with molecular data when estimating the origin of clades.

#### The rhynchocephalian phylogeny: fine-tuning and compromise

#### <u>Sofia Chambi-Trowell</u><sup>1</sup>, Agustin G. Martinelli<sup>3</sup>, David I. Whiteside<sup>1,2</sup>, Paulo R. Romo de Vivar<sup>4</sup>, Mike J. Benton<sup>1</sup>, Emily J. Rayfield<sup>1</sup>, Pamela G. Gill<sup>1,2</sup>

<sup>1</sup>University of Bristol, United Kingdom

<sup>2</sup>Natural History Museum, United Kingdom.

<sup>3</sup>Museo Argentino de Ciencias Naturales & "Bernardino Rivadavia", Argentina

<sup>4</sup>Universidade Federal do Rio Grande Do Sul, Brazil

Rhynchocephalia is the sister-group to Squamata (lizards, snakes, and their relatives), which are now represented by one living species, the tuatara of New Zealand. In the past however, they were a diverse, globally distributed group, with over 65+ known fossil species, a number that increases yearly. The phylogeny of Rhynchocephalia has never been well resolved, for many years their phylogeny was reconstructed by different authors based on a more-or-less shared taxon-character matrix, with few changes to characters or choice of

taxa. Here, we create the largest rhynchocephalian matrix yet, adding 19 further taxa – many of which have not been included in a phylogenetic analysis previously – and over 70 new characters to the matrix. In general, our trees recover similar topology to previous analyses, but the clade Opisthodontia (*Opisthias* + Eilenodontines) breaks down as we find greater similarities between *Opisthias* and the Sphenodontines. As in previous analyses, our Bremer support values remain low, we conclude this is a compromise that must be made as many rhynchocephalian fossils are highly fragmentary or described in little detail, and removing rogue taxa did little to change our support values or our trees' topology. Updating the descriptions of more obscure taxa – particularly the superbly preserved 'Solnhofen' rhynchocephalians of the Jurassic – using CT-scanning and high-resolution photography would greatly benefit future analyses.

#### A new *Toyotamaphimeia* and its implications for the late survival of Crocodylia in the Pleistocene of Taiwan

#### <u>Yi-Yang Cho<sup>1</sup>, Cheng-Hsiu Tsai<sup>1,2,3</sup></u>

<sup>1</sup>Institute of Ecology and Evolutionary Biology, National Taiwan University, Taiwan <sup>2</sup>Department of Life Science, National Taiwan University, Taiwan <sup>3</sup>Museum of Zoology, National Taiwan University, Taiwan

Toyotamaphimeia is a fairly large tomistomine crocodile (up to 7 m long), monotypic genus (T. machikanensis), and previously only known from the Pleistocene of Japan. A recent re-description of an almost-century-old and fragmentary specimen proposed the existence of Toyotamaphimeia in the Pleistocene of Taiwan – the first record outside Japan. However, the evolutionary history of Toyotamaphimeia outside Japan or along the eastern margin of Eurasia remains poorly explored. Here, we describe a newly-discovered specimen dredged from the sea bottom between Penghu and Taiwan; the geological horizon is uncertain but likely to be Middle to Late Pleistocene based on previous studies. The specimen preserves the posterior portion of the skull and shows the Toyotamaphimeia affinity by having: the posterior tuberosity of supraoccipital visible in dorsal view, quadrate with expanded medial hemicondyle, exoccipital ventral process robust and participating in occipital tubera, capitate process of laterosphenoid oriented lateromedially, lateral carotid foramen opening posteroventrally, and basisphenoid anteroposteriorly long and exposed ventrally. Interestingly, our specimen also differs from Toyotamaphimeia machikanensis in: skull table surface sloping ventrally, opening of the lateral carotid foramen dorsal to basisphenoid lateral exposure, and thick posterior edge of the supratemporal fenestra. Given the distinct morphology and geologically young age (Middle to Late Pleistocene), our fossil reveals the hidden diversity of the Toyotamaphimeia lineage and suggests the late survival of Toyotamaphimeia along the eastern margin of Eurasia. Our discovery promises future research on the speciation, extinction, and paleoecology of Toyotamaphimeia, a critical member to understand the megafauna extinction and turnover in the Pleistocene.

# Bryostromatolites – enigmatic shallow water reefs from the Silurian of Gotland

#### Anna Lene Claussen<sup>1</sup>, Axel Munnecke<sup>1</sup>, Andrej Ernst<sup>2</sup>

<sup>1</sup>GeoZentrum Nordbayern, Friedrichs-Alexander University Erlangen-Nuremberg, Germany <sup>2</sup>Institut für Geologie, Universität Hamburg, Bundesstr. 55, D-20146 Hamburg, Germany

Bryozoan-stromatolite associations were formed in specific intervals of the Wenlock to Ludlow of Gotland. Although the Silurian reefs on Gotland are well studied, these bryostromatolites have just been discovered and described recently. In contrast to "classical" Silurian reefs which are mainly formed by stromatoporoids, corals, and tabulates, the bryostromatolites are dominated by encrusting bryozoans intergrowing with poro- and spongiostromate microbes. The bryozoan community is surprisingly diverse and accompanied by stenohaline reef-dwelling organisms such as echinoderms, trilobites, brachiopods, sponges, and scarce tabulates, corals, and stromatoporoids. During the reef development the environmental conditions changed for metazoans, from favourable settings in the initial stage to more hostile in the developed stage. This caused a typical growth succession documented in all bryostromatolites. Features of these reefs on Gotland are cauliflower-like growth providing abundant cryptic habitats, a high bryozoan diversity, enhanced bioerosion, abundant phosphatic components (inarticulate brachiopods and bryozoan pearls), and Palaeomicrocodium crusts. On Gotland ten localities exposing bryostromatolites were discovered so far. They are small, from a few decimeters up to one meter in size, and occur in very shallow marine areas, presumably directly at the palaeosea surface as indicated by the presence of *Palaeomicrocodium*. Stable isotope analysis revealed that the bryostromatolites were formed solely in times of strongly elevated  $\delta^{13}C$ values. The high stable carbon isotope ratios as well as the unusual combination of sedimentological and palaeontological features are evidence that the bryostromatolite development was directly related to the climatic and oceanographic changes expressed by the - still enigmatic - isotope excursions.

# 3D model of the extinct giant shark *Otodus megalodon* suggests ability to undertake long migrations and a preference for large prey

### <u>Jack Cooper</u><sup>1</sup>, John Hutchinson<sup>2</sup>, Rory Wilson<sup>1</sup>, Jeanette Pirlo<sup>3</sup>, Matt Dicken<sup>4,5</sup>, Jan Menzel<sup>6</sup>, Stephen Wroe<sup>7</sup>, David Bernvi<sup>4</sup>, Geremy Cliff <sup>4,8</sup>, Catalina Pimiento<sup>1,9,10</sup>

- <sup>1</sup>Swansea University, Swansea, United Kingdom
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Computer modelling combined with exceptional fossil specimens has given palaeontologists the unprecedented ability to reconstruct entire bodies of extinct animals. Given its low preservation potential, no complete skeleton exists for the extinct giant shark Otodus megalodon; however, the existence of an exceptional 141-centra vertebral column from Belgium (IRSNB P 9893) allowed us to reconstruct a 3D model of this individual's entire body using a previously established "hoop-based" methodology in Blender. From the completed model, we estimated body length (15.93 m) and mass (61,500 kg), revealing that IRSNB P 9893 was larger than hitherto proposed. We then used body mass-related equations from literature to make novel ecological calculations for this O. megalodon individual, including cruising speed (1.39 m/s), stomach volume (9,600 L), gape size (1.81 m in height) and daily energy requirement (98,100 kcal/day). Our measurements, compared against living sharks, indicate that while this large O. megalodon individual was slower than some smaller sharks, it was an adept swimmer able to move across oceans. Although small cetaceans of 2-5 m would have provided calories beyond its daily requirement, prey as large as 9 m could have been entirely eaten. Thus, a preference for large prey could have been a strategy for the largest O. megalodon individuals to avoid competition with more agile sharks. Excess calories consumed from such large prey may have been used to fuel and sustain prolonged migrations, as seen in extant sharks. The extinction of this highly mobile super-predator likely impacted global nutrient transfer and trophic food webs.

#### "Kindergarten science?"

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Palaeontologists and artists have worked together since dinosaurs were first excavated; my research explores how the visual arts interpret palaeontology for the public. This paper aims to show that questions about the validity of using images that show prehistoric creatures as living animals have been fundamental to palaeontology throughout its history, and asks how much attention palaeontologists should pay to such questions today. To explore this, I discuss a meeting that was held in Bristol, United Kingdom, in 1898, in which an argument broke out about these very questions. Why is this particular meeting interesting? It was one of many held by the British Association for the Advancement of Science, but among those present were American palaeontologists Othniel C. Marsh of Yale and Henry Fairfield Osborn, of the AMNH. Osborn presented four paintings by artist Charles Knight to show how the AMNH displayed palaeontology to the public. The lively discussion that followed was reported in The Times and in correspondence between Marsh and British geologist Henry Woodward. Marsh was vehemently opposed to speculating on the appearance of prehistoric animals and stigmatised this as "Kindergarten science" but opinions varied on the validity of such speculation, summarising questions that resonate through to today. Osborn wanted to change how palaeontology was presented to the public but met significant resistance from other palaeontologists. Was Marsh right? Is this "Kindergarten science?" I suggest that palaeontologists should still question how much speculation is valid. Is palaeontology helped or harmed by its partnership with palaeoart?

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

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The evolution of quadrupedality from a bipedal ancestral state is unique to Dinosauria and its closest relatives, convergently occurring at least three times in Ornithischia. By using 3D multi-body dynamic models, we are investigating changes to forelimb muscle moment arms (muscle leverages around a joint) in quadrupedal ornithischians that may be mechanistically associated with changes to their posture and locomotion. Photogrammetric, CT, and laser scans of forelimb fossil material from key ornithischian taxa across a range of groups and body sizes were used as the basis for our models. The attachments and 3D pathways of the muscles were reconstructed using the archosaur extant phylogenetic bracket. Our analyses suggest that across the estimated ranges of motion, the moment arms of humeral protractors increased relative to humeral retractors between basal bipedal ornithischians and quadrupedal ornithischians, with hadrosaur-line ornithopods showing the greatest increase. The moment arms of humeral abductors were greater in ceratopsids and stegosaurs than in guadrupedal ornithopods. These changes to the moment arms and overall lines of action of the pectoral musculature appear to result from disparate changes to the shape of the scapulocoracoid and humerus between the different quadrupedal ornithischian groups, each of which may have consequently developed distinct locomotor styles.

# Changes in corallite sizes of scleractinian corals across major hyperthermal events

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Global warming today is taking its toll on coral reefs globally, particularly affecting scleractinian corals which rely on their symbionts for nutrition. In the past, hyperthermal events have probably triggered evolutionary losses and gains of symbiosis in corals. Accordingly, we expect photosymbiotic corals to be more strongly affected than non-symbiotic corals. Corallite sizes have been used as a proxy for the efficacy of photosymbiosis with smaller corallite sizes associated with higher photosymbiotic autotrophy in colonial corals. Using a new database on corallite sizes of fossil corals collected from existing literature and data on modern corals from the Coral Trait Database combined with occurrences from the Paleobiology Database, we test how the dependency on photosynthetic diet in corals may have increased their extinction risk. We expect corals to be selected against small corallite sizes during hyperthermal events. Based on a survey of 353 fossil and recent coral genera we establish trends in corallite sizes across the Triassic–

Jurassic, Pliensbachian–Toarcian, Barremian–Aptian, Cenomanian–Turonian, and Paleocene–Eocene. We find a significant increase in corallite diameter of all corals at three of these events. Colonial corals had 0.8 times larger corallites in the Aptian than in the Barremian suggesting stronger heterotrophy at this hyperthermal event. However, generalized linear modelling suggests that the extinction of scleractinian corals seems to be non-selective with regards to their corallite sizes. This indicates that processes other than warming, such as increased sediment input could be the cause of this change.

# A new phylogeny of the cladoxylopsid plexus – contribution of an early cladoxylopsid from the Lower Devonian (Emsian) of Quebec

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Cladoxylopsids represent one of the two main groups of euphyllophytes recognized in the Devonian based on xylem architecture - the moniliformopsids. Cladoxylopsids formed earth's earliest forests and are thought to have given rise to sphenopsids and ferns. Emsian strata of the Battery Point Formation on the Gaspe Peninsula (Quebec, Canada) contain anatomically preserved cladoxylopsids. We describe a new cladoxylopsid from this unit and we evaluate the phylogenetic position of this plant. The phylogenetic study also addresses broader questions of cladoxylopsid systematics and evolution. The new plant is preserved anatomically and consists of small actinostelic axes bearing dichotomously-branched, helically-arranged ultimate appendages and fusiform sporangia. This plant provides the oldest evidence of cladoxylopsid anatomy, including ultimate appendages and sporangia. To evaluate phylogenetic relationships, we use a dataset of 36 new morphological characters and 31 species in parsimony-constrained analyses. In agreement with nonphylogenetic classification schemes, our analysis resolves a basal grade of iridopterids and a clade of cladoxylopsids s.s., which includes a pseudosporochnalean cladoxylopsid clade and a cladoxylalean cladoxylopsid clade. The new plant is resolved as part of the cladoxylopsid s.s. clade. Our phylogenetic analysis illuminates aspects of tempo and mode of evolution in the cladoxylopsid plexus. Originating prior to the Emsian, cladoxylopsids reached global distribution by the Frasnian. Iridopterids and cladoxylopsids s.s. radiated in the Emsian-Eifelian. The sequence of character changes recovered by our phylogeny supports a transition from actinostelic protosteles to dissected steles, associated with an increase in xylem rib number and medullation generating a central parenchymatous area.

#### Acrothoracid barnacle borings in Late Devonian heterocoral skeletons

#### Patrycja G. Dworczak<sup>1,2</sup>, Matthias López Correa<sup>2,3</sup>, Emilia Jarochowska<sup>2</sup>, Błażej Berkowski<sup>1</sup>

<sup>1</sup>Institute of Geology, Adam Mickiewicz University, ul. Bogumiła Krygowskiego 12, 61-680 Poznań, Poland <sup>2</sup>Geozentrum Nordbayern, Universität Erlangen-Nürnberg, Loewenichstr. 28, D-91054 Erlangen, Germany <sup>3</sup>Consiglio Nazionale delle Ricerche, Istituto di Scienze Marine, via Gobetti 101, I-40129 Bologna, Italy Rogerella de Saint-Seine (1951) borings are narrow, pouch-shaped pits with tapering slitlike openings. They are produced by acrothoracid barnacles, which do not have a shell and bore into hard substrates to protect their "naked" body. The bioerosional activity of barnacles has a long fossil record and the ichnogenus Rogerella is known from the Upper Ordovician to the Recent and occurs only in carbonate hard substrates such as rock or shells and skeletons of other organisms. Here, we provide the first report of the occurrence of Rogerella sp. in skeletons of the heterocoral Oligophylloides maroccanus Weyer 2016 from the upper Devonian Tafilalt Platform (Jebel Bou Ifarherioun, Anti-Atlas, Morocco). Acrothoracid borings were found on the basal part, but also on broken branches of the heterocoral corallum and occurred post mortem. There is no indication for a syn vivo coralbarnacle interaction as borings in tissue-covered areas. X-ray microcomputed tomography was used to visualize the morphology of the pits, their orientation and distribution. Albeit being current-dependent, owing to their filter-feeding habit, we did not find a preferential orientation of the borings. Our samples are the best preserved Devonian material to date. The trace morphology ranges from rounded symmetric to asymmetric basal outlines, without ontogenetic shape transitions. In asymmetric specimens the deepest point occurs below the widest part of the surface perimeter.

# Diversity dynamics through deep time: overcoming the hurdle of spatiotemporal sampling bias

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Analysing large-scale diversity trends through geological time has been a staple of palaeontological enquiry for over 70 years. The data underpinning such analyses, along with the methods used to mitigate variation in sampling intensity through time, have become increasingly sophisticated. It is now apparent, however, that variation in the geographical distribution of palaeontological data continues to distort relative and absolute diversity trends, even when temporal variation in sampling intensity is accounted for. While methods to address this issue have been proposed, they all produce point-wise diversity estimates from spatially-standardised subsamples and cannot provide the temporally continuous datasets needed for the calculation of speciation, extinction and preservation rates - the variables which ultimately determined true palaeo-diversity and its manifestation in the geological record. To overcome these hurdles, I present an alternative approach to accounting for spatial sampling bias, employing the geometry of palaeoocean basins as a priori biogeographic regions and natural sampling units which can provide temporally continuous datasets that can then be standardised by a number of different geographic extent metrics. I apply methods which account for temporal sampling bias within these regional samples, where the resultant diversity trends show no relationship to geographic extent and may be considered to reflect the true signal through time. I showcase this approach using the Triassic marine fossil record, highlighting individual biogeographic histories and the coordinated diversity changes which reflect emergent global events, including the Permo-Triassic and Triassic-Jurassic mass extinctions and the Carnian Pluvial Episode.

# Insect herbivory in the middle-late Paleocene (58–60 Ma) neotropical rainforests of the Bogotá Formation, Central Colombia

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Plant predation by insects is a major driver of the high plant diversity observed in modern Neotropical rainforests, yet plant-insect herbivore interactions are poorly known in the early evolution of this biome. The earliest known records of Neotropical rainforests date back to the middle-late Paleocene of Colombia: the coastal-floodplain deposits of the Cerrejón Formation (58-60 Ma, northern Colombia) and the lowland fluvial environments of a recently discovered flora in the Bogotá Formation (58–60 Ma, central Colombia). Here, we studied insect damage in leaf fossils from the Bogotá flora to test whether a high abundance and low richness of insect damage -the pattern seen in previous reports from Cerrejón- typified early evolving Neotropical rainforests. The Bogotá flora records the highest frequency and richness of insect damage among comparable floras in Europe, North America and Patagonia, in addition to the highest number of galling and mining associations. This indicates that, by the middle-late Paleocene, insect herbivory was more intense and host-specialized in the Neotropical rainforests of the Bogotá flora than elsewhere, reflecting a rich suite of herbivorous insects. The highly abundant and rich galls, a distinctive feature of the Bogotá flora, is consistent with the preferential use of upper canopy leaves by galling insects, as seen in modern Neotropical rainforests. Furthermore, our results show differences between the Cerrejón and Bogotá floras, both early Neotropical rainforests, suggesting differential recovery from the end-Cretaceous ecological crisis and/or that, by the middle-late Paleocene, there were marked differences in the ecology of Neotropical rainforests.

#### Biological complexity in sauropod dinosaurs

#### Emily Green<sup>1</sup>

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The concept of complexity in biology seems intuitive and easy to grasp. The so-called first law of evolution posits that organisms increase in complexity over time. Rooted in empiricism, the notion of increasing complexity is corroborated most famously by the origin of multicellularity. However, whether complexity evolves according to sustained directional processes occurring in parallel lineages remains a moot point. Overlooked as an independent research area, the evolution of complexity is now being assimilated in analyses of macroevolutionary change in deep time. In particular, complexity increases have always been assumed in macroevolutionary studies but never rigorously tested with an aim to establish whether they are ubiquitous and, therefore, whether they represent a pervasive rule. Complexity, here defined as the sum-total of internal variation, is quantified by comparing homologous serially repeating structures. For this particular investigation, I chose the vertebral column of sauropods as an exemplary case study. Sauropods' unique necks allow study of morphological complexity by looking at patterns of count and shape change across the lineage. Ecological information indexes, such as the Brillouin index, have been repurposed here to characterize complexity as well as a landmark analyses study of shape change between vertebral region. The results support a driven trend in increasing complexity over time. Additionally, both analyses show that the peculiar sauropods in the family Dicraeosauridae demonstrate independence in their complexity compared to their relatives.

# Biases in the early actinopterygian fossil record obscure underlying patterns of diversity

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Actinopterygians (ray-finned fishes) are the most diverse living group of vertebrates, but the mechanisms of their rise to dominance and patterns of diversity in the earliest part of their evolutionary history are far from understood. There have been limited attempts to investigate biases in the early actinopterygian fossil record, and previous studies of 'global' diversity have conglomerated regional fossil records, with results subject to significant spatial biases. As biases influence face-value richness, palaeontologists have sought to tease apart sampling biases and estimate true diversity patterns, leading to the advent of new subsampling and extrapolation techniques. These have been applied to numerous vertebrate groups, but never to ray-finned fishes. Here we present raw occurrence data for Palaeozoic actinopterygians as both a 'global' curve and local richness plots, and identify major spatial biases, gaps in sampling and correlations of richness with sampling. We also attempt to accurately deduce diversity trends using estimation techniques. We find that biases in the Palaeozoic actinopterygian record effectively swamp any underlying signal, and our relative richness estimates show explicable, though likely inaccurate, temporal variation. Available methods are therefore unable to produce accurate trends in Palaeozoic

actinopterygian diversity due to compounding taxonomic, temporal, geographic and researcher biases that plague the actinopterygian fossil record. Future work addressing problematic taxonomy, exploring underrepresented regions, and harnessing unpublished museum data will be vital to understanding the rise of ray-finned fishes. More broadly, our work highlights that researchers should take care that their data are suitable for estimating diversity.

The internal cranial anatomy of the large geosaurine metriorhynchid *Plesiosuchus manselii*, and implications for body size evolution in Metriorhynchidae

#### Robert Higgins<sup>1</sup>, Mark Young<sup>1</sup>, Steve Brusatte<sup>1</sup>

#### <sup>1</sup>University of Edinburgh, United Kingdom

During the Mesozoic, metriorhynchid crocodylomorphs extensively radiated in shallow marine ecosystems. Given that they are the only known obligately pelagic crocodylomorphs, and archosaurs, their endocranial anatomy has been of great interest. With large cranial salt glands, compact inner ears, hypertrophied vasculature canals, and dramatically reduced braincase sinuses, metriorhynchid neurosensory systems were radically different from those of all other crocodylomorphs. However, until now only smaller-bodied species had been studied. In order to determine if large body size impacted metriorhynchid endocranial anatomy, we micro-CT scanned and digitally segmented the largest known metriorhynchid skull (belonging to *Plesiosuchus manselii*). Segmentation is still progressing (due to scanning artefacts), but thus far we have not found any size-related morphologies in *Plesiosuchus*. However, *Plesiosuchus* does have a pronounced forebrain/midbrain endocast flexure similar to that described for "*Metriorhynchus*" cf. *brachyrhynchus*. Given that this pronounced forebrain endocast flexure has only been observed in geosaurines, it could suggest a split in brain endocast morphology within Metriorhynchidae.

#### Modelling the effects of erosion, sedimentary condensation and dilution on paleontological data

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Accumulations of skeletal remains are common in the fossil record and easily recognizable in outcrops. They can be evidence for ecologically important events, such as changes in biological productivity or mass mortality. However, they can also be generated by low sedimentation rates, which reduce the amount of sediment placed between individual skeletal remains. This sedimentary condensation applies to all types of data that is derived from particles that are part of the sedimentary rock record. We present the R package DAIME to (1) model the effects of sedimentary condensation and dilution on paleontological data and (2) incorporate available information on sedimentation rates into paleontological analyses. The model is available as an interactive web application that does not require any knowledge of R Software, available at https://stratigraphicpaleobiology.shinyapps.io/shellbed\_condensator/. This application is developed for teaching purposes, visualization, and self-study. Using the model and the app, we discuss how different types of data such as isotope ratios, skeletal abundances, taxon last occurrences, and changes in morphology are affected by depositional settings such as high/lowstands, shallowing upward and deepening upward successions as well as hiatuses. We discuss the implications for interpreting rates of environmental changes, stratigraphic correlation, diversity analyses, origination and extinction rates and other research applications with a focus on the introduction of apparent rapid changes due to sedimentological controls.

# Postcranial traits differentiate species of the late Cenozoic kangaroo genus *Protemnodon* better than teeth

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Prior to their extinction ~40,000 years ago, kangaroos of the genus Protemnodon Owen, 1874 (Marsupialia: Macropodidae) were widespread across the Australian continent during the Pliocene and Pleistocene. Large and robust, they were among the largest kangaroos ever, with body mass estimates of up to 180 kg. The Pleistocene Australian species are poorly delimited, diagnosed on slight, inconsistently recognisable dental differences, resulting in 150 years of taxonomic confusion that negatively affected broader studies of historic trends, e.g. palaeoclimate. 3D scans and photographs were taken of 735 specimens from 13 institutions in four countries. Digital measurements were collected, and morphometric data visualised, while detailed morphological comparisons were made. These analyses found that only some species could be differentiated on dental characteristics. However, profound morphological and proportional differences in hindlimb and cervical vertebrae not attributable to sexual dimorphism were evident between specimens with indistinguishable dentitions Some specimens have long, gracile hindlimbs, proportionally similar to the arid-adapted, fast-hopping red kangaroo. Others have shorter, robust hindlimbs and very short, broad cervical vertebrae, suggestive of slow hopping through dense vegetation. The geographic distribution of these morphotypes, interpreted as distinct species, is consistent with such ecomorphological inferences and a reminder that herbivore divergences may be driven as much by varying locomotor adaptations to different habitats as diet. The overriding focus on teeth in mammalian taxonomy is often due to their higher chance of preservation, but where elemental associations exist we must interrogate further and generate a more complete understanding of evolutionary patterns and processes.

Morphological changes in reticulate Nummulites across the Eocene– Oligocene transition – comparisons from 2-D thin sections and 3-D image segmentations

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The Eocene-Oligocene transition event was one of the most prominent climatic shifts of the Cenozoic era, associated with climatic cooling, oceanographic change and biotic turnover. Within the shallow marine realm, the larger benthic foraminifera are known to suffer extinctions of several long ranging and widespread genera, but some taxa pass through this event apparently unscathed. One such lineage is the reticulate Nummulites fabianii lineage. Preliminary work using equatorial thin-sections of the reticulate N. fabianii lineage species from Tanzanian Drilling Project records show that they occur continuously through the EOT and show increasing variation in their morphology. However, the extent of the morphological change and whether it was driven by the climate change taking place at the EOT remained uncertain. Here we study the morphological characteristics (proloculus length and volume, chamber counts and volume, number of whorls, test diameter, thickness) of the Tanzanian reticulate Nummulites across a ~1 Myr interval spanning the EOT. These are then coupled with climatic data (d<sup>18</sup>O, d<sup>13</sup>C) from the same core record to identify potential drivers. Measurements from equatorial thin-sections (2-D) and micro-computed tomographic segmented models (3-D) were compared to determine whether data loss during sectioning significantly impacted trends. Positive trends in proloculus size, number of chambers and whorls along with test expansion were found to coincide with the transition. These trends were consistent across both 2D and 3D datasets. We conclude these adaptations likely occurred as a result of changing ecological responses to sea-level fall and increasing nutrient conditions across this event.

#### Geometric evolution of the galloanseran quadrate

#### Pei-Chen Kuo<sup>1</sup>, Roger Benson<sup>2</sup>, Daniel Field<sup>1</sup>

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In birds and other reptiles, the quadrate acts as a hinge connecting the lower jaw and the skull, and plays an important role in avian cranial kinesis. Though previous studies have qualitatively described its substantial morphological variability, none have tried to quantify evolutionary changes in its shape. Here, we investigate shape changes of the quadrate in Galloanserae, a major clade of living birds uniting relatives of living chickens and ducks. We quantified morphological variation in the quadrate across 35 extant galloanseran taxa using three-dimensional geometric morphometrics, and performed ancestral shape reconstructions in the context of an up-to-date neornithine phylogeny. Our results suggest the quadrate of ancestral galloanserans may have shared features associated with extant Galliformes and Anseriformes. For example, the ancestral condition of the orbital process is

reconstructed as robust and strongly protruding (anseriform-like) with a pointed tip (galliform-like). The quadratojugal contact is reconstructed as a shallow fossa (anseriform-like), but the squamosal and otic capitula are more similar to the condition in galliforms. This three-dimensional ancestral reconstruction facilitates comparisons with early galloanseran fossil quadrates, such as *Asteriornis* (a ~67 Ma possible stem galloanseran) and *Presbyornis* (a ~52 Ma probable stem anseriform). Notably, our ancestral galloanseran quadrate reconstructions closely approximate aspects of quadrate morphology observed in these early fossil galloanserans, suggesting that both these fossils and our reconstructions may provide useful insight into the plesiomorphic galloanseran condition. We hope our approach will help elucidate important aspects of the morphology and function of the feeding apparatus early in crown bird evolutionary history.

#### New data on glomeromycete spores associated with early tracheophytes in the Lower Devonian (Emsian; c. 400 Ma) of Gaspé (Quebec, Canada)

#### Madison Lalica<sup>1</sup>, Mihai Tomescu<sup>1</sup>

#### <sup>1</sup>Humboldt State University, United States of America

Fossil assemblages preserved in fluvial-coastal Emsian strata of the Battery Point Formation of Gaspé Bay (Quebec, Canada) are among the most diverse occurrences of Early Devonian permineralized plants. The plants host fungal material with affinities to the Glomeromycotina. A survey of over 200 specimens reveals the presence of spores (90-240 µm) that may represent a new species of *Glomites*. These spores exhibit four wall layers, of which two are more resilient: a thick, dark layer to the outside of a thin, membranous layer. The spores are globose and have subtending hyphae with varying occlusion. Circumstantial evidence suggests that the spores were metabolically active within their plant hosts and that the plants were alive at the time of infection: hyphae and vesicles, indicative of metabolically active fungi co-occur with the spores; the tissues of some host plant axes are notably affected in the vicinity of the spores; within individual axes, spores show varying levels of preservation, consistent with continued spore development (and subsequent breakdown). Compared to other fossil glomeromycetes and considering the traits of living glomeromycetes, our observations of the Battery Point Formation material suggest that the fungi had an endomycorrhizal role. This occurrence is one of the few reports of fungi in the Battery Point Formation and the only Early Devonian glomeromycete occurrence documented outside the hot spring deposits of the Rhynie chert. The presence of glomeromycetes in plants of fluvial-coastal environments and their putative mycorrhizal role suggest that glomeromycetes were relatively ubiquitous symbionts of tracheophytes by the Early Devonian.

#### Growth and feeding ecology of coniform conodonts

#### Isabella Leonhard<sup>1</sup>, Bryan Shirley<sup>1</sup>, Duncan J E Murdock<sup>2</sup>, John E Repetski<sup>3</sup>, Emilia Jarochowska<sup>1</sup>

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Conodonts were the first vertebrates to develop mineralized dental tools, known as elements. Recent research suggests that "complex" euconodonts fed as macrophagous predators and/or scavengers, but we do not know how this feeding habit emerged in the earliest coniform conodonts. We focus on the primitive Proconodontus muelleri from the late Cambrian and the more derived Panderodus equicostatus from the Silurian. We tested the following hypotheses: (1) Panderodus and Proconodontus processed hard food and (2) both species shifted towards higher trophic levels during ontogeny. We employed backscatter electron imaging, energy-dispersive X-ray spectroscopy and synchrotron radiation X-ray tomographic microscopy to identify growth increments and Sr/Ca ratio as proxy for the trophic position. Growth increments (27 in Pa. equicostatus and 58 in Pr. muelleri) were formed in bundles of 4-7 increments in Pa. equicostatus and 7-9 in Pr. *muelleri*. We interpret the bundles as analogous to Retzius periodicity in vertebrate teeth. Based on optimal resource allocation models, internal periodicity might explain indeterminate growth in both species. We interpret the almost linear growth of both individuals as an indicator that these taxa were not prey to higher-level predators. Our findings show that periodic growth was present in early conodonts and preceded tissue repair. We found no microwear and the Sr/Ca ratio did not change substantially during ontogeny. Trophic ecology of coniform conodonts differed from the predatory lifestyle of "complex" conodonts. We propose that conodonts adapted their life histories to top-down controlled ecosystem during the Nekton Revolution.

# Appendage specialization in the Cambrian trilobite **Olenoides serratus** from the Burgess Shale and implications for trilobite reproduction

#### Sarah Losso<sup>1</sup>, Javier Ortega-Hernández<sup>1</sup>

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Trilobites are a dominant group of Paleozoic euarthropods that despite boasting an impressive diversity of over 20,000 described species; however, details of their appendicular morphology are only known from 31 taxa. All known trilobites with preserved appendages feature a pair of uniramous antennae followed by a homonomous series of biramous appendages. All the biramous trunk limbs have the same morphology, and the only evidence of differentiation consists of the presence of progressively smaller posterior appendage pairs and some variability in the proportions of the proximal region that affect food mastication. *Olenoides serratus* is a well-known corynexochid trilobite from the Burgess Shale (Wuliuan, Miaolingian) with preserved appendages known from over 70 specimens. However, *O. serratus* is unique among trilobites in having preserved cerci, thus showing a higher degree of limb tagmosis than other representatives. Here, we

demonstrate the first evidence of substantial morphological differentiation of the biramous appendages in *O. serratus* based on undescribed material from the Burgess Shale. An exceptionally preserved specimen shows differentiated appendages on the seventh thoracic and first pygidial segments consisting of greatly reduced endopods, composed of seven podomeres with unique morphology, and a large sub-circular protopodite without endites, but with an otherwise conventional exopod. These differentiated appendages demonstrate an unparalleled degree of limb tagmosis in trilobites, and carry broader implications for trilobite biology and reproduction. The functional morphology of the reduced endopods resembles that of claspers, which have convergently evolved in adult male arthropods to grasp onto females prior to or during mating.

#### A theoretical morphospace approach to understanding the evolution of the mammalian mandible

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The evolution of the mammalian dentary-only mandible, with a dentary/squamosal jaw joint, is well documented in the fossil record, yet the functional consequences and drivers of this innovation remain unclear. The clade in which this transition occurs, Therapsida, also provides an ideal case study for investigating morphospace occupation on a macroevolutionary scale. We constructed a theoretical morphospace from empirical jaw shapes and used this to quantify both realized and the unrealized mandibular morphologies across ~300 million years of therapsid evolution. Functional performance surfaces, adaptive landscapes and phylomorphospaces were used to compare the impact of functional and phylogenetic constraints on the exploration of this theoretical morphospace. Despite multiple adaptive radiations, therapsids have not explored the entirety of possible mandibular morphospace. Most taxa are associated with areas of morphospace with high functional optimality. The distribution of taxa across morphospace appears to be best explained by their feeding ecology. The base of the clade Eucynodontia was associated with a shift in morphospace occupation. Eucynodonts occupy an area of morphospace which is better optimised for the trade-off between increased bite speed and reduced biting stress in the mandible relative to other therapsids. The expansion of the coronoid process, reduction of the post dentary bones, and appearance of a dual jaw joint, in eucynodonts is associated with increasing functional optimisation of the mandible, suggesting that functional optimisation was an important driver of the evolution of the mammalian mandible. Functional factors related to feeding ecology appear to constrain the exploration of possible mandibular morphology amongst therapsids.

#### Convergent evolution of body shape in tetrapods

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Morphological convergence is often explained as the result of adaptation to similar mechanical functions and/or ecological niches. However, quantitative tests of this hypothesis and comparisons across a diverse array of taxa and ecotypes are uncommon. We use dietary and locomotor data to classify the ecology of tetrapods and identify patterns of convergent evolution in body segment proportions. Convergence measures were calculated using a modified form of the Wheatsheaf index. The Wheatsheaf index (w) yielded relatively low values and high P values P >0.05 for most dietary and locomotor categories suggesting weak convergence overall. This does not imply that convergence has not occurred, but that it is not very strong in most linear and volumetric measurements of body proportions, especially within dietary groups. There are however a few exceptions to this: mechanically demanding or specialised forms of locomotion such as fossoriality and flight (active and soaring) show significant convergence in certain aspects of morphology. This suggests that locomotor ecology has had a bigger influence than diet on the convergent evolution of tetrapod body shape over time.

# The oldest Neogene sediments in Wales: palaeoenvironment and palaeoclimate of the Trwyn y Parc solution pipe complex

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The Trwyn y Parc solution pipe is one of only four onshore United Kingdom Miocene deposits; it is both a Regionally Important Geological site, and part of the GeoMôn UNESCO Global Geopark. Previously, the pollen and spore flora from Trwyn y Parc was dated to the Miocene. Here we present a revision to that age and show that these are the oldest onshore Miocene sediments in the United Kingdom. The palaeoclimate under which this flora grew has been reconstructed using three different nearest living relative approaches: the Coexistence Approach (CA), Climate REconstruction SoFTware (CREST) and Climate Reconstruction Analysis using Coexistence Likelihood Estimation (CRACLE). All three produce comparable reconstructions and show that a warm-temperate climate existed during the Langhian of northwest Wales. The reconstructed mean annual temperature of 9.4 °C. Mean annual precipitation is reconstructed between 1134 – 1356 mm per annum as compared to the modern rainfall of 898 mm per year. Finally, we place the Trwyn y Parc flora in the context of other Neogene floras from the United Kingdom to present a long-term development of floras and climate.

# Functional morphology of the oviraptorosaurian dinosaur cranium and adaptation for a powerful bite

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Oviraptorosaurians were a theropod dinosaur group from the Cretaceous of North America and Asia that evolved highly modified lightweight crania with robust toothless beaks, leaving their cranial function, diet, and ecosystem position uncertain. To investigate oviraptorosaurian cranial functional morphology, we used CT-scans and photogrammetry to create digital 3D models of four oviraptorosaurian crania: Incisivosaurus, Citipati, Khaan, and Conchoraptor. This required detailed restoration and retrodeformation using specialist software packages Avizo, Landmark, and Blender. These 3D models form the basis for volumetric reconstruction of jaw adductor musculature to estimate bite force. Using finite element analysis (in Hypermesh and Abaqus), we assessed how the crania perform in resisting bite reaction forces and accommodating muscle forces, looking at resulting patterns of stress and strain within the crania and energetic efficiency. The three more derived oviraptorid crania appear adapted for a strong symmetrical bite in multiple positions; greater stress is produced when force is applied asymmetrically. Stresses are channelled away from pneumatic areas and the skull roof by the robust premaxilla and palate. In contrast, the early diverging oviraptorosaurian Incisivosaurus exhibits higher and more generalised stress patterns; its prominent incisor-like teeth appear adaptive for feeding. Estimated bite forces are significantly greater for the more derived oviraptorid oviraptorosaurians compared to the early diverging Incisivosaurus and other herbivorous theropods (of larger body size), both absolutely and relatively. These results hint at a transition from a generalised feeding style in early oviraptorosaurians towards a more specialised condition focused on stronger bite forces in the later-diverging oviraptorids.

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

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Benthic foraminifera are a group of calcifying marine organisms that play a significant role in global carbonate production and the structure of marine ecosystems. A large body of work has focused on their potential physiological and community responses under future climate change, however, there has been little research focusing on the potential impact on their structural integrity. Finite element analysis (FEA) is a mathematical technique that allows for the assessment of the strength of a structure. Here, this technique was implemented to test how the form of benthic foraminifera is affected during periods of environmental stress. Biologically accurate 3-D geometric models for different morphological groups of benthic foraminifera were generated from computed tomography (CT) scans and were used to produce simplified 3-D geometric models based on individual cross-sections, to which they were then compared. The simplified models were then altered based on morphological changes observed in the fossil record of the Palaeocene Eocene Thermal Maximum (PETM), a useful geological analogue to future climate change. The results indicate that the simplified cross-sections were incapable of accurately capturing the strength of the whole organisms, however, do demonstrate that the robustness of the organism varies between morphological groups. The results also indicate that if similar morphological changes to those of the PETM were to occur in the future, it would lead to benthic foraminifera producing weakened forms, with variability amongst species. Resultantly, future climate change may result in lowered biodiversity of benthic foraminifera subsequently leading to negative impacts on ocean ecosystems.

# Where the fossil record falls flat: using novel cophylogenetic methods to unravel platyhelminth evolution

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Understanding how hosts and parasites have coevolved through time is a major goal in evolutionary biology. Previous approaches relied on the assumption that cospeciation was the dominant evolutionary process driving their shared history. Recent studies, however, have suggested this assumption may not hold true for many host parasite associations. As such, new models are now being developed to reconstruct the evolutionary processes involved without making this prior assumption of cospeciation. Here we investigate the coevolutionary history of neobatrachian polystomes and their anuran hosts using model-based approaches. These polystome parasites are considered to be host specific and as such have been hypothesised to have evolved mainly through cospeciation. Using a DTL model we estimated the relative contribution of cospeciation. Our results show that while there does seem to be an evolutionary preference towards cospeciation, a number of host switching events have occurred. The results indicate that studying host parasite interactions through time, including molecular dating studies that rely on the host fossil record for calibrations, must consider host switching as an important evolutionary process.

# The impact of broader sampling of character space on zosterophyll relationships

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Important constituents of Siluro-Devonian floras, zosterophylls gave rise to the lycophytes. We explore the relationships of 20 genera that maximize sampling of anatomy. Using phylogenetic and phenetic analyses we (1) assess the influence of tree rooting, taxon

sampling, and morphological vs anatomical characters on the stability of relationships; (2) compare phylogenetic and phenetic methods in terms of relationships recovered. Phenetic analyses show sensitivity to taxon sampling, recover Huia+Nothia highly similar and support placement of Renalia among zosterophylls. Phylogenetic analyses demonstrate that taxon sampling and tree rooting significantly influence resolution. Trees rooted with Renalia have higher resolution than trees rooted with Psilophyton. Inclusion of the lycopsid Sengelia and exclusion of Stolbergia (highest percentage of missing data), also yield higher resolution. We recover three clades: Huia+Nothia sister to the rest of the ingroup, wherein two clades correspond to the previously recovered sawdonialean and "nonterminate" groups. The position of Sengelia supports earlier ideas that the lycopsid ancestor had nonterminate fertile axes. Exclusion of morphological characters diminishes phylogenetic resolution. Morphology-only analyses recover a tree that differs from that obtained using morphology+anatomy in the membership of sawdonialean and "nonterminate" clades, highlighting the importance of broader sampling of the morphological character space. Because both anatomy and morphology are part of the evolutionary history of a species, relationships recovered using morphological+anatomical characters more likely reflect natural evolutionary relationships. Thus, breadth of character sampling and not the amount of phylogenetic resolution should be the primary criterion for selecting between alternative hypotheses of relationships.

# Functional trade-offs in multituberculate theoretical jaw morphology between stress response and jaw speed

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The question of how function constrains morphology has long been interrogated by palaeontologists. For example, multituberculates, an extinct mammal group that first arose in the Mesozoic, are defined by their unique tooth morphology, which has led to questions about why their teeth and, in combination, jaws take the shape that they do. Here, I attempt to examine this particular relationship between form and function by examining the breadth of potential theoretical morphologies of multituberculate jaws, and determining the functional optima among these morphologies for stress response and rotational efficiency. I first collected 2D multituberculate jaw images from the available literature, and then used Elliptical Fourier Analysis to take the outlines of each jaw and produce a grid of theoretical morphologies for multituberculate jaws. Using this theoretical shape data, two performance landscape tests were conducted. The first test used Finite Element Analysis to determine stress response, and the second used rotational inertia calculations to determine rotational efficiency among jaw shapes. Our results indicate that multituberculate jaw morphology primarily differentiates based on the prominence of the coronoid process and the height of the dentary. Additionally, Cimolodonts appear to exhibit a greater stress response than other multituberculates, while rotational efficiency is evenly distributed across the order. These results suggest a presence of potential trade-offs between stress response and jaw speed. I hope to follow this research by constructing a phylomorphospace and use it to estimate hypothetical ancestral jaw morphologies, which in turn may be able to be mapped to diet.

# Early Devonian euphyllophyte anatomy reveals a mosaic pattern of expression of regulatory modules responsible for secondary growth

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Recent plant fossil discoveries have uncovered previously unrecognized anatomical diversity among Early Devonian (390 Ma) euphyllophytes. These new plants inform hypotheses of relationships and reveal unexpected complexity in the early stages of the first vascular plant radiation. A prime character that contributes to plant structural diversity and complexity is secondary growth from a vascular cambium, a process that produces secondary xylem (wood). Vascular cambial growth is controlled by a set of interacting but independent regulatory modules, which, in different combinations, result in different modes of secondary growth. The activity of some of these modules can be recognized in extant and extinct plants based on key structural fingerprints, such as radially aligned tracheids, presence of rays (or, more generally, of a radially polarized tissue component), and multiplicative (anticlinal) divisions. The recognition of such fingerprints in recently discovered Early Devonian euphyllophytes demonstrates that secondary growth originated and diversified rapidly in the Early Devonian and lends support to the modular view of cambial growth regulation. We describe a new Early Devonian plant that adds yet another type to the growing list of modes of secondary growth documented in the Early Devonian. This new plant and the other euphyllophytes that mark the earliest occurrences of secondary growth possess structural fingerprints that illustrate different combinations of regulatory modules acting in secondary growth. Considered together, these plants demonstrate different degrees of canalization of regulatory modules controlling secondary growth and their mosaic pattern of expression in coeval Early Devonian tracheophytes.

# *Charniodiscus* and *Arborea* are separate genera within the Arboreomorpha

#### Daniel Pérez Pinedo<sup>1</sup>, Duncan McIlroy<sup>1</sup>

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*Charniodiscus* is one of the most iconic Ediacaran fossil fronds. Since the description of the holotype *C. concentricus* Ford, 1958 the scarcity and poor preservation of unequivocal specimens has resulted in taxonomic uncertainty within the genus. Since the reinterpretation of *C. concentricus* as a multifoliate frond, other *Charniodiscus* species—all of which are bifoliate—have been left in a taxonomic limbo, with most authors comparing them to the Arboreomorpha. Study of the taphonomic mode of the holotype of *C. concentricus* has revealed significant morphological differences between *Charniodiscus* and the somewhat similar *Arborea*; specifically the presence of a conical bifoliate frond. Our emendation of the generic diagnosis of *Charniodiscus* to encompass bifoliate arboreomorphs with a conical petalodiums allows the retention of the taxa *Charniodiscus* and *Arborea*. While the genus *Arborea* has for many years been touted as a possible junior

synonym of *Charniodiscus*, our work recognizes similarities between *Charniodiscus* and *Arborea* but restricts the latter genus to encompass taxa with flat bifoliate petalodiums. Additionally, we find no evidence for rangeomorph-type fractal branching in *Charniodiscus* and thus reject its inclusion in the Rangeomorpha.

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

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Crocodilian jaw morphology is the result of a trade-off between hydrodynamics, strength and closure speed, a clear example of the relationship between form and function. However, the morphological and ecological diversity of modern crurotarsans is vastly outstripped by their extinct relatives, which included multiple convergent examples of active terrestrial forms, herbivores and fully marine species. These lifestyles may have imposed different functional demands such as the need for additional stress resistance or greater hydrodynamic efficiency, but the effect that this had on morphology is largely unquantified. In this study, we combine Elliptical Fourier analysis with functional testing to build a performance landscape of theoretical jaw shapes to investigate the drivers of morphological evolution in crurotarsan jaws. We found that the realised jaws of 242 crurotarsans generally occupy the most optimal regions of theoretical morphospace for rotational efficiency, resistance to Von Mises stress and hydrodynamic efficiency, though some viable shapes remain unrealised. Jaw speed is optimised only in a narrow region of morphospace whereas many shapes possess optimal jaw strength, which may act as a minimum boundary rather than a strong driver for most species. Morphology and ecology are closely linked in crurotarsans; shape variation shows little phylogenetic signal and functional convergence is common throughout the clade. The jaws of aquatic taxa are confined to shapes with high hydrodynamic efficiency, whereas some terrestrial taxa evolved stronger shapes. Within these environments, diet appears to play a crucial role in determining jaw shape, largely dictated by the importance of rotational efficiency in feeding.

### An enigmatic jawless vertebrate from the Silurian of Scotland with soft tissues

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The origin of vertebrates is one of the major evolutionary events, recorded by a diverse assemblage of fossil taxa. Understanding this transition requires a well-supported phylogeny, yet this is hindered by conflicting interpretations of soft tissue taxa that results in poor resolution. One key problematic taxon is *Lasanius*: a small, primarily soft-bodied,

jawless genus that exhibits unusual areas of localised mineralization. Potentially *Lasanius* represents a transitionary form, bridging the morphological gap between nonbiomineralizing and biomineralizing taxa. However, due to poor knowledge of its anatomy, the affinity of this genus is unclear, as is its importance in the evolutionary history of vertebrates. To resolve some of the uncertainty, an array of modern approaches and techniques were used to reassess the anatomy of *Lasanius*. EDS-XRF analysis provides support for a bone-like composition of the mineralised regions, but fails to find evidence for proposed dermal armour. Numerous vertebrate synapomorphies are confirmed, including a notochord, paired sensory organs and a digestive tract, but no evidence is found for an anal fin noted in previously descriptions. Phylogenetic analysis recovers *Lasanius* in a stem-cyclostome position, yet further analysis suggests this position is still unstable, and potentially unreliable. Although the work here creates a more robust reconstruction of the anatomy of *Lasanius*, it highlights the need both for further work on this genus, and the understanding the ambiguous taphonomy of soft-tissue vertebrates.

### Priority effects and the macroevolutionary dynamics of biodiversity

#### Bouwe Reijenga<sup>1</sup>, David Murrell<sup>1</sup>, Alex Pigot<sup>1</sup>

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Inhibitory priority effects—the phenomenon where the prior local establishment of species may inhibit other species from colonising—are a major source of historical contingency in the assembly of ecological communities. However, how they shape the dynamics of biodiversity over macroevolutionary timescales remains unclear. Here we develop and analyse a metacommunity model combining local priority effects with niche evolution, speciation and extinction, and present three key results. We show that by promoting the persistence of rare species, local priority effects cause the evolution of higher global diversity as well as major disparities in richness among evolutionary lineages. However, we also show how classic macroevolutionary patterns of niche incumbency—whereby rates of regional diversification and invasion slow down as ecological niches are filled—do not depend on local priority effects, arising even when invading species continuously displace residents. Together, these results clarify the connection between local priority effects and the filling of ecological niche space, and reveal how the impact of species arrival order on competition fundamentally shapes the generation and maintenance of biodiversity.

### The quality of the fossil record of Palaeozoic chondrichthyans

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The chondrichthyans or cartilaginous fishes are a highly successful group of predominantly predatory fishes that originated and first diversified in the early Palaeozoic. They possess an endoskeleton made mainly out of cartilage rather than bone which rarely fossilises. As a

consequence, their evolutionary history is poorly understood and often dominated by disarticulated and isolated mineralised remains such as teeth, scales and fin spines. Here, we use a variation of the previously defined Skeletal Completeness Metric (SCM) to assess and quantify the quality of the Palaeozoic chondrichthyan fossil record. This metric calculates how complete the skeletons of individuals are compared to their theoretical complete skeleton. Information from museum collection visits and literature were compiled into a database of 838 chondrichthyan species from the Ordovician to the end-Permian. Chondrichthyan completeness peaks in the Lower Devonian, late Mississippian and middle Pennsylvanian as well as early and middle Permian, with lowest scores throughout the Silurian and in the early Mississippian. Chondrichthyans show a significantly lower completeness distribution than any published tetrapod group. However, completeness increases significantly when isolated material such as teeth, scales and fin spines are excluded and is similar in range to that of pelycosaurs and parareptiles. Completeness of chondrichthyans from freshwater deposits is higher in the Lower Devonian, around the Devonian-Carboniferous boundary and again throughout the Permian while marine environments yield more complete skeletons throughout the Carboniferous. Our assessment of completeness reveals only weak spatial biases influencing the Palaeozoic chondrichthyan fossil record while environmental and temporal biases are much stronger.

## The cono-dos and cono-don'ts of phosphatic microfossil preparation and chemical characterisation

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Scanning electron microscope (SEM) based analysis of fossils allows us to unlock ultrastructural information about their skeletal tissues, but sample preparation of the biominerals forming their skeletons requires time, patience, and knowledge. SEM and associated analytical methods allow the observation of internal microstructure, shedding light on function, growth, and chemistry. Sample preparation is the process by which material is fixed within a medium (e.g. epoxy resin), a transect created and surface defects removed. This step is arguably the most important in any SEM based analysis, allowing for the acquisition of reliable, high quality data sets. Surfaces with topography will both induce charging effects and also compromise the reliability of data acquired. This is particularly apparent when utilising energy dispersive x-ray spectrometry (EDX). Techniques from material science are continuously adapted to palaeontological applications, in particular with respect to calcareous and phosphatic microfossils. This case study focuses on conodonts, the tooth-like remains of marine vertebrate group ranging from the late Cambrian to Late Triassic. They have been chosen as a model due to the abundance of material, complexity of internal tissues and previous work focused histological features. With these phosphatic microfossils, we attempt to outline the process of sample preparation and provide information on how to avoid and overcome common pitfalls. Once addressed we quantify the extent of the inaccuracies in the acquisition of EDX data both due to issues with sample preparation and user defined parameters.

# Investigating Deccan-induced environmental changes, prior to the K/Pg mass extinction

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~66 million years ago, the Earth experienced two major events – the Chicxulub impact and the eruption of the Deccan Traps Large Igneous Province. Whereas the former is widely implicated as the main driver of the Cretaceous-Paleogene (K/Pg) mass extinction, the exact environmental impacts of the preceding Deccan trap volcanism requires further research. My MScR project will use paired planktic and benthic trace element (B/Ca, Mg/Ca) and stable isotope ( $\delta^{11}B$ ,  $\delta^{13}C$ ),  $\delta^{13}C$ ) analyses to quantify the changes in climate and carbonate chemistry during the Late Maastrichtian Warming Event (LMWE) at ODP 1262. I will investigate: (a) whether ocean acidification occurred during the Late Maastrichtian Warming Event (LMWE), (b) the magnitude of temperature changes that occurred during the latest Maastrichtian, and (c) if similar trends in  $\delta^{18}$ O and  $\delta^{13}$ C occurred in both the surface and deep ocean during the Late Maastrichtian Warming Event (LMWE) in ODP 1262 samples. I anticipate: (1) a positive correlation when the new B/Ca and  $\delta^{11}$ B data are compared to established % CaCO<sub>3</sub> records, but a negative correlation when compared to established Fe intensity records at ODP 1262. (2) a positive correlation between the new Mg/Ca trace element data and the established  $\delta$ 180<sub>Benthic</sub> record at ODP 1262. (3) a positive correlation between both the planktic and benthic  $\delta^{18}$ O and  $\delta^{13}$ C records at ODP 1262. The results of my research project will contribute to improving our understanding of the environmental response to Deccan volcanism, prior to the K/Pg mass extinction.

# The 'apatite' of conodonts: a multivariate reconstruction of the dietary range and specialisms of the stem vertebrates

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Conodonts have one of the most complete and abundant fossil records of any group and their evolutionary significance as early vertebrates is well-recognised. However, despite exhibiting a wide diversity of 'tooth' morphologies, hypothesised as adaptations to different diets, their trophic ecology is poorly understood, and the role of conodonts in deep time ecosystems remains largely unconstrained. While some studies have suggested a broadly carnivorous diet, investigation has been limited to a handful of species and specimens by time-consuming and costly methods. We provide the first large scale analysis of conodont dietary ecology, using multivariate analyses of dental topographic metrics known to correlate with dietary composition across vertebrate and invertebrate taxa, allowing informative comparisons between non-homologous food processing structures. To make inferences about conodont diet, we analysed the food processing P1 elements of 48 species

representative of the taxonomic and temporal range of conodonts. In a combined analysis with vertebrate and invertebrate feeding elements we tested the hypothesis that conodont element morphologies reflect functional adaptations to dietary specialisms. Our analysis demonstrates that conodonts were carnivores and provides strong support for the hypothesis that element morphology is strongly linked to dietary adaptation – ranging from soft-prey carnivory to specialists processing food with a tougher chitinous exoskeleton (comparable to insectivory in terrestrial vertebrates). Using this time and cost-effective approach to reconstruct conodont trophic guilds, we can begin to shed light on the roles conodonts played as important components of ancient ecosystems, and how this changed through their 300 million year fossil record.

## How to identify a senile dinosaur? The importance of age-related diseases for the age determination in non-avian dinosaurs

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Senile non-avian dinosaurs are extremely rare in the fossil record. The study presents a Late Cretaceous duck-billed dinosaur exhibiting advanced age in its anatomy, bone microstructure, and non-traumatic bone pathology. The specimen, aside from its large size, shows the external fundamental system (closely spaced growth marks) in the external cortex of its bones and closure of transcortical channels indicating growth cessation, nearly complete remodelling of bone tissue (evidence of long time passing since skeletal maturity), and primary calcium pyrophosphate deposition disease (CPPD) on its vertebrae and foot. CPPD is an age-related pathology exceptionally rare in young animals, recognized here for the first time in a non-avian dinosaur. The presence of such pathology, clearly indicating senile age of the individual, allow us to verify the features previously used as indicators of advanced ontogenetical age in non-avian dinosaurs. This research project is supported by the National Science Centre, Poland, grant no. 2019/32/C/NZ4/00150.

## An unexpected biodiversity of bryophyte macrofossils in the Early Miocene of the Bílina Mine (Most Basin, Bohemian Massif)

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The macrofossil record of bryophytes is significantly sparser than that of other terrestrial plants, however there is a growing body of literature that recognises the importance of this group in completing a comprehensive overview of fossil plant assemblages. The purpose

of this study was to obtain the data which will help achieve that in the Early Miocene locality Bílina. Until this day, a total number of seven macroscopic bryophyte remains were found and deposited at the National Museum in Prague. Data were collected by a detailed observation of both anatomical and morphological features (such as branching, type and position of leaves, presence of stem leaves etc.) and their comparison with modern representatives. Six samples were classified into five different recent taxa. The last one was placed in the fossil genus *Muscites*, which stands outside the recent system. This shows a high level of bryophyte diversity in fossil history, opens a question of the group's assumed low fossilization potential and changes the view of evolution of this group.

## Historical material of cf. *Thoracosaurus* from the Maastrichtian of Denmark provides new insight into the K–Pg distribution of Crocodylia

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Crocodylia is one of the distinctive groups that survived the K-Pg mass extinction event. New material from Late Cretaceous-early Palaeogene deposits is therefore important to understanding shifts in crocodylian distribution and ecology. This paper describes and assesses a fragmentary mandible of a marine crocodylian from the lower Maastrichtian (Late Cretaceous) of Møns Klint (Denmark). Based on features including narrow rami and curved, slender, and conical teeth, the specimen is referred to cf. Thoracosaurus (Gavialoidea). Although collected in 1968, the material has not yet been described. However, given its importance to crocodylian palaeontology, the specimen warrants further attention. This research aims to systematically present the palaeobiogeographical significance of the fossil material, assessed using digital palaeolatitudinal reconstruction. The Møns Klint specimen represents the oldest gavialoid record in Europe, with all other material deriving from upper Maastrichtian and Danian deposits. This indicates that Gavialoidea were present in the European Chalk Sea throughout the Maastrichtian, rather than being a latest Maastrichtian arrival. Furthermore, the Møns Klint 'Thoracosaurus' represents one of the only lower Maastrichtian gavialoids, the other two being from Mississippi and New Jersey (United States of America). The specimen thus extends the palaeogeographical range of lower Maastrichtian gavialoids across the proto-Atlantic and by ~7° in palaeolatitude. This reveals a transatlantic distribution of Gavialoidea dating back to the earliest Maastrichtian, providing further evidence for distributional communication between vertebrate faunas of the Western Interior Seaway and of the Chalk Sea. These factors therefore make the Møns Klint Thoracosaurus specimen particularly valuable to understanding distributional patterns of K-Pg crocodylians.

# Oceanographic and biotic changes in Australia during the Oceanic Anoxic Event 2

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My research examines marine anoxia in a 'super-hot-house' Cretaceous world - a time of polar forests and atmospheric CO<sub>2</sub> concentrations of >2000ppm. At peak warmth (~93 Ma), many ocean basins experienced a period of low, or even non-existent, oxygen. This ~500,000 year event is called Oceanic Anoxic Event 2 (OAE 2). It represents one of several major upheavals in the global carbon cycle, with huge changes to ocean chemistry and increased biotic turnover. Despite being one of the largest events of its kind, data on OAE 2 from the Southern Hemisphere are lacking, making a true global understanding of the event impossible. In this project, I identify the OAE 2 in marine sediments from offshore SW Australia (palaeolatitude ~62°S) using stable bulk C and O isotopes. These data demonstrate the global extent of low oxygen ocean basins and indicate short-term relative sea surface temperature changes over OAE 2 itself. Changing Nd and Sr isotope values over OAE 2 indicate shifts in sediment provenance - highlighting a change in weathering or sediment source/transport in terrestrial environments during this period of oceanic upheaval. Ongoing work examines the biotic response to changes in climate and ocean chemistry, using dinoflagellate cyst (resting cysts of marine phytoplankton), pollen and spore assemblages to track oceanic productivity and terrestrial vegetation change, respectively. Combined, these proxies will determine the extent and extremity of climate change in the mid-Cretaceous over OAE 2, and provide insights into marine and terrestrial biotic responses to high global temperatures of the past.

### The evolution of mandible morphology in the paravian bird lineage

#### Stephanie Woodgate<sup>1,2</sup>, Emily Rayfield<sup>2</sup>, Philip Donoghue<sup>2</sup>, William Deakin<sup>2</sup>

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The incredible diversity of extant birds and the extreme anatomical transitions of their paravian ancestors, underwent to achieve powered flight, makes them an excellent candidate lineage to analyse the constraints on the evolution of biological shapes. Here we investigate mandibular morphological evolution in the paravian bird lineage according to Seilacher's theory of morphodynamism. Elliptical Fourier Analysis is used to quantify mandible outline shapes and generate a morphospace of theoretical (unrealised) morphologies, from which constraints are investigated. 'Biological function', modelled using Finite Element Analysis, reveals a strong trade-off between mandible strength and rotational efficiency, with taxa showing little convergence on functional optima (identified using Pareto Optimality techniques). Assessing 'phylogenetic tradition' via ancestral state reconstruction shows a strong yet mostly non-directional signal. While flight and miniaturisation allowed new morphologies to be explored, overall, 'effective

environment' enacts a weak constraint on shape. Preliminary investigation into 'morphogenetic fabrication' shows a largely unconstrained ontogenetic path through morphospace. Behavioural transitions including singing and cranial kinesis are likely important in explaining the weak convergence on functional optima and ecological niche, showing the importance of examining both behavioural and anatomical shifts in macroevolutionary studies. The 'form-function' relationship of extant bird jaws is controversial in current literature; our work is significant in elucidating this relationship over a broad evolutionary timescale, and extending study of this relationship to the mandible, which is often excluded from studies of dinosaur-bird skull shape and biomechanics.

### Micromorphology of sediments from Lida Ajer and Ngalau Gupin cave, West Sumatra

### <u>Holly Smith</u><sup>1</sup>, Mike Morley<sup>2</sup>, Conor Mcadams<sup>3</sup>, Jahdi Zaim<sup>4</sup>, Yan Rizal<sup>4</sup>, Aswan<sup>4</sup>, Mika Puspaningrum<sup>4</sup>, Agus Trihascaryo<sup>4</sup>, Gilbert Price<sup>5</sup>, Julien Louys<sup>1</sup>

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This study is the first sedimentological analysis of the fossil-bearing cave deposits in Lida Ajer and Ngalau Gupin caves in the Padang Highlands of western Sumatra, Indonesia. Lida Ajer cave is best known for yielding fossil evidence that *Homo sapiens* arrived in Southeast Asia 20,000 years earlier than previously considered. Ngalau Gupin cave in west Sumatra recently produced the first record of hippopotamid Hexaprotodon on the island; representing the only globally extinct taxon in deposits from Sumatra. Thus, the provenience of the remains from these cave sites is a critical question regarding the archaeological and natural history of the region. The cave sediments were studied using the soil science of micromorphology coupled with geochemical analyses to extract taphonomic data and determine the timing and order of events leading to these deposits. Results show the sediments in Ngalau Gupin to have been derived from the interior of the cave where the matrix has become partially phosphatized and derived from bat habitation. The sediments in Lida Ajer have been subjected to a suite of natural sedimentation processes ranging from water action to carnivore occupation. Revealing these previously unidentified taphonomic agents using this method generates a more complete model of Pleistocene sedimentation in the cave sites. These geoarchaeological observations can be used to test hypotheses about the integrity of incorporated vertebrate remains and to aid in local palaeoenvironmental reconstructions. Our robust reconstruction of complex sedimentary cave evolution provides clear insights into the environmental background in west Sumatra across an important transition in human history.

### Digital Reconstruction of the brain and inner ear of Leptictis haydeni

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Leptictis is an extinct mammalian genus that remains enigmatic to this day due to the fact that its relationship to crown-group placental mammals is still highly contentious. It lived during the Eocene/Oligocene along with many crown-group mammals that survived until today. Not much is known about the neurosensory system of *Leptictis* in general, let alone whether the reason for its extinction is related to its neurosensory system. The last in-depth description of the brain of Leptictis dates back to the 1980s, before the use of modern reconstruction techniques became mainstream. Nowadays, Computed Tomography (CT) and 3D image segmentation software have become a widely available tool for palaeontologists, opening the door for detailed descriptions and volumetric measurements of parts of the brain, which was not easily done on natural endocasts. This study aims to describe and reconstruct the brain and inner ear of *Leptictis haydeni* and to quantify the condition and volume of Leptictis' cranial features. The study will make use of CT scanning and 3D image segmentation software to create a virtual endocast of the cranium of the fossil specimen. Volumetric calculations of key brain structures will be made and a range of equations will be used to determine palaeobiological metrics such as the encephalization quotient, locomotor agility scores and hearing frequency range. The outcomes of these calculations will be used to compare *Leptictis* to contemporaneous mammals.

### **Lightning Talks**

### A well-developed callus in an iguanodontian femur from England

#### Filippo Bertozzo<sup>1</sup>, Alastair Ruffell<sup>1</sup>, Eileen Murphy<sup>1</sup>

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Our understanding of the palaeobiology of ornithopod dinosaurs has increased in recent years due to the discovery of new specimens and development of novel analytical techniques. However, information regarding the physical response to injuries as well as overall pathological frequencies are still limited for non-hadrosaurid iguanodontians compared to hadrosaurids. Here, we analyse a large and well-developed overgrowth on the laterodistal margin in NHMUK PV R6609, a right femur from a mid-sized ornithopod, referred to as Iguanodontia indet., discovered in southern England. The specimen shows anatomical affinities with *Mantellisaurus atherfieldensis*, and *Iguanodon bernissartensis*. The expanded overgrowth was first scanned with a CT-scan, and then sectioned at three positions (for palaeohistology), corresponding to: (i) the unaffected area, (ii) the rising margin of the overgrowth, and (iii) the central point of the domed area. The overgrowth is

formed by a highly vascularized primary bone, with radially oriented vascular canals at 90° in relation to the lining of the cortex, differing from the woven parallel fibered complex of the unaffected cortex. Based on these features, the overgrowth corresponds to a healing callus that presumably originated as a consequence of a traumatic impact to the individual's thigh. No fracture lines were detected in the CT-scans, thereby suggesting that the impact occurred several months before death and that the bone was almost fully healed. A peculiar endosteal bone tissue is visible in the medullary cavity that resembles medullary bone. The trauma would have had a debilitating effect on the locomotion of the individual.

## The palaeoecology of the Wenlock (Silurian) arthropods of Buttington Quarry, Wales

#### Harry Blake<sup>1</sup>, David Loydell<sup>1</sup>

#### <sup>1</sup>University of Portsmouth, United Kingdom

The Silurian period was long considered a time of prolonged environmental stability with consistently high sea levels. Since the 1990s, however, new data have emerged suggesting the presence of four major positive carbon isotope excursions. One of these excursions, the Early Sheinwoodian Carbon Isotope Excursion (ESCIE), can be seen in the Wenlock Series of Buttington Quarry. Prior work at Buttington Quarry has focused on graptolites and palynomorphs and their reaction to environmental changes. This new study focuses on the arthropod fossils, which have received little attention. Buttington Quarry extends a chance to study a rare eurypterid from deeper waters and aechminid ostracods, providing an opportunity to investigate their poorly understood ecology. The abundance of trilobite fossils and excellent biostratigraphical resolution of the Buttington Quarry succession allows the controls on their distribution to be investigated. 1914 specimens of arthropod have been identified and catalogued, comprising 1659 ostracods, 254 trilobites and one eurypterid. Important examples have been imaged in an SEM. Construction of a range chart of the arthropods, which also shows abundances, has then allowed for correlation with isotope, trace fossil and biostratigraphical data from Loydell & Large (2019). It appears that bottom water oxygenation was the primary control on trilobite distribution. Eurypterids are very rare within the Buttington Quarry material, with the only confidently identifiable specimen being assigned to the family Carcinosomatidae, based upon its morphology. Previous studies of eurypterid associations suggest carcinosomatid eurypterids usually occur in open marine/brackish waters.

## Reassessment of a toothed pterosaur from the Early Cretaceous Romualdo formation of Brazil

#### Hebert Campos<sup>2</sup>, <u>Michael Sprague<sup>1</sup></u>

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The toothed pterosaur Cearadactylus? ligabuei from the Early Cretaceous (Albian) Romualdo formation of the Araripe Basin of Brazil is based on a single specimen (MSNVE-21530) consisting of a rostrum. This specimen was tentatively referred to the genus Cearadactylus when it was described by Dalla Vecchia in 1993. After reevaluating this partial skull, we conclude that C. ligabuei does not represent a valid taxon. A review of taxonomic characters revealed that Cearadactylus? ligabuei is a junior synonym of Cearadactylus atrox, supported by eight diagnostic autapomorphies. Further, seeing as the holotype of C. atrox was lost in 2018, we propose designating this specimen (MSNVE-21530) as the neotype for the species. In addition to synonymizing C. ligabuei with C. atrox, the species Camposipterus sedgwickii from the Cambridge Greensand of England and Ludodactylus sibbicki from the Crato formation share important synapomorphies with the genus Cearadactylus including an upturned incline of the rostrum and a rounded rostral profile, and we propose merging these species into Cearadactylus colorhinus comb. nov. The redescription of a second specimen of *Cearadactylus atrox* indicates that crestless anhanguerian pterosaurs are less frequent in the fossil record and constitute the minority of the toothed pterosaur taxa from the Romualdo assemblage. Pterosaurs lacking a bony premaxillary crest are considerably scarcer in the Romualdo formation than crested anhanguerians. Although the Romualdo assemblage is host to a rich diversity of pterosaur species, this study indicates a more restricted number of crestless taxa than previously thought.

### Discretising continuous morphological phylogenetic character data

#### James Chester<sup>1</sup>, Chris Knight<sup>1</sup>, Russell Garwood<sup>1</sup>, Robert Sansom<sup>1</sup>

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Morphological phylogenetics use two types of phenotypic character – discrete and continuous. Discrete characters are more common in the literature, due to a combination of philosophical beliefs about their improved usefulness in conveying phylogenetic signal, and their ease of use. Continuous measurements are routinely discretised before analysis, however, there exists no consensus as to best practice for doing so. Here we investigate the effect of different approaches to discretisation of continuous characters. Continuous morphological data from 4 empirical studies were discretised at multiple levels using a maximum gap coding approach and evaluated in terms of their homoplasy relative to molecular trees. Levels of homoplasy were found to be generally higher and more variable across all levels of discretisation when compared to raw continuous data. Raw continuous characters were also compared to original categorical and binary discrete characters from 2 empirical datasets, and were found to exhibit higher homoplasy relative to the originally

discrete characters. As such, our results indicate that discretisation of continuous characters can lead to the introduction of additional homoplasy in phylogenetic analyses, and that the choice of discretisation method can impact phylogenetic estimation.

## How can Holocene benthic foraminifera be used for modern environment characterization?

#### Kamila Faizieva<sup>1</sup>, Guillaume Arnouts<sup>1</sup>, Eric Armynot du Châtelet<sup>1</sup>

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Benthic foraminifera, marine and brackish unicellular eukaryotes, are considered as promising tools for environmental monitoring of modern transitional areas, due to their short life cycle, large abundance, sampling and analysis simplicity. As a part of the Interreg North-West Europe, SURICATES (Sediment Uses as Resources In Circular And Territorial EconomieS) project has the goal of studying and assessing the bottom sediment quality in the port of Calais (France, Hauts-de-France region). Foraminifera are used to estimate the sediments quality status before their reuse as coastal flood protection or replenishment of beaches undergoing a high erosion rate. Calais harbor presents an industrial dock, a leisure basin, and busy boat traffic point causing local ecosystem pressure. Here we present a provisional study of living foraminifera (Rose Bengal stained) from sediment samples collected in the port in March, 2019. Amongst the 30 species recorded from the area, three key species were identified as abundant and opportunistic: Haynesina germanica, Cribroelphidium excavatum and Ammonia tepida. Their spatial distribution showed a dependence on both abiotic and biotic factors: local hydrodynamic conditions, substrate characteristics, organic matter quantity. Species richness is reduced in the areas with the highest level of arsenic (As). Note that Cribroelphidium excavatum and C. magellanicum showed test abnormalities: aberrant chamber shape and size, abnormal additional chambers. They could be considered as a consequence of local disturbance caused by anthropogenic impact. Preliminary results have shown that Holocene foraminifera have potential for modern environment characterization.

### Global scale marine diversity dynamics through the Early Cretaceous and the magnitude of the Aptian extinction event

#### Przemyslaw Gruszka<sup>1</sup>

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Early Cretaceous (145–100.5 Ma) marine ecosystems were strongly influenced by a series of significant environmental fluctuations. The Aptian extinction event is widely held to have occurred during that time. However, the importance, magnitude and causes of this event remain a subject of considerable debate. Therefore, this research aims to assess the global marine diversity changes in the Early Cretaceous and determine the physical causes influencing them. Such an approach will show the Aptian event in the necessary context of

the whole epoch. Fossil occurrence data has been obtained from the Paleobiology Database. Taxonomic richness, extinction and origination rates have been calculated from time-binned fossil data using various measures to get reliable results. Obtained diversity data will be correlated with changes in eustatic sea level, water oxygenation and sea surface temperature using statistical tests. Preliminary results show a minor extinction event in the late Aptian and a possible one in the Valanginian. There was also a significant diversity drop in the Albian that was not induced by an extinction event. Further analysis will possibly show more prominent extinctions among specific fossil groups and will reveal their physical triggers. As the oceans in the Aptian experienced similar trends to presentday oceans in terms of sea-level rise, deoxygenation and water temperature increase, it is significant to understand the causes and real magnitude of the Aptian extinction, regardless of its size, to preserve current biodiversity and aid our knowledge about extinction events.

### The functional adaptation of the turtle jaw

#### Eloise Hunt<sup>1,2</sup>, William Deakin<sup>3</sup>, Emily Rayfield<sup>3</sup>, Philip Donoghue<sup>3</sup>

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A key goal of life science is to understand the drivers of morphological variation. This study aims to investigate whether function constrains turtle jaw morphology. Elliptical Fourier Analysis (EFA) was used to characterise the 2D lower jaw shape of 97 species of extant and fossil turtles. This empirical data was used to generate theoretical lateral and dorsal mandible morphologies. Our comparative functional testing included the estimation of jaw closure speed, resistance to stress, and hydrodynamic efficiency of these theoretical jaw morphologies which were plotted as three performance landscapes. These performance landscapes were all combined using Pareto ranking; the resultant Pareto adaptive landscape reveals the zone of morphospace where the theoretical jaw shapes lie with the most optimal compromise between the three functional constraints. Additional controls on form were investigated using our empirical jaw dataset combined with ecological traits and phylogenetic relationships. Our results suggest that the shape of turtle jaws are constrained by a trade-off between speed, strength and hydrodynamic efficiency. Our empirical jaws plot in a region of morphospace associated with optimum hydrodynamics, but suboptimal stress dissipation and jaw speed. This research also provides an example of a pipeline which can be used to disentangle the complex relationship between environment, form, and function.

## Did changes in body size allow Sauropsida to survive the Permian–Triassic mass extinction event?

#### Adhiyan Jeevathol<sup>1</sup>, Xin Yi<sup>1</sup>, Krisztian Horvath<sup>1</sup>, Philip Mannion<sup>1</sup>, Sebastian Groh<sup>1</sup>, Paul Upchurch<sup>1</sup>

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With approximately 80–96% of all species lost, the Permian–Triassic mass extinction (PTME) was the largest loss of life on record. Analytical work on survivorship across the PTME has mainly focused on marine invertebrates, despite vertebrates also having suffered substantial losses. Among the vertebrate clades that survived were the Sauropsida, which gave rise to all reptiles. During the Permian and Triassic, sauropsids already occupied a wide array of ecological niches and showed a high morphological disparity. This included a substantial range of body sizes, from the 7 cm long *Phaanthosaurus* to the >2 metre long Pareiasaurus. Studies that have looked at the change in the body size of marine organisms through time show significant reductions before and after the PTME. However, no equivalent study has evaluated such patterns in Sauropsida during this interval. Using phylogenetic generalised least squares, we tested whether there is an association between body size and the Sauropsida lineages that survived into the Triassic. Preliminary results, focusing mostly on parareptiles, indicate such an association is present and that this includes a strong phylogenetic effect. Procolophonids, the only parareptile lineage that survived the PTME, had smaller body sizes relative to other parareptiles, which might be the reason they survived. To confirm whether body size was really a determinative factor in survival, more taxa from Eureptillia will need to be included. The results from this study could prove useful for predicting the responses of different body size groupings of reptiles to anthropogenic climate change.

# The palynology of the Canna Lava formation (Paleocene) on the Isle of Canna and Sanday, Scotland

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The Isle of Canna and Sanday, north west Scotland, exposes important examples of volcaniclastic intercalations amid flows of basalt lava deposited during the Paleocene, approximately 60Ma. The Canna Lava formation was first described from exposures on the islands by Geikie (1897); however, the palynological contents of its sedimentary lenses have remained unstudied until now on Canna itself. As the majority of the exposed geology on Canna and Sanday is basaltic, these deposits offer the only fossil insights to the Paleogene flora and environment here. This study focuses on the smaller lenses of volcaniclastic material deposited by a river flooding across a lava field, with sediment collecting in small pools. Systematic sampling of these beds revealed that palynomorphs are present, which indicate that the prominent vegetation was ferns and other plants adapted to flood plains and frequently disturbed environments. Distributions of several palynomorphs across the localities compare with the palynofacies described by Jolley (2009), from exposures of the Canna Lava formation on Skye. This suggests a warm temperate to tropical climate on Canna, also observed across the British Paleocene Igneous Province prior to the PETM.

### A novel quantitative method to landmark complex fossils

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Landmarking techniques are useful and accurate tools for quantifiably comparing the shapes of fossil specimens. However, it is difficult to use them effectively on complex, rounded fossils such as brachiopods, bivalves and endocasts because they lack homologous points which can be used as accurate landmark positions. We propose an accessible methodology to reliably landmark fossil specimens, such as those above. The methodology utilises the free software Blender and employs the vertices of a 'shrinkwrapped' UV Sphere on each model as reliable semi-landmark coordinates. This methodology was validated using principal component analysis (PCA) on landmark data of brachiopods and bivalves. To show the applications of this methodology, author bias in constructing endocasts was investigated using the Early Triassic cynodont Thrinaxodon liohornus, an early relative of mammals, and extant rodent endocasts constructed by different authors. PCA results successfully distinguished between morphologies of brachiopod and bivalve specimens but were inconsistent in grouping specimens based on genera. The PCA results also show significant differences in morphology in *Thrinaxodon* endocasts, suggesting a high amount of author bias when constructing endocasts. Future research into author bias will illuminate its extent and how it can be reduced effectively. This methodology achieves its aims of reliability and accessibility but is limited in its applications by its inability to landmark finely detailed structures on specimens and its inclusion of structures which are usually ignored present in some specimens but not in others. Therefore, this methodology may be best used in conjunction with traditional landmarking techniques.

# Extrapolating ammonite hemisuture analysis from partial (lateral) suture components

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Ammonite sutures have been measured for their fractal dimensions based on hemisutures (half-suture, from venter to umbilicus) that are visible on some shell surfaces. Due to the pandemic and subsequent lack of access to specimens in institutional collections, measuring full hemisutures has not been possible. Here, we propose a revised fractal measurement method requiring only the lateral lobe and saddle (LLS), the part of a suture not distorted by shell curvature near when viewed in profile. Unlike the traditional Richardson fractal step method, which requires entire hemisutures, our approach uses measurements taken from photographs of sutures, as well as lateral lobe-saddle (LLS) data taken from the ammonite literature. The LLS method produces fractal-dimension results that differ from those calculated using hemisutures. To circumvent this issue, one must convert LLS-method fractal dimensions to those of the Richardson (hemisuture) method.

The factors needed to perform these conversions are specific to ammonite genera. We provide these factors for some common ammonite taxa. The original purpose of the LLS method was to circumvent loss of access to specimens during the pandemic by enabling use of photographic data for ammonites. However, results of the LLS method are independent of shell size, and can be used to evaluate ontogenetic trends in fractal complexity from single whole conches. Such conversion values thus may also have implications for unresolved taxonomic questions. Therefore, the LLS method will undoubtedly still be relevant beyond COVID.

## Craniofacial and vertebral neurovascular complexes of *Tethysaurus nopcsai* (Mosasauridae, Squamata) from the Upper Cretaceous of Morocco

#### Kyle Marson<sup>1</sup>

#### <sup>1</sup>University of Portsmouth, United Kingdom

Mosasaurs were secondarily aquatic reptiles closely related to snakes and lizards from the Upper Cretaceous. They developed paddle-like limbs, streamline bodies and hydroceral tails. Recent studies have investigated the craniofacial neurovascular complexes of derived taxa from the Campanian and Maastrichtian. However, data is lacking in pre-Campanian taxa and furthermore post-cranial anatomy. Here, we investigate the neurovascular complexes in the craniofacial and vertebral anatomy of several specimens of *Tethysaurus* nopcsai, a basal mosasaur from the lower to middle Turonian of Morocco. Micro CT scanning will be performed on an isolated maxilla and isolated dentary. A new systemic technique, foramina mapping, was developed and utilised to correlate patterns of craniofacial neurovascular foramina of mosasaurs and other marine reptiles. Thin-section osteohistological observations of Tethysaurus vertebrae are also utilised. We conclude that Tethysaurus exhibited anterior and mid maxillary concentrations of neurovascular foramina and likely utilised them for ambush predation. Comparison with other russellosaurines indicated the development of an increased premaxillary concentration of neurovascular foramina in derived subfamilies. Additionally, data suggests a potential of dichotomy in the craniofacial neurovascular foramina concentrations in Mosasauridae. Observations of the neurocanal displayed a unique structure projecting from the floor of the canal suggest an adaptation for spinal cord stability. These results improve implications of neurovascular complexes in basal mosasaurids, including locomotory factors in terms of the vertebral column and the role of craniofacial neurovascular foramina in mosasaur palaeoecology.

# The effects of latitude on Eocene seasonality and on the growth rates of *Nummulites* from Tanzania and South England

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The Eocene was a dynamic time of environmental and climatic change, with ocean temperatures up to 9°C warmer than today. There are numerous geochemical temperature proxy records from open ocean sites, however, relatively few records exist from shallow water sites. Larger benthic foraminifera (LBF) are abundant in the Eocene, inhabit shallow marine platform environments and form calcareous shells in equilibrium with the sea water. Additionally, their large size (up to 15cm) and longevity means they have the potential for not only recording temperature, but variations in temperature through their lifespan. Here we present magnesium-calcium ratios obtained by LA-ICPMS of reticulate Nummulites specimens from the upper Eocene of Kilwa, Tanzania and specimens of Nummulites prestwichianus from the Isle of Wight and Bracklesham Bay, United Kingdom. The temperature variation shown by this data allows for a latitudinal comparison of Eocene seasonality. The seasonal cycles will also enable growth rates to be determined in both an optimum environment (Tanzania) and at the edge of their geographic range (United Kingdom). This research may facilitate predictions of how our own seasons and temperatures may vary with future climate change, on a more regional scale.

## The fourth trochanter across early archosauriforms: morphological decoupling between locomotor habit and body size influence

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The fourth trochanter is an attachment site for the caudofemoral musculature that is located on the posterior side of archosauriform femora. Its morphology is commonly used as a synapomorphy for various archosauriform clades such as its pendant shape in some ornithischian dinosaurs. The fourth trochanter presumably was subjected to strong mechanical loading during the retractation of the hind limb toward the tail, which played an important role in locomotion and balance. Herein, we studied 72 Triassic archosauriform femora using a 3D geometric morphometrics approach in order to better understand how these two highly disparate factors impacted femoral morphology, including the fourth trochanter. We found that morphological variation of the fourth trochanter was decoupled in two independent components: 1) a more distally located fourth trochanter with a

rounder medial ridge in the largest archosauriforms, which was strongly convergent between pseudosuchians (crocodile lineage) and avemetatarsalians (dinosaur lineage) and implied similar mechanical loading; 2) an asymmetric fourth trochanter in bipedal archosauriforms with a steeper slope on the distal ridge than on the proximal ridge, which had a strong phylogenetic signal. In addition, we also uncovered that the morphological distinction between bipedal and quadrupedal femoral morphology increased among the largest Triassic archosauriforms. Our results provide new insights about the evolutionary history of the fourth trochanter among early diverging archosauriforms. These insights are essential in order to better understand the fourth trochanter's wide morphological diversification along the dinosaur radiation as well as the convergent origins of gigantism and secondary quadrupedality in ornithischian and saurischian dinosaurs.

Preliminary study on the organic petrology of graptolite fragments from the Ordovician-Silurian black shale of Tanjung Dendang formation, Langkawi, northwest Peninsular Malaysia

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The morphology and optical properties of the graptolite fragments from the Ordovician– Silurian graptolitic black shale of the Tanjung Dendang formation, Langkawi was examined using reflected white light microscopy. The mean random reflectance was measured on samples that were orientated perpendicular to the bedding. The graptolite fragments show a non-granular surface morphology and are mostly present in a long stipe-like, lath shape. Bitumen-like fragments and pyrite were also present in some samples. The mean random reflectance of non-granular graptolite in sections perpendicular to the bedding ranges from 1.73% to 2.70% with a standard deviation of 0.195% to 0.413%. Equivalent vitrinite reflectance ranges from 1.79% to 2.75% which suggest a mature to overmature stage in terms of hydrocarbon generation. No discernible reflectance pattern across the Hirnantian (Upper Ordovician) to Aeronian (Llandovery, Silurian) sequence can be identified which could be attributable to the slow accumulation of sediment over a long time period resulting in a relatively thin sequence. The present study acknowledges that the graptolite reflectance can be used to determine the thermal maturity of the sediment and distinguishes the Ordovician–Silurian Tanjung Dendang formation as a condensed section. The bovids from the Villafranchian locality of Karnazeika (Argolis, Southern Greece).

#### Panagiotis D. Sianis<sup>1</sup>

#### <sup>1</sup>University of Patras, Greece

The Early Pleistocene (Villafranchian) locality of Karnazeika is located in Argolis in the northeastern part of Peloponnese, Southern Greece. It consists of the southernmost Villafranchian locality of Greece. The locality was initially discovered during an excavating operation of a nearby mining facility and the fossiliferous rock was removed by miners in the form of grand blocks. The fossils were enclosed in red, fine grained sediment, along with debris of the surrounding rock, which filled a carstic cavity in a late Triassic limestone. The studied material was prepared with the purpose of conducting taxonomical, taphonomical and palaeoecological analyses of the site. Herein, the taxonomy of the bovids is discussed. For this purpose the morphology and metric characteristics of the material were examined and compared with other relevant taxa known from the bibliography. The bovid fauna was found to consist mainly of a small sized representative such as the Gazella, G. bouvrainae and the possible occurrence of one additional, mentioned currently as Gazella sp.. Additionally, a large part of the studied material was found to belong to the large Rupicaprini Gallogoral meneghinii. A relatively small sized form of Gazellospira torticornis has been recorded, as well as scarce dental material of a Caprini mentioned herein as Caprini gen. et sp. indet.. These taxa are typical of the middle Villafranchian of Greece (2.6-1.8 Ma).

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

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The major crown bird subclade Passeriformes (passerines) comprises >6,000 extant species, making up over half of extant avian diversity. However, despite constituting one of the most diverse clades of living vertebrates, limited work has targeted passerine comparative anatomy on a broad phylogenetic scale. As such, many components of the passerine skeleton are understudied, and existing morphological matrices tend to identify relatively few phylogenetically informative characters for each skeletal component. This has hindered interpretation of the passerine fossil record, as many isolated fossils of passerine bones remain unassigned beyond the ordinal or subordinal level. Here, we present a detailed analysis of the passerine fossil record. We identify morphological synapomorphies for major passerine subclades, sampling >100 taxa distributed across extant passerine diversity. We used both published characters and a substantial amount of

previously undescribed anatomical variation, resulting in >50 phylogenetically informative characters that were optimized across a robust published phylogenomic scaffold. Our results show high levels of homoplasy within the passerine carpometacarpus. Despite this, we identify numerous diagnostic character combinations for key passerine clades. The character matrix from this study will aid in future diagnoses of isolated passerine carpometacarpus fossils, enabling insight into when and where representatives of major passerine clades first appear in the fossil record. This work provides a starting point for large-scale comparative analyses of the passerine skeleton, and reveals a substantial degree of previously unrecognized morphological variation among Passeriformes.

### A new pterosaur tracksite from the Upper Jurassic of the Wiehengebirge, Northwestern Germany

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Over the past few decades, pterosaur tracks have been proven to be a valuable source of information on the ecology and terrestrial locomotion of these extinct flying reptiles. The most widely reported pterosaurian ichnogenus Pteraichnus Stokes 1957 frequently occurs in Upper Jurassic marginal marine deposits mainly from North America and Europe. Trackways consist of laterally facing, tridactyl manus and tetradactyl, roughly triangleshaped pes imprints. The manus tracks are typically positioned anterior to the pes tracks. The Wiehengebirge in Northwestern Germany has been known for regular discoveries of dinosaur tracks from Kimmeridgian tidal flat deposits for several decades. One such locality, producing isolated tracks sporadically, is the Störmer guarry north of the village Bergkirchen. In 2019, a sandstone slab with large pterosaur manus and pes hyporeliefs, referrable to the ichnogenus Pteraichnus, was reported to the LWL-Museum of Natural History Münster. Subsequent explorations yielded more finds. The manus tracks range from 20 to 60 mm in anteroposterior length. The pes imprints have anteroposterior lengths from 20 to 90 mm. The majority of tracks occur isolated. However, there is at least one trackway consisting of two manus-pes-sets. Further finds include potential swim tracks and beak scrapes. This is the second report of German pterosaur tracks and the first record of Pteraichnus from Germany. The discovery of at least a dozen tracks during only a few dedicated prospections as well as their remarkable size range show the potential of the Störmer quarry as another important pterosaur track locality.

### The evolution of functional disparity in the avian skull

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#### <sup>1</sup>University of Hull, United Kingdom

Bird beaks exhibit remarkably diversified morphology. Beak morphology is commonly associated with diet, but recent studies indicate this relationship is far from straightforward, and there are likely numerous factors influencing the shape of bird beaks. For example, within Aequorlitornithes ('core waterbirds'), the diet of many species is predominantly fish, but a range of beak morphologies and feeding behaviours are present. An often overlooked aspect in bird evolutionary studies is the role that cranial kinesis plays in ecological disparity. Cranial kinesis allows birds to move their upper beak relative to the skull. The mechanism behind cranial kinesis may align more closely with avian ecological correlates such as diet and feeding method, as it is not subject to the additional selective pressures that beak shape is (e.g. preening, heat transfer, vocalisation). Four-bar linkage models of the kinetic system were used to calculate kinematic transmission (KT), a ratio expressing how the system amplifies motion between the input and output links. We compared these values with data on diet and feeding method. Our results highlight the differences in KT across the group, illustrating the complex relationship between form and function and many-to-one mapping of structure and function. This gives an insight into which aspects of morphology are actually related to mechanics and diet. Investigation into the mechanical sensitivity of the system reveals KT is correlated with input link (quadrate) length. Comparison of mechanical sensitivity analysis with non-avian clades enables increased understanding of variation in biological linkage systems more broadly.

### New taxon *Nilssonia mirovanae sp. nov.* as indicator of water stress in the palaeoenvironment

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Plant cuticle is an important component in the palaeoenvironmental detection system. This study aims to analyse the relationship between micromorphological structures of plant cuticles and their environmental requirements. The newly described taxon *Nilssonia mirovanae sp. nov.* comes from the Late Cretaceous, Cenomanian of the Bohemian Cretaceous basin, from the best-exposed portion of the Peruc-Korycany formation, in the Pecínov quarry, 50 km west of Prague, Czech Republic. Data were collected using cuticle analysis, which consists of chemical maceration (hydrofluoric acid, Schulze's reagent and potassium hydroxide) and observation of the cuticular epidermal structures (light microscope and scanning electron microscope). This study is founded on a single specimen. Although preserved only as a fragment of a pinna, it clearly shows haplocheilic stomata, papillae arranged in rings around sunken stomata, wrinkles on the periclinal wall and thick cuticle, characteristic features indicating adaptation to drought among

gymnosperms. Micromorphology relates closely to palaeoenvironmental conditions, and the purpose of the study is to identify such relationships. Observation of special features, such as the above-mentioned xerophytic characters, allows us to reconstruct some palaeoecological conditions of the Late Cretaceous in the Bohemian Massif, and state with a fair degree of certainty that they included mesic to xeric environments.

### **Posters**

#### Silica replacement of rudist shells

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Evaluating shell preservation of Campanian rudists (Macgillavryia sp., Vaccinites sp., Torreites sanchezi) by investigating their microstructure and mineral composition, allows tackling the development of silica replacement as a crucial diagenetic feature prior to sclerochronological and geochemical analyses. Understanding the silicification spatial distribution allows those shell parts to be avoided during stable isotope sampling. Shell microstructure, mineralogy and silica distribution were investigated by SEM, EDX elemental mapping and Raman spectroscopy. Silicification occurred either as large crystal filling in primary pores or as partial replacement of the calcitic layer. This fine replacement often occurs together with preservation of the primary microstructure and delicate meshwork structures. Resulted from the differences in origin of mineral composition, microstructure, and crystal orientation of each part. There are two potential sources of silica, either siliceous organisms like sponges, or silica-rich diagenetic fluids percolating through the rocks. The first source would argue for an early, the second one for a late diagenetic silicification. The organic matrix in the shell played a role in the distribution and replacement of silica within the rudist shells arguing for an early diagenetic silicification. The organic matter decay locally changed the pH in pore water fluid by releasing CO2, and this is considered as a catalyst to dissolve the metastable minerals and create voids, which then act as a preferential zone for the replacement by silica. The fine substitution with synchronous preservation of initial shell microstructure implies a reaction front within the shell, without going through a "void" stage from dissolution.

### A comprehensive review of phylogenetic characters in early dinosaurs

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Many early dinosaurs have questionable phylogenetic positions. Such uncertainties on the dinosaur tree have been intensively discussed and several hypotheses came to light, with phylogenetic studies frequently reaching different results. An evaluation of the quality of the phylogenetic characters employed to study the rise of dinosaurs has been conducted through revising 129 publications, from 1970 to 2020. A list of 6827 "raw" phylogenetic characters describing the morphology of early dinosaurs was collected, based on the revision of 65 phylogenies from 1993 to 2020 that have been chosen among the total reviewed publications. The characters were collected from the phylogenies of early Archosauria (9.9%), Pseudosuchia (1.8%), Ornithodira (5.3%), Dinosauromorpha (6.2%), Dinosauriformes (4.2%), early dinosaurs (22.5%) Sauropodomorpha (25.3%), Theropoda (17.9%) and Ornithischia (6.8%). The sampled characters covered all the anatomical regions of the body, in which (38.2%) of those are related to the cranial skeleton, (14.4%) to the axial skeleton, (46.5%) to the appendicular skeleton, besides (0.9%) to the integumentary tissues. In general, most problematic characters are related to (1) definitions that are too anatomically ambiguous, (2) different terminology used to describe the same anatomical feature, (3) precise identification of the anatomical measurements, (4) inappropriate mixing of neomorphic and transformational characters, (5) mixing of quantitative and qualitative states, (6) unnecessary use of multistate, in cases which binary states would be more precise, (7) ratio characters differently used. A final list of ca. 1.000 unambiguous characters related to the appendicular skeleton is expected to compose a comprehensive dataset to back-up early dinosaurs' phylogenies.

# The effect of environmental change on the structural integrity of Southern Ocean and K/Pg boundary bivalves

#### Samuel Bulmer<sup>1</sup>, Leanne Melbourne<sup>1</sup>, Daniela Schmidt<sup>1</sup>

#### <sup>1</sup>University of Bristol, United Kingdom

As a major regulator of global climate, the Southern Ocean is extremely important to the planet. Not only that, but the Southern Ocean is a major complex ecosystem supporting over 9000 species from tiny, microscopic plankton to top predators like penguins and whales. However, climate change is a major threat to this ecosystem. Ocean warming is leading to increased predation pressures through poleward migration of invasive species, such as king crabs. While aragonite undersaturation events are particularly detrimental to calcifying organisms, such as bivalves, making it harder for these organisms to build their shells. Climate induced shell changes ultimately will affect structural integrity and the ability of organisms to withstand external pressures. Therefore, it is important to assess the impact of environmental change on bivalve morphology and subsequently how morphology affects structural integrity. This study takes a theoretical approach, by creating simple 3D ellipsoid shapes, to assess how parameters such as length, width, and height may alter under current climate change in modern Southern Ocean bivalves. Using Finite

Element Analysis, we assess how these morphological changes affect structural integrity to give us an insight into which morphologies may lead to a weakened structural integrity. Using this knowledge, we can then assess whether morphological changes under extreme environmental change such as at the K/Pg boundary were down to functional constraints. Ultimately this will give us an insight into which bivalve shapes are more susceptible to environmental change, potentially leading to predictions to which species may survive under future climate change.

### Quantifying avian post-cranial skeletal pneumaticity

#### Maria Grace Burton<sup>1</sup>, Roger B.J. Benson<sup>2</sup>, Daniel J. Field<sup>1</sup>

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Skeletal pneumaticity is defined as the presence of air-filled chambers within bones, a characteristic that is unique to birds (post-cranially) amongst extant vertebrates. Previous studies have attempted to characterise the extent of avian skeletal pneumatisation by categorically assessing the presence or absence of air in bones across the skeleton, allowing hypotheses to be articulated regarding associations between pneumatisation and avian ecology (e.g., a general reduction in aquatic diving taxa) and body size (i.e. a general increase in larger-bodied birds). Other studies have investigated links between pneumatisation and bone cortical thickness and mechanical properties. However, the true extent of skeletal pneumaticity, in terms of the fractional volume of a bone occupied by air, is yet to be investigated. Here, we investigate high-resolution 3D images of the internal structure of the long bones of a broad phylogenetic range of extant bird taxa that had been posthumously frozen. Components of a bone's volume occupied by bone, air, and marrow were segmented from high-resolution CT scans, and quantitative volumetric measurements of these models were taken. Our results show that there is considerable variation in the relative fraction of air within the internal cavities of avian long bones, even among closely related taxa. This work tests existing hypotheses surrounding the evolution of avian post-cranial pneumaticity using quantitative volumetric measurements for the first time, and may shed light on the extent to which bone cortical thickness may be predictive of the presence of pneumaticity in long bones.

# Investigating morphological variation and convergence in the passerine foot

#### Matthieu Chotard<sup>1</sup>, Elizabeth Steell<sup>2</sup>, Roger Benson<sup>3</sup>, Daniel Field<sup>2</sup>

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Passeriformes (passerine birds) is a major extant clade comprising >6,000 species distributed across 137 recognised family-level clades, representing more than half of extant avian species richness. Recent phylogenetic studies based on genomic data have shed light on the evolutionary origins and interrelationships of passerines. Nevertheless, a morphological study of crown Passeriformes is required to incorporate information from the fossil record into our understanding of passerine evolutionary history. At present, the tarsometatarsus (avian foot) has received more research attention in terms of characterising anatomical variation than any other passerine post-cranial skeletal element. The tarsometatarsus incorporates two regions exhibiting considerable anatomical variation: the proximally positioned hypotarsus and the trochleae that articulate with the pedal digits. Synapomorphies for major passerine subclades have previously been hypothesised for the hypotarsus, and both the hypotarsus and trochleae may exhibit homoplasy across passerine clades resulting from convergent behavioural specialisations such as climbing, which has evolved multiple times independently across Passeriformes. Here, we evaluated and illustrated published tarsometatarsus characters, highlighting morphological variation among major passerine clades, as well as investigating characters associated with climbing adaptations. We found extensive variation in the hypotarsus across Passeriformes, including intrafamilial variation. We also identify cases of homoplasy and its implications for previously published higher clade synapomorphies. This work is based on observations from high-resolution 3D models of tarsometatarsi from a large taxon sample. This study contributes to the ongoing effort to characterise passerine skeletal variation, facilitating future work that will enable fossil passerines to be incorporated into large-scale phylogenetic analyses.

## Locomotion in legged whales: modelling muscle moment arms in transitional archaeocetes

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The evolution of Cetacea from terrestrial ancestors to an obligate aquatic lifestyle is an iconic evolutionary transition. Among secondarily aquatic tetrapods, the aquatic specialisation of cetaceans is relatively well-preserved. This sequence offers the opportunity for rare insights into how locomotion evolved across the land-water transition. Among archaeocetes, significant variation in the anatomy of the hindlimb is clearly visible - with seemingly different functions in both terrestrial and aquatic locomotion in different archaeocete groups. To quantify any mechanical changes resulting from this variation, we

used 3D computational modelling to approximate pelvic muscle moment arms in a variety of archaeocete species. Muscle moment arms, the distance from the joint centre of rotation to the line of muscle action, can be used to provide insight into muscle function in extinct taxa. In this study, we used the extant phylogenetic bracket to produce hindlimb muscle reconstructions of the archaeocete species *Pakicetus attocki*, *Maiacetus inuus* and *Aegicetus gehennae* - a temporal span covering 15–20 million years of archaeocete evolution. To provide context and identify functional trends, equivalent models were produced for related extant mammal species. The extant species investigated were *Tragulus javanicus*, *Hippopotamus amphibius* and *Eubalaena glacialis*, selected for their range of locomotion strategies and reasonably close relatedness to the archaeocetes under investigation. The moment arms of equivalent muscles were subsequently compared between groups.

## The spatial distribution of spotted hyena (*Crocuta crocuta*) dens during the Middle and Upper Pleistocene of Britain

#### Jenna Amy Davenport<sup>1</sup>, Andrew Chamberlain<sup>1</sup>

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Pleistocene spotted hyenas are one of the most important taphonomic agents in the fossil record due to their bone accumulating behaviours, especially within cave localities. The primary aim of this study was to investigate the spatial distribution of spotted hyena dens in Britain during the Middle and Upper Pleistocene. Utilising museum catalogues and literature reports, caves possessing Pleistocene remains were identified and then divided into those containing spotted hyena remains and those where they were absent. The sites yielding spotted hyena remains were then collated and studied in detail to identify whether the localities were dens of spotted hyena. The results from this study showed that there was a random distribution of the eighty-five denning localities throughout Britain. However, within specific areas, a high proportion of the available caves were used, for example at Creswell Crags (Derbyshire/Nottinghamshire) and the Gower Peninsula (South Wales). Surprisingly, there was only one spotted hyena den site in Ireland and none in Scotland. The overall dates of occupation at these localities spanned long time periods, yet the accumulations often created a palimpsest within the caves and are frequently aggregated together within museum collections, meaning any information such as seasonal/year round occupation of the caves, or whether there was multiple occupation events, was lost. To conclude, this study is the first to identify the spatial distribution of Middle and Upper Pleistocene spotted hyena dens in Britain.

## What can digital populations teach us about the maintenance of recombination?

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The maintenance of sexual recombination is a macroevolutionary phenomenon which has troubled evolutionary biologists for over a century. Through modelling and empirical studies, numerous hypotheses have been proposed to explain why this seemingly disadvantageous phenomenon is wide-spread. No definitive answers have been found. Individual-based models are a tool to bridge the gap between deterministic models and empirical data from living systems and hence better understand the mechanisms that maintain sexual reproduction. Examples include the Red Queen co-evolutionary dynamics and competing theories such as the Court Jester. Here, we use the computational model REvoSim to observe how antagonist interactions and environmental conditions, as well as organismal life history traits, affect the amount of sexual recombination over macroevolutionary timescales. We show, within this system, antagonist relationships have a greater effect on the amount of recombination than frequency and magnitude of environmental change, but that both parameters work synergistically to maintain a higher proportion of life cycles spent sexually when combined than separately. In addition, life history traits such as dispersal, mutation and length of life affect on the amount of sexual recombination maintained. In conclusion, within this system, whilst Red Queen dynamics play an important role, pluralistic explanations of sexual reproduction are important and need further exploration. These results have implications on our understanding of the evolution of sexual recombination.

# Testing hypotheses on heterostracan feeding using computational fluid dynamics

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Teeth constitute a key innovation underpinning the evolutionary and ecological development of jawed vertebrates. As the earliest jawed vertebrates already possess teeth, we have to study tooth-like structures in stem gnathostomes to learn more about the evolutionary origin of teeth. Heterostracans are a group of extinct, jawless vertebrates, that possess denticle-covered plates in their oral cavity. However, virtually nothing is known about the structure, development or function of these. How did heterostracans feed? Did they use their oral plates as actual teeth for predation or are these structures an adaptation to suspension feeding? The lateral sides of the anterior part of the heterostracan oral plates are covered with rows of forward-pointing denticles. The forward-facing orientation of these denticles has previously been hypothesised to be a specific adaptation to suspension feeding. To test this hypothesis, we used computational fluid dynamics (CFD). CFD allows us to model fluid flow and visualise turbulences and velocity patterns around 2D models of

heterostracan oral plate denticles. In our analyses we compare flow and velocity patterns of different models with forward-facing denticles to alternative models with rear-facing denticles. Independent of denticle orientation, similar velocity and turbulence patterns develop in the spaces between the individual denticles as well as on the upper surface of the denticles. In general, the models do not show substantial differences in their flow and velocity patterns. We therefore reject the hypothesis of the forward-facing heterostracan oral plate denticles being a specific adaptation to suspension feeding.

### A new framework for reconstructing the diet of fossil birds

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Birds are some of the most diverse organisms on Earth, with species inhabiting nearly every niche across every major biome. As such, birds are key to understanding modern ecosystems. Our understanding of the evolutionary history of modern ecosystems, then is limited by knowledge gaps in the origin of modern bird ecosystem ecology. A crucial part of addressing these shortcomings is coming to understand the earliest birds, the non-avian avialans (i.e. non-crown birds), particularly their diet. The diet of non-avian avialans has been largely uncertain, in large part because of the ambiguous qualitative approaches that have been used to reconstruct it. After reviewing ways to determine diet in modern and fossil avians (i.e. crown birds) as well as non-avian theropods, we propose a set of comparable, quantitative approaches to determine fossil bird diet. While no single approach is consistent in separating birds by diet, each can exclude some diets and narrow the dietary possibilities. We recommend combining (1) dental microwear, (2) landmark-based muscular reconstruction, (3) stable isotope geochemistry, (4) body mass estimations, (5) traditional and/or geometric morphometric analysis, (6) lever modelling, and (7) finite element analysis to reconstruct fossil bird diet. While currently the ancestral avialan diet is unknown and dietary evolution outside of crown birds is obscure, the framework we propose provides a clear way forward to answer these key evolutionary questions.

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

#### Roisin Mooney<sup>1</sup>, Aodhán Ó Gogáin<sup>1,2</sup>, John Murray<sup>1,2</sup>

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Petalodontiforms are a clade of cartilaginous fish, which were major components of Late Paleozoic marine communities. With the exception of rare body specimens, petalodontiforms are known mostly from disarticulated teeth. This is particularly true for *Petalodus*, which is one of the most common and cosmopolitan genus of petalodontiform. The teeth of petalodontiforms are distinct as they possess large petal-shaped crowns with deep roots. Here, a new specimen of petalodontiform (TCD. 31087) is reported from a disused coastal quarry at Doon Point, near Ballybunion in County Kerry. The quarry section reveals a series of interbedded limestones and shales which are assigned to the Corgrig Lodge Formation and are late Viséan in age. TCD. 31087 itself was extracted over 20 years ago but was unable to be properly examined as it began to disintegrate. This is why it was scanned using micro-computed tomography. Resultant CT-slices were rendered in SPIERS to produce 3D models from which the anatomical characters were described. The crowns of the teeth are petal-shaped and labio-lingually flattened, with concave lingual surfaces. Cristae are present towards the base of the crowns, with the crown-base over twice the width of the roots. TCD.31087 is identified as *Petalodus cf. ohioensis* and the relative completeness of the specimen allows for tooth variation within *Petalodus* to be assessed, which is highly important for petalodontiform taxonomy. It was found that the teeth were heterodont in nature and some were part of a tooth replacement whorl. These findings disagree with the current literature for this species.

Origin, provenance and depositional environment of the stratigraphic sequence of the Cerro del Pueblo Formation (Campanian, Late Cretaceous) in the localities "La Parrita" and "Las Águilas" in Coahuila, Mexico

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The Cerro del Pueblo Formation has yielded a wide palaeontological record of vertebrates (dinosaurs, crocodiles, turtles, etc.), so its geologic interpretation is of vital importance for understanding the environment in which these organisms flourished. The formation is present in the localities of "La Parrita" and "Las Águilas", in the southeastern portion of the state of Coahuila, within the area of the Parras Basin. The sedimentary rocks at these locations are Campanian in age, so their origin, provenance and the sedimentary environment of their lithology (sandstones, shales, limestones), is crucial for understanding the fauna at this time. Petrographic interpretation, analysis of provenance by point count, and identification of the sedimentary facies, have resulted in the classification of the sediments as lithic sandstone from a massif. These sandstone deposits were deposited in a sequence of alluvial fans in the middle and distal zones of a continental marine transition zone. The deposits led to the formation of bodies of fresh and salt water, in which vertebrates roamed in the area of "La Parrita" and "Las Águilas". During the Campanian there was a series of shallow seas in different parts of Mexico and the rest of North America, which provided ideal conditions for the distribution of vertebrates widely recorded in this type of environment.

### Modelling marine ecosystem structure from palaeoecological trait data in the Middle Jurassic Peterborough Member (United Kingdom)

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

## Investigating allometric relationships between face length and forelimb mobility in mammals

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The Cranio-Facial Evolutionary Allometry (CREA) 'rule' states that face length scales with size in closely related mammal groups, so that bigger mammals demonstrate relatively longer faces than smaller ones. However, some mammal clades appear to break this 'rule', among them the sthenurines or "short-faced kangaroos". Here, the results of a 2D geometric morphometrics analysis on 10 sthenurine and 31 macropodine jaws are presented. Additionally, linear measurements (along the mandible and tooth row), body size and phylogenetic information of each taxon was compiled. Put together, these data were used to test whether within these macropod subfamilies, larger animals tend to have longer faces. This will also help explore the significance of stance in the evolution of longer faces and larger sizes, as many large terrestrial mammals tend to feature derived postures for improved weight-bearing potential while sacrificing forelimb mobility. This is rarely the case in smaller mammals as less strain must be transmitted through the forelimbs, allowing for advanced movements (pronation and supination) but less efficient loadbearing. Studies have revealed that sthenurines were likely bipedal at all gaits and were unable to adopt any stance that necessitated forelimb weight-bearing, which is observable

in extant macropodines. The absence of a need for forelimb load-bearing likely allowed sthenurines to develop higher forelimb mobility and shorter faces. This study proposes that forelimb mobility (and consequently food manipulation potential) might be an important factor related to facial length in mammals.

Modelling of morphotypic transitions and intermediary developmental stages between species of rugose corals using Steiner trees and Maximum Parsimony

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Standard phylogenetic trees are useful for many organisms but may not accurately represent relationships between morphotypes and species. A phylogenetic tree of the Rugosa shows parsimony but fails to consider intermediaries or hybrids with insufficient characteristics for them to be considered as independent species. Steiner tree problems are used to find connections of minimal length in Euclidean space. One such application is in the construction of evolutionary trees, where a Steiner point represents an intermediary stage between species in a parsimonious tree. Here we consider the Zaphrentis delanouei species of the order Stauriida, and its taxonomic lineages: Cyathophillina and Stereolasmatina (suborders), and Zaphrentidae, Hapsiphyllidae and Zaphrentoididae (families). The genus Amplexizaphrentis is considered a variation of Zaphrentis, classified using the shape of the cone relative to the cardinal fossula. This genus occurs in two families: Zaphrentidae and Hapsiphyllidae and such complications hinder phylogenetic tree construction but may be resolved with Steiner trees. Our provisional results suggest Steiner points between species are indicative of morphotypes, short-lived because of rapid adaptation, selection pressure and environmental constraints. Therefore, we do not see the complete phylogenetic relationship between generations, and it may leave room for hybrid variants which produced recognised species as abundant offspring. This technique resolves intermediary and short-lived species, missing from anagenetic or cladogenetic solutions. An understanding of relative time-space positions and taxonomy is also required when interpreting evolutionary mechanisms. Thus, in line with other quantitative models, Steiner trees can lead to further understanding of a hitherto hidden phylogeny.

Testing hypothesis of habitat preferences among early sauropodomorph dinosaurs

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Initially during the Mesozoic, a paraphyletic assemblage of sauropodomorphs became widespread and abundant in the Late Triassic and Early Jurassic before eventual extinction by the early Middle Jurassic. In contrast, the gigantic sauropods, increased in diversity and

abundance during the Early Jurassic, apparently replacing the early-branching sauropodomorph grade. Recent studies suggest that non-sauropods preferred aridic habitats and sauropods preferred mesic ones: increasingly mesic climates have then been linked to the decline of non-sauropods and the rise of sauropods. However, body and trace fossils indicate that both groups were present in both arid and mesic environments for over 50 million years of their coexistence. Here, we assemble a large data set on non-sauropod and sauropod occurrences for the Late Triassic to Middle Jurassic and carry out numerous analyses to test such habitat preferences. The results strongly indicate significant statistical support that non-sauropod sauropodomorphs occurred in arid environments, and sauropods in semi-mesic and mesic environments, more than expected by chance. These results persist when the data are time-sliced, though the Late Triassic and Middle Jurassic show lower levels of support for habitat preferences than does the Early Jurassic. Examination of the effects of phylogenetic relatedness reveals that very early-branching sauropods (such as the lessemsaurids) display the weakest evidence for habitat preference. Thus, biotic and abiotic factors that drove early sauropods to invade more mesic niches, combined with subsequent climate change in the Early Jurassic, hold the key to understanding the decline and extinction of non-sauropods and the early rise of sauropods.

# Spatiotemporal variation in completeness of the early cynodont fossil record and its implications for mammalian evolutionary history

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Mammals are the only surviving group of Cynodontia, a synapsid clade that first appeared in the fossil record in the late Permian, ~260 million years ago. Using metrics that capture skeletal completeness, we quantify the quality of the early cynodont fossil record in time and space to evaluate the impact of sampling and preservational biases on our understanding of the group's evolutionary history. There is no consistent global sampling signal for early cynodonts. Completeness of the cynodont fossil record increases across the Permian-Triassic boundary, peaking in the Early to early Late Triassic. This peak is dominated by Gondwanan specimens, where a highly seasonal climate probably favoured preservation. Completeness is generally lower thereafter, correlating with a shift from a Gondwanan to a predominantly Laurasian fossil record. Phylogenetic and stratigraphic congruence in early cynodonts is high, although their fossil record exhibits less skeletal completeness overall than other tetrapod clades, including the contemporaneous anomodont synapsids. This discrepancy could be due to differences in the diagnosability of their fossils, especially for small-bodied species. Establishing the timing and assembly of derived ('mammalian') anatomical features in Cynodontia is obscured by sampling. Two of the major nodes at which acquisition of mammalian features is concentrated (Cynodontia and Mammaliamorpha) suffer from lengthy intervals of poor sampling before becoming abundant parts of tetrapod faunas. Low completeness in these intervals limits our ability to determine when certain 'key' mammalian characteristics evolved, or the selective pressures that might have driven their origins.

## Body proportions in extant crocodilians and estimation of size and body mass of Caimaninae from the Miocene of South America

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In recent years, size and body mass analysis have been increasing in palaeontology mainly within Crocodyliformes. However, in some groups this attention is deflected, such as Caimaninae. This lineage includes the living caimans, but their diversity and morphologic disparity were much richer with their relatives that existed in the Miocene from South America, that included huge sizes, unique cranial formats with peculiar forms, such as Acresuchus, Mourasuchus and Purussaurus, that represent such diversity in the group and made part of this study. Previous searches with body dimensions have been based on cranial measurements, mostly. But a more accurate analysis of the body proportions based on extant species has not been done yet. Here, we present a total length of a hypothetical extant crocodilian in different body masses based on morphometric measures of the database, to see if the extinct caimans were in the standards of the living crocodilians. So, it was estimated the size and mass of them based on the regressions. It demonstrated a positive correlation of body mass vs. cranial width, cranial length, snout-vent length and total length, reaching from medium to giant body sizes, and weight of more than 10 tons. We note that some specimens have shown to be within the standards of the living crocodilians, being the cranial width the most accurate. The use of a large dataset and a refined analysis of these body proportions are excellent proxies to forward an estimating body size and mass.