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**MORPHOLOGY, TAXONOMY, AND PHYLOGENETIC RELATIONSHIPS OF THE MONTEVIALE CROCODYLIANS (OLIGOCENE, ITALY).**

**This is the author's manuscript**

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(Article begins on next page)



**The 66<sup>th</sup> Symposium on  
Vertebrate Palaeontology and  
Comparative Anatomy**

**Universities of Manchester  
September 5<sup>th</sup>-8<sup>th</sup> 2018**

**PROGRAMME AND  
ABSTRACTS**

# **Welcome to Manchester for SVPCA and SPPC 2018, the 66<sup>th</sup> Symposium on Vertebrate Palaeontology and Comparative Anatomy with the Symposium of Palaeontological Preparation.**

Herein you will find information about the schedule and programme of events including the line-up of oral and poster presentations, details about the social events, and a guide to the conference. The abstract booklet is available as a PDF only (emailed to delegates and at [www.svPCA.org](http://www.svPCA.org))

## **Local Host Committee:**

Robert Sansom, University of Manchester (Chair)

Robin Beck, University of Salford

Charlotte Brassey, Manchester Metropolitan University

Robert Brocklehurst, University of Manchester

Leah Callender-Crowe, University of Manchester

Joe Keating, University of Manchester

Dean Lomax, University of Manchester

John Nudds, University of Manchester

Elsbeth Wallace, University Manchester

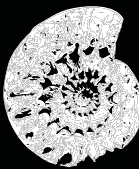
## **SVPCA Steering Committee**

Robert Sansom, University of Manchester; Richard Butler, University of Birmingham; Emma Dunne, University of Birmingham; Richard Forrest, [plesiosaur.com](http://plesiosaur.com); Cindy Howells, National Museum Wales; Jeff Liston, Bayerische Staatssammlung für Paläontologie und Geologie; Graeme Lloyd, University of Leeds; Susannah Maidment, Natural History Museum London; Martin Nunn, Dinosaur Isle Museum

We extend our deep thanks to the official sponsors of the meeting, the Palaeontographical Society and PLOS ONE.

# The Palaeontographical Society

Established 1847



MONOGRAPH OF THE PALAEOGEOGRAPHICAL SOCIETY

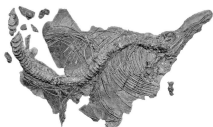
## ICHTHYOSAURS OF THE BRITISH MIDDLE AND UPPER JURASSIC

BENJAMIN C. MOON & ANGELA M. KIRTON

PART 2

### BRACHYPTERYGIUS, NANNOPTERYGIUS, MACROPTERYGIUS AND TAXA INVALIDA

Pages 85–176; Plates 31–40



© THE PALAEOGEOGRAPHICAL SOCIETY, LONDON  
August 2018

BRACHYPTERYGIUS EXTREMUS

89

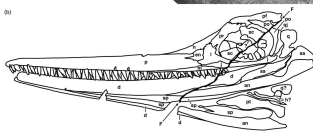
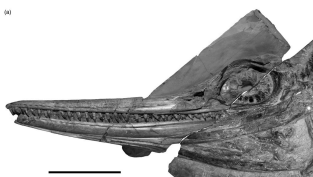


FIGURE 30. *Brachypterygius* skull (BRSMU C6 16090) in left lateral view composite photograph (a) and interpretation (b). The skull is preserved in two portions separated by the line of fracture (F); the anterior portion is completely preserved, while the posterior portion has been incompletely preserved, as does (b) despite a well-developed. Photographs in a true orthosthous view to the specimen are also provided. (c) Bone blocks of these two pieces separately and are outlined in (a). Measurements: F fracture line between two blocks of the specimen (thickened line); an, angular; d, dentary; em, external naris; hc, postorbital hook; j, jaw; l, lateral; m, maxilla; m, mandible; pm, premaxilla; pt, postorbital; pp, postorbital; pr, prefrontal; p, parietal; q, quadrate; qd, quadratoquadrate; sc, suprascapula; sc, scapula; sp, suprascapula; un, unguis; v, vomer. Scale bar represents 500 µm. From courtesy Simon Powell (University of Bristol), used with permission; illustration by Benjamin Moon.

All of the above specimens are from the Kimmeridge Clay Formation unless noted (Table 3). The material is assigned based on the similarity with the type limb material – three distal humeral facets, large dorsal and ventral processes, polygonal limb elements – as in comparison with skull material of CAMSM J09316 and UN 57.111 – basiscapital with narrow extracondylar area and dorsally positioned notochordal pit; basihyoid with well-defined basihyoid processes, ventrally positioned carotid foramen, and pentagonal form posteriorly.

**Diagnosis.** Moderately large to large (jaw length up to 1230 mm) member of Ophthalmodontidae characterized by: robust rostrum, snout ratio 0.567–0.905 (more

*Extracts from a recent Monograph of the Palaeontological Society, Moon and Kirton, ©The Palaeontographical Society*

Our sponsor, **The Palaeontographical Society** is a historic body that exists for the purpose of figuring and describing British fossils by publishing monographs. Benefits of membership include receipt and access to high quality monographs. They also have annual prizes for and funding for palaeontological research. [www.palaeosoc.org](http://www.palaeosoc.org)

## Schedule of Events in Brief

	Wednesday 5th	Thursday 6th	Friday 6th	Saturday 7th
9.00	Registration	Ahlberg	Moreno-Azanza	Coach from Oxford Road to Buxton
9.15		Clack	Atterholt	
9.30	Bayesian	Castiello	Maharaj	
9.45	SPPC Workshop	Cupello	Martin-Silverstone	
10.00	Larkin	Dobson	Unwin	Buxton museum including guided tour of Pleistocene mammal collections
10.15	Smith	Dearden	Bestwick	
10.30	Nunn	Tea		
10.45	Tea	Tea		
11.00		Chiarenza	Bullar	
11.15	Forrest	Brocklehurst	Chatterji	
11.30	Graham	Maidment	Jones	
11.45	Henderson	Butler	Lomax	
12.00	Carrio			
12.15	Open			
12.30		Lunch Break	Lunch Break	Lunch (Old Sun Inn)
12.45				
13.00	Lunch Break			
13.15				
13.30		López-Arbarelo	Brocklehurst	
13.45	Special Symposium	Callender-Crowe	Troelsen	
14.00	SVPCA Intro	Sookias	Marek	Poole's Cavern tour
14.15	Coates	Beck	Sharp	
14.30		Lloyd	Karoullas	
14.45	Davis	Tea		
15.00			Tea	
15.15	Giles	Regalado		
15.30		Barrett	Henderson	Return Coach
15.45	Tea	Johnson	Clements	
16.00		Mannion	Wallace	
16.15	Asher	Armfield	Zhang	
16.30			MacLaren	
16.45	Randle		Lautenschlager	
17.00		Poster Session		
17.15	Rauhut			
17.30				
17.45				
18.00				
18.15				
18.30	Museum Reception	Annual Auction	Conference Dinner	
18.45				
19.00				

Details and talk titles can be found below

## **SVPCA and SPPC Code of Conduct**

The SVPCA and SPPC meetings welcome all those who are interested in vertebrate palaeontology, comparative anatomy, and care of fossil collections. Symposium organisers and the steering group are committed to maintaining a meeting environment that encourages the free expression and exchange of scientific ideas through open and respectful dialogues at oral and poster presentations, workshops, fieldtrips, and associated social events. Diversity in all its forms is celebrated and meeting attendees are expected to be respectful and considerate of fellow attendees, meeting organisers, and facility staff.

*Behavioural expectations.* Throughout the meeting and associated events, attendees are expected to behave in a courteous, collegial, and respectful manner to each other, volunteers, exhibitors, and 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 the intellectual property of presenters. Demeaning, abusive, discriminatory, harassing, or threatening behaviour will not be tolerated, in either personal or electronic interactions.

*Social media and digital images.* At the time of the meeting, open discussion on social media and other outlets is encouraged (#SVPCA2018). While the default assumption is to allow discussion of presentations on social media, attendees are asked to respect any request by an author to not disseminate the contents of their talk or poster. Authors should use the icons available on the SVPCA website (examples below) to clearly express when content from their talks/posters should not be recorded, photographed, or posted online.



*Misconduct.* Any attendee who believes that an incident of scientific or ethical misconduct has taken place, or who experiences/witnesses any form of harassment is encouraged to contact the lead Symposium organiser (Robert Sansom) or designated members of the steering group (Emma Dunne, Graeme Lloyd). Reports of such incidents will be treated in the strictest confidence and will be investigated by the Symposium organiser with support from the Steering Group and, if a complaint is upheld, appropriate action will be taken. This action may include, in the most severe cases, the banning of individuals found to have behaved inappropriately from presenting at or attending SVPCA and SPPC meetings in the future.

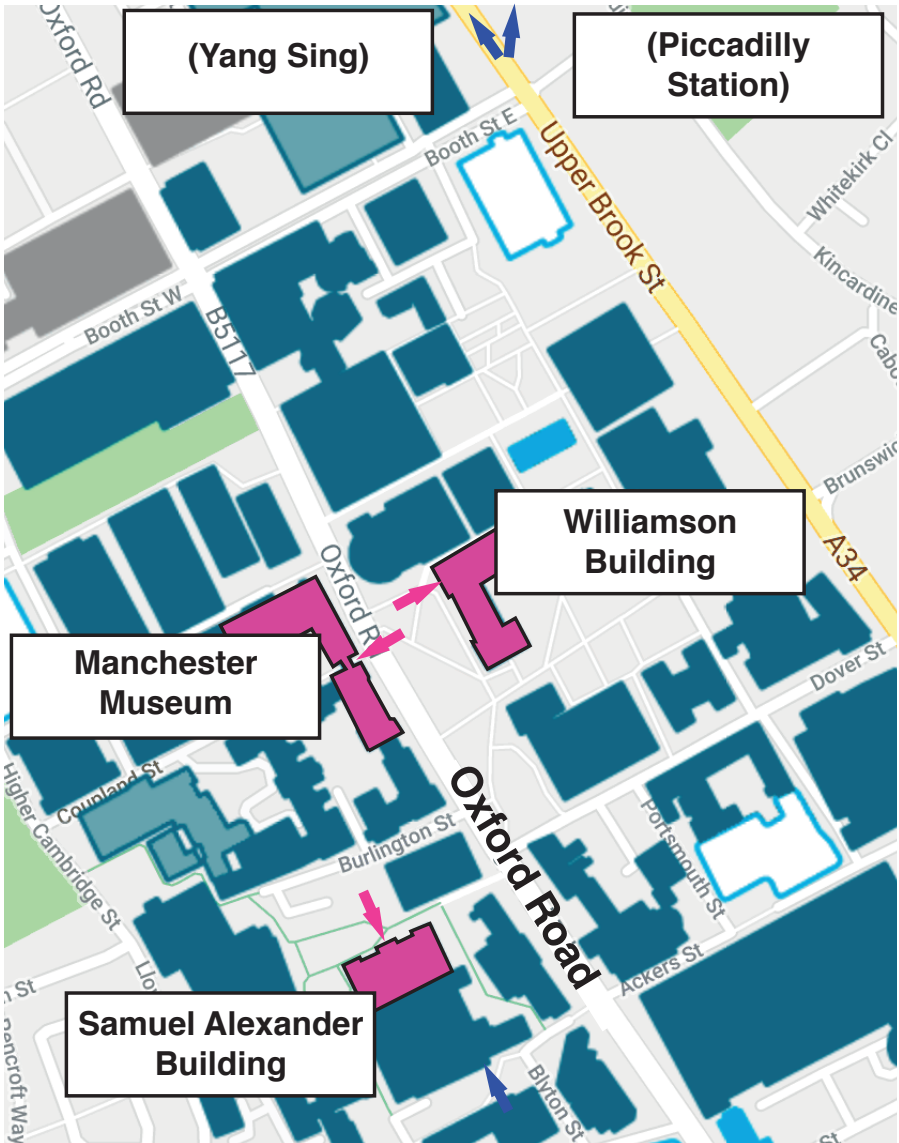
## **Meeting Venue and Facilities**

SVPCA and SPCC will take place at the University of Manchester Oxford Road Campus. Oral sessions will take place at the Samuel Alexander Lecture Theatre in the Samuel Alexander Building (M13 9PP, map below). Registration and tea breaks will take place in the foyer of the same building. The workshop, poster session, and annual auction will take place in the Williamson Building (map below) whilst the welcome reception (18.00 Wednesday 5<sup>th</sup>) will take place in the Manchester Museum fossil gallery (map below).

Step free access to the Samuel Alexander Lecture Theatre is to the rear (purple arrow in the map). The main campus is a short walk (1 mile) or bus ride (#147) from Manchester Piccadilly railway station, which has frequent trains to Manchester Airport. The welcome reception is being held at the fossil galleries of Manchester Museum and the annual dinner is being held at Yang Sing in Manchester's historic China town (34 Princess Street, M1 4JY).

Oxford road has plenty of eating and drinking establishments available. Lunch is not provided to delegates, but we recommend Kro bar (Oxford Road) for those wanting a sit down lunch, or just south on Oxford Road is a Sainsbury's local, Costa Coffee, and a Subway. Each evening has social events, but for after we recommend either Kro bar again, Big Hands (Oxford Road) or Sandbar (Grosvenor Road). You will likely find the local hosting committee at one of these after hours! For evening meals, Manchester's famous "Curry Mile" is a short walk (0.6 miles) south of the University Campus and has no shortage of options.





**(Yang Sing)**

**(Piccadilly Station)**

**Williamson Building**

**Manchester Museum**

**Samuel Alexander Building**

**Lunch options**

## Poster Session

Posters will be presented during the dedicated poster session (16.30 -18.00 of Thursday 6<sup>th</sup>), during which we ask presenters to be in attendance. This will take place in G12 of the Williamson building, just across the road from the Samuel Alexander Building. For logistical reasons **posters will be on display for this day only**, so we ask delegates to please attend the dedicated poster session. Snacks, wine, beer, and other refreshments will be provided.

## Annual Auction

The annual auction will immediately follow the poster session, starting at 18.00 in the Williamson Building (G03 lecture theatre). Proceeds of the auction will go to the Jones-Fenleigh Fund, to support future SVPCA and SPPC attendance by those without institutional funding. Please do think of things you have to donate, be they specimen replicas, books, monographs, artwork, clothing, toys – anything will be gratefully received! **Unfortunately the lecture theatre will not be able to accommodate all delegates. Places have been allocated on a first-come first-served basis to delegates who email** [SVPCAMAN2018@listserv.manchester.ac.uk](mailto:SVPCAMAN2018@listserv.manchester.ac.uk).

## Annual Dinner

The annual dinner will take place at the award winning Yang Sing in Manchester's historic China town. It can be found at 34 Princess Street (M1 4JY). This is a short walk (1 mile) from the conference venue. Simply head north on the A34 (Upper Brook St), which becomes Princess Street. Please arrive at 18.30 for dinner at 19.00. The event has proved quite popular and is now at full capacity – thank you to those who already registered for this event.

## **PLOS ONE Student Presentation Prizes**

Following the generous support of PLOS ONE, cash prizes will be awarded to the best student talk and the best student poster (£100 each). The prize will be judged by a committee of members of the hosting committee and SVPCA steering group. Winners will be announced at the annual dinner.

## **Fieldtrip – Saturday September 8th**

The ‘field’ trip this year will begin with a morning visit to the recently refurbished Buxton Museum and Art Gallery. Here we will have an opportunity to view the new galleries, including the ‘Wonders of the Peak’, and will also be given a guided tour of the palaeontology stores, housing the important archive and collections of the Victorian ‘Cave Hunters’ Sir William Boyd Dawkins and Dr J. Wilfred Jackson. Lunch will be taken at a local pub after which we will walk the short distance to Poole’s Cavern, where will have a guided tour underground into the spectacular caves and caverns. This natural cave in Carboniferous Limestone, was occupied from the late Neolithic Period, and was opened as a showcave in 1853. Coach leaves Oxford Road at 9.00 and returns to Manchester for 17.00. The cost of the field trip (£30) will cover coach travel to and from Manchester, as well as admission to the Museum and Cavern.

## **Social Media**

The official hashtag for the meeting is #SVPCA2018, and we encourage people to discuss the meeting and talks on social media. Our default assumption is that discussions of presentations on social media are allowed. However, please respect any request by an author not to disseminate the contents of their talk or poster. Authors should use a “no tweeting” symbol (see code of conduct) on their slides or posters to clearly express that they do not want their presentation posted or discussed online.

# FULL SCHEDULE OF ORAL PRESENTATIONS

## WEDNESDAY September 5th

### Symposium of Palaeontological Preparation and Conservation (SPPC)

Chair Cindy Howells

- 10.00 **Nigel Larkin** The Biddulph Grange geology gallery project: restoring a unique display from 1862 that encapsulates an important stage in the history of the development of geological thinking.
- 10.15 **Adam Smith** From China to Nottingham: the making of Dinosaurs of China
- 10.30 **Martin Nunn** Using theatre skills in a science exhibition: Dinosaurs of China in Nottingham
- 10.45 *Tea Break (Samuel Alexander Building Foyer)*
- 11.15 **Richard Forrest** Challenging preparation of a plesiosaur skeleton from a stressed nodule
- 11.30 **Mark Graham** The air-abrasive technique: re-evaluation of its use in fossil preparation
- 11.45 **Don Henderson** Rescuing an Early Cretaceous plesiosaur from an active tar sand mine
- 12.00 **Vicen Carrió** An introduction to “The Association for Materials and Methods in Palaeontology” (AMMP) meeting.
- 12.15 SPPC open session
- 12.30 *Lunch Break*

## Special Symposium "Advances in the Vertebrate Tree of Life"

Chair Robert Sansom

- 14.00 SVPCA opening remarks
- 14.15 **Mike Coates** Sharks uprooted - new perspectives on early chondrichthyans
- 14.45 **Katie Davis** Shaping the avian (super)tree of life
- 15.15 **Sam Giles** Unravelling osteichthyan relationships: evolutionary tales from the head of forgotten fishes.
- 15.45 *Tea Break (Samuel Alexander Building Foyer)*
- 16.15 **Rob Asher** Confidence in palaeontological systematics: lessons from mammals
- 16.45 **Emma Randle** Tackling jawless fish: continuous characters, rooting and patterns of evolution in Heterostraci
- 17.15 **Oliver Rauhut** Dinosaur origin and success in the early Mesozoic: insights from the distribution of homoplasy
- 18.00 **WELCOME RECEPTION** (*Fossil Galleries, Manchester Museum*)

## THURSDAY 6th September

### SVPCA Session 1: Early Vertebrates Chair Joseph Keating

- 9.00 **Per Ahlberg** An extremely primitive miniature tetrapod from The Late Devonian (Early Famennian) of North Timan, Russia
- 9.15 **Jenny Clack** *Acherontiscus*, the earliest durophagus tetrapod redux
- 9.30 **Marco Castiello** 3D investigation of the head and shoulder of a stensioellid fish reveals Stensioellida to be a valid group of placoderm-grade affinity
- 9.45 **Camilla Cupello** Lung evolution in osteichthyans: insights from synchrotron phase-contrast microtomography
- 10.00 **Claire Dobson** Cranial osteology of *Pachycormus*, and relationships and divergence times among pachycormiforms
- 10.15 **Richard Dearden** A third “acanthodian” stem-chondrichthyan endoskeleton in a uniquely well-preserved specimen of *Diplacanthus crassissimus*
- 10.30 *Tea Break (Samuel Alexander Building Foyer)*

### SVPCA Session 2: Macroevolution and Palaeobiogeography

Chair Graeme Lloyd

- 11.00 **Alessandro Chiarenza** Climatic drivers behind the demise of non-avian dinosaurs at the end Cretaceous mass extinction
- 11.15 **Neil Brocklehurst** Physical and environmental controls on Paleozoic tetrapod dispersal across Pangaea

- 11.30 **Susie Maidment** North Africa's first stegosaur and the armoured dinosaurs of Gondwana
- 11.45 **Richard Butler** Standardising for spatial sampling bias demonstrates constrained diversification of Phanerozoic terrestrial tetrapods
- 12.00 *Lunch Break*

**SVPCA Session 3: Morphology and Molecules** Chair Sam Giles

- 13.30 **Adriana López-Arbarello** Non-random distribution of homoplasy and the definition of actinopterygian clades
- 13.45 **Leah Callender-Crowe** Evaluating the performance and correlation morphological characters in reconstructing avian and squamate evolutionary history
- 14.00 **Roland Sookias** Reconciling morphology and molecular data in inferring phylogeny for extant crocodylians
- 14.15 **Robin Beck** Improvements in the fossil record may largely resolve the conflict between morphological and molecular estimates of mammal phylogeny
- 14.30 **Graeme Lloyd** Meta-analytical integration of fossil and molecular data in phylogenetic inference and the first truly comprehensive phylogeny for Cetacea
- 14.45 *Tea Break (Samuel Alexander Building Foyer)*

**SVPCA Session 4: Sauropsid Phylogeny** Chair Susie Maidment

- 15.15 **Omar Regalado** Impact of continuous character coding on the reconstruction of the evolutionary history of Basal Sauropodomorpha
- 15.30 **Paul Barrett** Those feathers won't stick: maximum likelihood modelling supports scales as primitive for Dinosauria
- 15.45 **Michaela Johnson** What is '*Steneosaurus*'? evolutionary relationships within Teleosauroidea (Crocodylomorpha, Thalattosuchia)
- 16.00 **Phil Mannion** New insights on the phylogenetic relationships and biogeographic history of eusauropod dinosaurs
- 16.15 **Roxanne Armfield** Cranial anatomy of the Palaeocene snake *Helagras prisciformis*; early implications for crown macrostomatan snakes

**SVPCA POSTER SESSION** (Williamson Building)

- 16.30- **All Poster Presenters** See below for poster titles

18.00 **ANNUAL AUCTION** (Williamson Building)



## FRIDAY 7th September

### SVPCA Session 5: Archosaur\* Anatomy Chair John Nudds

- 9.00 **Miguel Moreno-Azanza** The crystallography of the alligatorid eggshell. Insights from the EBSD.
- 9.15 **Jessie Atterholt** A CT-based survey of supramedullary diverticula in extant birds
- 9.30 **Iyra Maharaj** A comprehensive description of *Endothiodon bathystoma* (Anomodontia, Therapsida), a dicynodont from the late Permian of the Karoo Basin of South Africa
- 9.45 **Liz Martin-Silverstone** A 3D reconstruction and mass estimation of a well-preserved pterosaur from Brazil
- 10.00 **Dave Unwin** A quantitative protocol for assessing the developmental stage of embryos and its implications for pterosaurs
- 10.15 **Jordan Bestwick** Reconstructing the dietary ecology of pterosaurs using quantitative 3D textural analysis of tooth microwear
- 10.30 *Tea Break (Samuel Alexander Building Foyer)*

### SVPCA Session 6: Sauropsid Crania Chair Paul Barrett

- 11.00 **Claire Bullar** Ceratopsian braincase morphology and palaeoneurology through ontogeny.
- 11.15 **Ray Chatterji** A quantitative analysis of cranial growth and evolution in sea turtles (Testudinata: Cheloniaidea)

11.30 **Marc Jones** Brain structure supports interpretations of an active lifestyle in a small, iconic British dinosaur

11.45 **Dean Lomax** Odd narial features in *Ichthyosaurus* suggest the presence of salt glands

12.00 *Lunch Break*

### **SVPCA Session 7: Biomechanics and Functional Morphology**

Chair Liz Martin

13.30 **Robert Brocklehurst** Modelling Avian Ventilation Mechanics with 3D Levers and Linkages

13.45 **Pernille Troelsen** Functional morphology and hydrodynamics of plesiosaur necks: Does size matter?

14.00 **Ryan Marek** An everyday tool: how the avian neck has adapted to (almost) every situation

14.15 **Alana Sharp** The role of soft tissues in a biomechanical model of the rat skull

14.30 **Carolina Karoullas** Estimating the Flight Capabilities of Fossil Birds from Extant Bird Data and Aerodynamic Theory

14.45 **Mariane Delaunay** Do birds have whiskers?

15.00 *Tea Break (Samuel Alexander Building Foyer)*

**SVPCA Session 8: Taphonomy and Mammals** Chair Robin Beck

- 15.30 **Don Henderson** Sediments, skulls and squishing – taphonomic investigations of ceratopsian skull deformation
- 15.45 **Thomas Clements** Uncovering the impact of palaeogeography on vertebrate taphonomy: an investigation of the Mazon Creek Lagerstätte.
- 16.00 **Elsbeth Wallace** Community preservation within the Late Jurassic Morrison Formation, Western Interior, USA
- 16.15 **Hanwen Zhang** *Elephas recki*: the wastebasket?
- 16.30 **Jamie MacLaren** Walking with Unicorns - metacarpal morphology of the Rhinocerotidae
- 16.45 **Stephan Lautenschlager** Morphological convergence and functional diversification of sabre-toothed vertebrates
- 17.00 **END**
- 18.30 **CONFERENCE DINNER** (Yang Sing, 34 Princess Street, M1 4JY)

## POSTER PRESENTATIONS

\*Denotes electronic poster; they will be displayed in separate room. Other posters will be arranged in alphabetical order.

- Eduardo Ascarrunz** Algorithmically-assisted selection of ratio characters for the phylogenetic placement of fossils of geoemydid turtles
- \*Sue Beardmore** Sticky fish as an indicator of specific palaeoenvironmental conditions
- Charlotte Bird** Brain morphology and intraspecific variation in the Triassic cynodont *Thrinaxodon liorhinus*
- Emily Brown** The use of CT in discerning the life habits of the Early Triassic archosauriform, *Proterosuchus fergusi*
- David Button** A three-dimensional virtual reconstruction of the skull of the problematic Early Jurassic theropod *Coelophysis? kayentakatae*, and the importance of evaluating uncertainty in retrodeformation studies
- \*Hannah Byrne** Synchrotron microtomography analysis of coprolites from the Obrutschew Bjerg Formation, East Greenland
- Savannah Cobb** Inferring mode of life for extinct avians and theropod dinosaurs using measurements of curvature for the ungual phalanx
- Sandra Chapman** Compactor storage for vertebrate collections at the NHM
- Ewan Chipping** Taming the cow: how have humans influenced morphological variation in wild and domestic cattle from prehistory to the present?
- Matthew Dempsey** A student-staff-museum collaboration to restore, image and display the skeleton of a Lower Cretaceous ornithomimid dinosaur (*Tenontosaurus tilletti* LL.1227)
- Emma Dunne** The Rise of Dinosaurs: Tetrapod diversity and climate during the Late Triassic

<b>*Hugo Dutel</b>	The biomechanical significance of the palatal fascia and quadratojugal ligament in the skull of the ornate monitor ( <i>Varanus ornatus</i> )
<b>Richard Forrest</b>	Vertebral proportions in plesiosaurs
<b>Struan Henderson</b>	Morphological conservatism and slow evolution under a new porolepiform phylogeny
<b>Jesse Hennekam</b>	Insular gigantism in Mediterranean dormice
<b>Thomas Henton</b>	A mystery fossil from the Kimmeridge (Upper Jurassic) of Dorset, UK – the oldest urolith on record
<b>Emily Hunter</b>	Tests of masticatory convergence within hard-object feeding primates
<b>Megan Jacobs</b>	Walking in the shadows of giants: The small dental assemblage of the Early Cretaceous Kem Kem beds of Morocco, North Africa
<b>*Zerina Johanson</b>	Microstructure and mineralogy in dental plates of the holocephalan chimaeroid <i>Harriotta raleaghae</i> : novel dentine and conserved patterning combine to create a unique chondrichthyan dentition
<b>*Miranta Kouvari</b>	Evolution of functional morphology of the <i>Suncus etruscus</i> Corsican shrew's mandible: a story between climate, man and island
<b>*Loredana Macaluso</b>	Morphology, taxonomy, and phylogenetic relationships of the Monteviale crocodylians (Oligocene, Italy)
<b>Stephan Spiekman</b>	A new Antarctic specimen of <i>Prolacerta cf. broomi</i> , its biogeographical implications and a revision of the taxon
<b>Euan Malpas</b>	The first Mosasaur (Reptilia: Squamata) remains from the Ulster White Limestone Group, Northern Ireland, and refinements to the Wastebasket taxon, ' <i>Mosasaurus gracilis</i> '.
<b>Robert Mansergh</b>	Global and regional sea-levels during the Late Cretaceous and the evolution and radiation of megaherbivorous dinosaurs

- \*Darius Nau** Postcranial Osteology of a New, Juvenile Skeleton of *Plateosaurus* (Dinosauria: Sauropodomorpha) from Frick, Switzerland
- Tom Raven** A Phylogenetic Supermatrix of the Armoured Dinosaurs
- Francesco Santini** A macroevolutionary look at the history of fishes in coral reefs
- \*Tim Smithson** Traquair's lungfish from Loanhead: dipnoan diversity and tooth plate growth in the late Mississippian
- Marton Szabo** The Late Cretaceous (Santonian) ichthyofauna of Iharkút (Hungary), with a summary on the European Late Cretaceous continental fish faunas
- Lukardis Wencker** Phylogenetic value of jaw elements of lacertid lizards (Squamata: Lacertoidea): a case study with material from the Oligocene of France
- Mark Witton** Tyrannosaurid theropods: did they ever smile like crocodiles?

# SPPC TALK ABSTRACTS

## **An introduction to “The Association for Materials and Methods in Palaeontology” (AMMP) meeting.**

**Vicen Carrió**

*National Museums of Scotland, Edinburgh*

For more than 10 years I have been lucky to be able to attend the AMMP meetings. Originally known as Fossil Preparation and Collections Symposium, in 2015 the name was changed to AMMP to try to open the meeting to other areas of great importance when preparing fossils such as packing, adhesives, materials and preventative conservation. In my talk I would like to introduce you to this association and give you a taste of what a five day conference can provide. The conference is set up in a way to provide different activities to enhance and learn new techniques and tips in the conservation and preparation of fossil material. On the first day you are able to choose between workshops such as Jacketing and cradle, teaching observational, tactile skills and databases or undertaking fieldtrips to a Conservation Centre (if available) or a local “must see” visitor attraction. The second day is the Symposia - Two sessions on specific topics. This year the subjects were Conservation of In-situ Sites and Health and Safety (delegates are encouraged to attend). On the third day there are more workshops: Basic moulding and casting, advanced moulding and casting techniques and materials, consolidant/adhesive topics and various preventive conservation methods. The fourth day is the General Sessions Day, with oral presentations and posters on all aspects of fossil preparation, conservation and collections care. Finally, the main field trip – This year we visited the Ashfall Fossil -Miocene wildlife: Rhinos, horses, camels and other mammals preserved in-situ in their death positions.

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## **Challenging preparation of a plesiosaur skeleton from a stressed nodule**

**Richard Forrest**

*plesiosaur.com*

Preparation of fossil vertebrates can be a complex and demanding process. Every specimen presents a different suite of challenges. This talk is about the preparation of a partial plesiosaur skeleton in stellarated nodule from Bed 10 of the Oxford Clay, well-known for the number of well-preserved marine reptiles it has yielded over the past two centuries. This was a particularly challenging specimen. The nodule is riddled with veins of calcite, and highly stressed due to overburden pressure and the processes of nodule formation. It fractures unpredictably, sometimes for no apparent direct reason. The parts that break off are usually slightly distorted as their internal stress is released, and don't fit cleanly to the scar from which they originate. Parts of the nodular material are very pyritic and harder than the bone it contains. A number of different methods were attempted during the preparation, some successful others not. This is not intended as a demonstration on how to prepare such a difficult fossil. It is an account of the highs and lows encountered during the processes and the lessons learned from them. Despite all the problems, preparation has uncovered interesting information on the life history of the animal and its demise.

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## **The air-abrasive technique: re-evaluation of its use in fossil preparation**

**Mark Graham**

*Natural History Museum, London*

In 2017 new experiments were devised to assess the effect of air abrasion on matrix and fossil material using various types of powder across a range of delivery angles and differing air pressure settings. The experiments incorporated for the first time Scanning Electron Microscope (SEM) photography and 3-dimensional profiling on matrix coated with consolidant and copper powder to enable visual assessment and also on a piece of fossil bone. The abrasive effect of powder flow at the point of impact and immediately surrounding area on the test matrix, and damage across the surface of the bone fragment were revealed at the electron microscopic level and documented for the first time, together with microscopic comparison of the powder particles before and after use. The review incorporates information taken from the application of airabrasion in the fields of conservation and industry, as these provide valuable insights to the fossil preparator. Also part of the review, an international online survey of preparators was undertaken and 84 individuals from 12 countries contributed information about powder types used, micron particle size selection, the availability and use of equipment, preferred techniques, personal protective clothing and other health and safety related issues. The replies were drawn from professional, avocational and amateur preparators. The results of both the laboratory experiments and the international survey are soon to be published and will include practical advice on materials, techniques, laboratory set-up and health & safety considerations.

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## **Rescuing an Early Cretaceous plesiosaur from an active tar sand mine**

**Donald M. Henderson**

*Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta*

In June of 2018 the Royal Tyrrell Museum received notice of a fossil reptile being discovered in the Syncrude tar sand mine 25km north of Fort McMurray in northeastern Alberta, Canada. A team of four people from the Museum – one curator and three technicians – were dispatched to recover the specimen. Prior to commencement of work, all four museum staff had to complete an online safety course and complete a final exam with minimum pass score of 80%. Furthermore, one of the technicians had to complete a “mine safe driving course”. The specimen was found as a series of large (50+ kg) irregularly shaped blocks of a once whole concretion with bone exposed on the all broken internal surfaces. The fossil bone was not permineralized, so a penetrant stabilizer was immediately applied to all the exposed bone. Final bone protection was provided with medical grade plaster bandages (“Gypsonas”). Some of the exposed bone and broken edges required full plaster and burlap jacketing for protection during extraction and later transport. With the aid of a tracked excavator, its toothed bucket, and a skilled operator, each of the heavy blocks was wrestled into the bucket, lifted up, and then wrestled into the back of a Museum vehicle. The density and total mass of the concretionary blocks was seriously underestimated, and we found we were 800kg over the gross vehicle weight limit. Five of the offending blocks were shipped south at a later date.

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## **The Biddulph Grange geology gallery project: restoring a unique display from 1862 that encapsulates an important stage in the history of the development of geological thinking**

**Nigel R. Larkin**

*natural-history-conservation.com*

In 1862 just three years after Darwin published 'On the Origin of Species', Oxford-educated James Bateman (of the Royal Society) created a new entrance to his famous gardens at Biddulph Grange, near Stoke. This was a long stone corridor with 75 fossils set into the wall on one side, from graptolites and ferns to ichthyosaurs and a mammoth tusk in rough stratigraphical order. However, they were arranged in six bays titled Day 1 to Day 6 and represented the days of Creation. Bateman's thinking was directly influenced by Hugh Miller, in particular his theory of Genesis and Geology Compared, and the gallery was designed to show how the newly discovered fossil record could be reconciled with the bible. Although open to the public for several years, unfortunately the gallery became forgotten after Bateman sold his estate and apart from ten original specimens the fossils eventually deteriorated or disappeared. Now a National Trust property, over the last few years the gallery has been renovated. The ten original specimens have been cleaned, conserved and moulded to make casts for reinstating on the wall. With no records of the original gallery to guide us in filling the remaining 65 holes we have borrowed museum specimens of species described by 1862 that are from sites known by that date that are appropriate for their position in the gallery, to be as authentic as possible. Replicas of these were made to complete the gallery which uniquely captures a specific moment in the development of geology.

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## **Using theatre skills in a science exhibition: Dinosaurs of China in Nottingham**

**Martin Nunn** and Adam S. Smith

*Nottingham City Museums and Galleries*

Dinosaurs of China was a world-exclusive temporary exhibition of iconic, mostly feathered dinosaur fossils, which have revolutionised our understanding of dinosaur appearance and biology over the last twenty years. Hunter the *Sinraptor* was a puppeteer-operated semi-animatronic theropod dinosaur costume. Hunter, accompanied by Dinosaur Rangers, publicised the exhibition within Nottingham and beyond, visited schools to explore dinosaur ecology, and interacted with visitors to the exhibition. The process of putting this element of the exhibition into place included procurement of the costume, recruitment of volunteer Rangers, and Dino-Factor auditions to find a skilled puppeteer. Hunter and the Rangers contributed towards exhibition marketing and the public learning experience. However, the dinosaur had mixed impacts on visitor expectations. In conclusion, we show that if used with care, theatre and performance skills can enhance scientifically rigorous learning experiences.

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## From China to Nottingham: the making of Dinosaurs of China

Adam S. Smith<sup>1</sup> and Wang Qi<sup>2</sup>

1. Nottingham Natural History Museum, Wollaton Hall

2. University of Nottingham

In summer 2017, Nottingham hosted a collection of Chinese fossils that told the story of dinosaur evolution from scaly ground shakers to modern birds. This world-exclusive one-time-only Dinosaurs of China exhibition was the outcome of a multi-partnership between the University of Nottingham, Nottingham City Council, the Institute of Vertebrate Paleontology & Paleoanthropology, and the Longhao Institute of Geology and Paleontology Inner Mongolia. The exhibition combined Nottingham-based collections with loaned fossils and casts of Chinese dinosaurs and birds, including real type specimens of feathered dinosaurs (*Microaptor gui* and *Caudipteryx dongi*) and the tallest cast of a dinosaur skeleton ever displayed in the UK (a rearing *Mamenchisaurus*). Many of the specimens were on display outside of Asia for the first time. To bring the dinosaurs to Nottingham, the project team overcame the challenges of designing, curating, transporting, and installing an exhibition in the unusual setting of an Elizabethan mansion. Dinosaurs of China received 115,000 visitors in its four-month duration and has helped to foster the identity of Nottingham, especially Wollaton Hall, as a venue for natural science.

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# SVPCA SPECIAL SYMPOSIUM ABSTRACTS TALKS “ADVANCES IN THE VERTEBRATE TREE OF LIFE”

## Confidence in palaeontological systematics: lessons from mammals

**Rob Asher**

*Department of Zoology, University of Cambridge*

For many species, fossilizable data can accurately convey phylogenetic history. In other cases, they may be misleading about evolutionary affinities on the Tree of Life. An understanding of if and how fossilizable data (typically including hard tissues such as bones and teeth) might be statistically consistent or biased is important in palaeontology. Here, I draw on well corroborated phylogenetic trees and samples of fossilizable data for primates, rodents, eutherians, and mammals generally, in order to quantify the extent to which certain living species, with known phylogenetic affinities, are susceptible to error in phylogenetic reconstruction using only their hard-tissues. Predictably, certain species perform well (e.g., Lemur, *Sylvilagus*) and others are more problematic (e.g., *Erinaceus*, *Anomalurus*). When measured with metrics such as Robinson-Foulds and shared partitions, the former appear in phylogenies reasonably close to the well-corroborated tree, with relatively little variation across fragmentary to more complete fossil templates. The latter can show several times more conflict with the well-corroborated tree. These results can be explained by a number of intuitive factors, including branch lengths and taxon sampling, and likely entail at least some unique causes in any given dataset.

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## Sharks uprooted - new perspectives on early chondrichthyans

**Michael Coates**

*University of Chicago*

Rearrangements at the base of the gnathostome crown are changing our understanding of cartilaginous fishes: sharks, rays, and the chimaeroids. No longer resembling the hypothetical last common ancestor of jawed vertebrates (operculate, ossified and armour plated), early sharks *sensu lato* now include a populous stem lineage of acanthodians -and these are yet to be thoroughly explored for insight into the origins of classic shark characteristics such as tiny scales, tessellate calcified cartilage, broad-based fins, pelvic claspers, gill slits, and serial tooth production. Here, three projects are summarized to re-frame the origin of the modern clade. *Gladbachus*, from the mid-Devonian of Germany, provides yet another perspective on diversity and disparity in the chondrichthyan stem, raising the possibility of multiple early experiments with chondrichthyan-like conditions. *Dwykasselachus*, from the Permian of South Africa, spawned a newly detailed and revised hypothesis of chimaeroid origin, rooting the highly specialized holocephalans among symmoriiforms, including the textbook shark ancestor *Cladoselache*. And *Tristychius*, from the Lower Carboniferous of Scotland, reveals unprecedented skeletal and biomechanical sophistication among early elasmobranchs. If the emerging tree-shape is robust to further discoveries the challenge is to explore these new data and hypotheses within a palaeobiological framework. Crown chondrichthyans emerge against an increasingly detailed background of end Devonian extinctions, and the subsequent recovery seems to generate new levels of diversity and disparity. But, the implied, much deeper, origin of the total group remains murky, perhaps close to the base of the Silurian, and, therefore close to the base the entire jawed vertebrate record.

## Shaping the avian (super)tree of life

**Katie Davis**

*University of York*

Determining the patterns and processes that shaped the tree of life is one of the major goals in palaeobiology. To achieve this we need large inclusive phylogenies at the species level. Whilst large combined datasets – known as supermatrices – might be most desirable, in practise this is often not practicable due to the difficulties of combining disparate data types, including both extant and fossil taxa, and of reconciling character coding from different authors. An alternative is to make use of synthetic meta-tree methods, in which smaller phylogenies are combined to make a large inclusive phylogeny, usually termed a supertree. However, the question remains of whether supertrees are suitable alternatives for phylogenies based on primary character data. Birds are the most abundant land vertebrates on the planet and have been of great historical interest to systematists. They have been the focus of intensive study due to their economic and ecological importance and as a result we now have relatively complete species-level phylogenies built using both supertree and supermatrix methods. Birds are therefore an ideal group in which to compare and contrast these differing methodologies. Using examples from extant birds I demonstrate that phylogenies built using supertree and supermatrix methods recover the same macroevolutionary/macroecological signals, therefore justifying the use of supertree methods for large scale analyses in clades for which complete trees are not available. Finally, I consider ways in which global climate change through deep time may have contributed to shaping the avian tree of life.

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## Unravelling osteichthyan relationships: evolutionary tales from the head of forgotten fishes

**Sam Giles**

*University of Oxford, University of Birmingham*

Actinopterygians (ray-finned fishes) comprise 50% of living vertebrate diversity, with an evolutionary history extending back nearly half a billion years. However, fundamental issues preclude a robust understanding of their early history. Specifically, questions abound regarding the origin of the crown group, as well as the effects of the end-Devonian mass extinction on the group as a whole. The roots of the living radiation have long been accepted to be rooted in the Middle Devonian, necessitating a quarter-of-a-billion-year ghost lineage for the earliest diverging extant actinopterygian group, polypterids. In addition, placement of almost all Palaeozoic actinopterygians within the ray-fin crown has resulted in a highly depauperate stem lineage, contributing to confusion over the early evolution of the group. The advent of CT scanning permits an unrivalled view of internal anatomy in critically understudied early ray-finned fishes. Reinvestigation of three-dimensionally preserved Mesozoic fossils reveals unexpected anatomical features, shifting numerous Palaeozoic ray-fins to the actinopterygian stem and leading to a new phylogenetic hypothesis of relationships between extinct and extant actinopterygians. Recalculated divergence estimates posit a latest Devonian/earliest Carboniferous origin for the living ray-fin radiation, some 30 Ma younger than existing estimates. CT-led reinvestigation of small-bodied late Devonian taxa implies the divergence of many lineages prior to the Devonian-Carboniferous boundary, with important implications for patterns of evolution early in actinopterygian history and the impact of the Hangenberg mass extinction on ray-finned fishes. These results underline the importance of both CT scanning and fossil data for understanding deep divergences and the evolution of depauperate living groups. This new framework provides context to the overwhelming success of actinopterygians and paves the way for future macroevolutionary studies.

## **Tackling jawless fish: continuous characters, rooting and patterns of evolution in Heterostraci**

**Emma Randle**<sup>1</sup> and Robert Sansom<sup>2</sup>

<sup>1</sup>*Department of Life Sciences, Imperial College London*

<sup>2</sup>*School of Earth and Environmental Sciences, University of Manchester*

Evolutionary relationships give polarity and context to major transitions in anatomy and morphology in deep time. The first appearance of vertebrates with recognizable boney skeleton are from the middle Ordovician some 463 million years ago. These fish, together with the Heterostraci are interpreted as belonging to the deepest branching clade of boney vertebrates: the Pteraspidimorphi. However, the Heterostraci and Ordovician pteraspidimorphs lack a cladistic hypothesis of relationships. Difficulties such as the interpretation of homologous features, continuous variation of headshield anatomy and interpreting 'transitional taxa' has led to exploration of different coding techniques. Here I present phylogenetic hypotheses for the Pteraspidiformes, Cyathaspididae and the Pteraspidimorphs as a whole including different methods for interpreting their anatomy. Results from different phylogenetic analyses indicate discretising quantitative characters into ordinal states using a gap coding method produces the most stratigraphically congruent phylogenetic tree. Interpretation of transitional taxa gives resolution to the group they are interpreted as and relationships towards the root of the Pteraspidimorphi are still in conflict with two different rooting models identified using tree visualisation software. The differing rooting systems suggest either a tessellate head shield bauplan for the Heterostraci and Pteraspidimorphs or a headshield composed of two larger plates i.e. a dorsal and ventral. These novel phylogenies provide a framework for macroevolutionary studies and phylogenetic inferences.

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## **Dinosaur origin and success in the early Mesozoic: insights from the distribution of homoplasy**

**Oliver W.M. Rauhut**<sup>1,2</sup>, Adriana López-Arbarello<sup>2</sup> and Diego Pol<sup>3</sup>

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<sup>2</sup>*Department of Earth and Environmental Sciences and GeoBioCenter, Ludwig-Maximilians-University, Munich*

<sup>3</sup>*CONICET, Museo Paleontológico Egidio Feruglio, Trelew, Argentina*

Several important aspects related to the origin and early evolution of dinosaurs remain contested. The recently formulated Ornithoscelida hypothesis has renewed interest in the interrelationships of major clades, and re-analysis of the data indicated that none of the possible hypothesis is currently significantly better supported than any other. Patterns of homoplasy distribution might be of importance for understanding evolutionary events and areas of phylogenetic uncertainty. An important aspect is proximity of homoplasy to contested nodes, as proximal homoplasy indicates intrinsic difficulties in resolving the exact relationships at these nodes. In early dinosaur evolution we found especially high rates of proximal homoplasy close to their origin, considerably aggravating phylogenetic resolution here. This pattern might be due to rapid radiation of different dinosaur bauplans under functional constraints, such as bipedal locomotion. Early sauropodomorph and theropod phylogeny indicates that the Triassic/Jurassic boundary only had a minor impact on the evolution of these clades; their major radiation and success seems to have been triggered by the Pliensbachian/Toarcian extinction. An analysis of homoplasy distribution in theropod phylogeny found enhanced levels of proximal homoplasy at the origin and early radiation of averostran and tetanuran theropods, coinciding with the radiation of these clades in the latest Early and Middle Jurassic. An analysis of homoplasy distribution in evolutionary time shows a peak right after the Pliensbachian/Toarcian extinction event with subsequently lowering rates.

This pattern indicates relaxed selection following the extinction, with clades becoming more clearly defined with consecutive filling of available ecological niches.

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# SVPCA TALK ABSTRACTS

## **An extremely primitive miniature tetrapod from the Late Devonian (Early Famennian) of North Timan, Russia**

Per Erik Ahlberg<sup>1</sup> and Pavel Beznosov<sup>2</sup>

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<sup>2</sup>Institute of Geology, Komi Science Centre, Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia

The fossil record of the fish-tetrapod transition, from elpistostegids through to Late Devonian tetrapods, consists entirely of rather large animals with estimated body lengths ranging from a minimum of approximately 50 cm (*Tulerpeton*) to a maximum of more than 2 m (large individuals of *Tiktaalik*, and the largest Zachelmie trackmakers). This is somewhat surprising given the obvious advantages of small body size for a transitional fish-tetrapod in terms of weight support and ability to find moist and shady microhabitats on land. It also contrasts with the prevalence of small forms in the earliest parts of many other evolutionary radiations, for example among mammals and dinosaurs. Here we present the first miniature tetrapod from the Late Devonian, an apparently adult skull and associated shoulder girdle suggesting a body length of 15 cm, from the early Famennian delta plain deposits of Volonga River, North Timan, Russia. The specimen has been investigated by synchrotron microtomography, revealing a well-preserved braincase and branchial skeleton inside the skull. It is identified as a tetrapod by its stalked interclavicle, slender cleithrum, single pair of nasals, and characteristic dermal ornament. The lateral lines are poorly developed and the dentition does not look piscivorous, suggesting at least partial terrestriality. However, unlike all known tetrapods it retains an internal intracranial joint, cup-shaped basiptyergoid processes, postrostral bones and a deep precoronoid fossa. We tentatively interpret it as the sister group to all other tetrapods. It seems that terrestriality and ecological diversification of tetrapods started much earlier than has previously been thought.

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

Roxanne E. Armfield and Jason J. Head  
University of Cambridge

The majority of modern snake diversity falls within Macrostromata. Characterised by cranial specialisations enabling them to consume large prey whole, macrostomatan taxa possess increased jaw mobility and gape size. The origin, timing and sequence of acquisition of macrostomatan characters remains disputed due to a lack of consensus of the interrelationships within the clade and hindered by a poor Palaeogene fossil record deficient in diagnostic cranial material. The North American early Palaeocene snake *Helagras prisciformis* was first described based on isolated vertebral elements by Cope in 1883, recovered from the Nacimiento Formation of New Mexico. The taxon has been alternately considered a boiid, erycine, or a madstoid snake based on vertebral morphology, but the evolutionary implications of the taxon for inferring crown Macrostromatan history have not been previously explored. New specimens of *Helagras* include partial skulls, providing the first opportunity to resolve this taxon's relationships. Segmentation of microCT data reveals anatomy of the braincase, parietal, stapes, supratemporal, maxilla, vomer, pterygoid, palatine, compound bone, and dentary, as well as vertebrae and ribs. Phylogenetic analysis based on morphological datasets recovered a position stemward of Booidea within crown Macrostromata, based on skull roof

morphology. Addition of a molecular scaffold recovered the first anatomical support for synonymy of Alethinophidia with Macrostromata by joining *Helagras* with *Anilius scytale* and tropidophiids, based on stapedial and palatomaxillary morphologies. Our results provide the oldest unambiguous evidence for the dispersal of crown Macrostromata into Northern continents, and indicates dispersal connectivity of the Americas between the Late Cretaceous and early Palaeogene.

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## A CT-based survey of supramedullary diverticula in extant birds

Jessie Atterholt<sup>1</sup> and Matthew Wedel<sup>2</sup>

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Birds are unique among extant tetrapods in having pneumatic diverticula of the lungs and air sacs that pass among the viscera and muscles, under the skin, and into the skeleton. In addition, some birds also have supramedullary diverticula inside the neural canal, adjacent to the spinal cord. The anatomy of the supramedullary diverticula has only been documented in a handful of birds to date. Using CT scans, we surveyed the morphology of the supramedullary diverticula in a phylogenetically broad sample of extant birds. Although supramedullary diverticula are present in some small-bodied taxa such as hummingbirds and pigeons, the diverticula are typically larger and more complex in large forms such as ostriches and pelicans. Absence of these diverticula in loons and grebes is consistent with the lack of skeletal pneumatization in diving birds. Other absences, for example in the kestrel, are less explicable. When present, the supramedullary diverticula are best developed in presacral vertebrae, but only occasionally present in the synsacrum, and rarely present in caudal vertebrae. In most taxa we have surveyed, the diverticula are not continuous craniocaudally, but exist as separate segments extending fore and aft from each intervertebral joint, as documented by Müller for the pigeon. Occasionally supramedullary diverticula communicate with interosseous diverticula through foramina in the wall or roof of the neural canal. These foramina are osteological correlates of supramedullary diverticula and allow the presence of these diverticula to be inferred in dry skeletal material and fossil organisms.

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## Those feathers won't stick: maximum likelihood modelling supports scales as primitive for Dinosauria

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New discoveries over the past 25 years have revealed much about the nature of dinosaur epidermal structures. These data, especially the discoveries of non-avian dinosaurs with extensive plumage, have challenged long-standing dogma regarding the reptilian scalation of dinosaurs. Discoveries of filamentous structures in taxa positioned on many branches of their evolutionary tree have also led to suggestions of deep feather homologies among dinosaurs and the proposal that feathers were primitive for the clade as a whole. Here we test these proposed homologies using a dataset of 77 dinosaur species that preserve integumentary structures. We conducted a series of model-fitting and ancestral state reconstruction analyses to interpret the evolutionary history and ancestral integumentary condition in dinosaurs within a maximum likelihood framework, using the 'ace' function within the R package 'ape'. Our results provide the first empirical support for a model in which feathers evolved in an ordered fashion,



but reveal that these trends were not always towards 'more complex' character states. Ancestral state reconstructions demonstrate that irrespective of either 1) the preferred phylogenetic framework (e.g. Saurischia/Omnithischia vs Saurischia/Omnithoscelida), 2) the ancestral pterosaur condition (scaled/feathered/'naked'), or 3) whether any one major dinosaur lineage had a Late Triassic feathered representative, support values for a feathered dinosaur ancestor are low. More examples of dinosaur taxa with feathers from across the whole breadth of the tree and, in particular, the discovery of as yet unknown feathered Triassic taxa, would be needed to overturn support for a scaled dinosaur ancestor.

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## **Improvements in the fossil record may largely resolve the conflict between morphological and molecular estimates of mammal phylogeny**

**Robin M. D. Beck** and Charles Baillie

*School of Environment and Life Sciences University of Salford*

Morphological phylogenies of mammals continue to show major conflicts with the robust molecular consensus view of their higher-level relationships. This raises doubts as to whether current morphological character sets are able to accurately resolve mammal relationships, particularly for fossil taxa for which, in most cases, molecular data is unlikely to ever become available. We tested this under a hypothetical "best case scenario" by using ancestral state reconstruction (under both maximum parsimony and maximum likelihood) to infer the morphologies of fossil ancestors for all clades present in a recent comprehensive molecular phylogeny of mammals, and then seeing what effect inclusion of these predicted ancestors had on unconstrained analyses of morphological data. We found that this resulted in topologies that are highly congruent with the molecular consensus, even when simulating the effect of incomplete fossilisation. Most strikingly, several analyses recovered monophyly of clades that have never been found in previous morphology-only studies, such as Afrotheria and Laurasiatheria. Even when predicted ancestors are represented by dental characters only, their inclusion is sufficient to group morphologically disparate taxa that appear closely related based on molecular data, such as "insectivoran-grade" (tenrecs and golden moles) and "ungulate-grade" (proboscideans, hyraxes and sea cows) afrotherians. Our results suggest that, at least in principle, improvements in the fossil record may be sufficient to largely reconcile morphological and molecular phylogenies of mammals, even with current morphological character sets.

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## **Reconstructing the dietary ecology of pterosaurs using quantitative 3D textural analysis of tooth microwear**

**Jordan Bestwick**<sup>1\*</sup>, David M. Unwin<sup>1</sup>, Richard J. Butler<sup>2</sup>, Donald M. Henderson<sup>3</sup> and Mark A. Purnell<sup>1</sup>

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<sup>3</sup>*Royal Tyrrell Museum*

Pterosaurs were key components of Mesozoic terrestrial and coastal ecosystems for 150 million years, yet our understanding of their feeding ecology remains poorly constrained. Postulated pterosaur diets include insectivory, piscivory and/or carnivory, but many dietary hypotheses are highly speculative with little or no evidential basis. We have developed a robust approach to this problem based on quantitative analysis of the micron-scale 3D textures of worn pterosaur tooth surfaces – dental microwear texture analysis – never before applied to pterosaurs. Microwear is produced as scratches and chips generated by food items create characteristic surface textures on teeth that vary according to diet. Our analysis was based on

microwear from non-occlusal tooth surfaces of 13 species of pterosaur. This was compared with data from extant taxa with known diets: bats, monitor lizards and crocodylians, including insectivores, piscivores, carnivores and omnivores. The first axis of a principal component analysis of texture parameters which significantly differed between extant taxa negatively correlated with proportions of vertebrates in their respective diets, and positively correlated with proportions of dietary invertebrates and with degree of dietary generalism. Projecting pterosaur microwear data into this multivariate space allows robust inferences of respective pterosaur diets. Microwear from *Dimorphodon* for example, previously hypothesised as a piscivore, indicates a diet of vertebrates and invertebrates, while *Darwinopterus*, argued to be a carnivore or a piscivore, has microwear that indicates insectivory. Dietary analysis from microwear provides new evidence and novel insights into the ecological roles of pterosaurs and pterosaur dietary evolution.

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## Physical and environmental controls on Paleozoic tetrapod dispersal across Pangaea

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The Carboniferous and Permian were crucial intervals in the establishment of terrestrial ecosystems, which occurred alongside substantial environmental and climate changes throughout the globe, as well as the final assembly of the supercontinent of Pangaea. The influence of these changes on tetrapod biogeography is highly contentious, with some authors suggesting a cosmopolitan fauna resulting from a lack of barriers, and some identifying provincialism. Here we carry out a detailed historical biogeographic analysis of late Paleozoic tetrapods to study the patterns of dispersal and vicariance. A new supertree of tetrapods is generated, providing the most comprehensive phylogenetic hypothesis of this group during the Paleozoic. A likelihood analysis, used to infer ancestral geographic ranges, is combined with a novel stochastic mapping approach to assess rates of vicariance and dispersal. A decrease in dispersal rates and peak in vicariance rates are identified across the Carboniferous/Permian boundary, principally among amphibian-grade tetrapods. These are attributed to the increased orogenic activity occurring at this time, and a previous suggestion of the rainforest collapse as a driver of increased provincialism is rejected. Dispersal rates of amphibians remain low for the rest of the Permian, while those of amniotes recover through the Cisuralian (early Permian). A second trough in dispersal rates is noted at the end of the Guadalupian (middle Permian), also accompanied by a peak in vicariance rates, tentatively attributed to climate shifts observed at this time increasing environmental heterogeneity between equatorial and temperate regions.

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## Modelling Avian Ventilation Mechanics with 3D Levers and Linkages

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Modern birds have a derived respiratory system, which is associated with a highly modified ribcage. The ribcage, along with other parts of the trunk, has also undergone extensive

modifications due to the evolution of flight, and ribcage morphologies differ between birds with different locomotor modes. However, the functional implications of these morphological differences for the mechanics of ventilation remain unclear. We examine ribcage ventilator function across a diverse avian sample, by employing a new modelling approach where the ribcage is treated as a 3D linkage system. CT scan data were made available as part of the oVert project, and the linkage models were generated based on anatomical landmarks obtained from the CT data. For interspecific comparisons, we use the expansion advantage (EA) – the change in ribcage volume for a given movement of the sternum – as a metric of ribcage ventilation performance. When comparing EA across birds, our initial hypothesis was that species with more energetically demanding flight styles would have the most “efficient” ribcages (highest EA). However, there is no real observable difference between birds of different flight styles; instead, the highest EA values are present in flightless birds. We therefore put forward the alternative hypothesis that ventilation is constrained in volant taxa by the locomotor demands which flight places on the skeleton. We also present other possible applications of the models, such as estimating mechanical advantage of intercostal muscle fibres and exploring the functional consequences of variation in intercostal muscle architecture.

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### **Ceratopsian braincase morphology and palaeoneurology through ontogeny**

Claire Bullar<sup>1</sup>, Qi Zhao<sup>2</sup>, Mike Benton<sup>1</sup> and Michael Ryan<sup>3</sup>

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The development of cognitive abilities throughout ontogeny is of particular interest for the Ceratopsia; a group of non-avian dinosaurs for which many behavioural theories have previously been posited. Regrettably, ceratopsian braincases are often neglected in contemporary palaeontological studies due to the high level of fusion and consequent obscurity of sutures. Characterising any major changes occurring in this area during growth may further inform theories of mental development. Due to their basal evolutionary position, Asian ceratopsians represent an important set of taxa within Ceratopsia. Here we use an ontogenetic series of *Psittacosaurus lujiatunensis* specimens as a basis for a study into morphological disparity levels within ceratopsian palaeoneurological architecture during growth. Through the examination of high resolution CT scans, we find that the braincase alters significantly as ontogenesis progresses. For example, as *P. lujiatunensis* grows, the supraoccipital undergoes dramatic morphological changes and shrinks to make way for the expanding parietal. We also explore semi-circular canal plasticity in relation to the posited postural shift of this species during ontogeny. There appears to be some change in semi-circular canal morphology that might support previous postural shift theories. This has been a rare opportunity to acquire detailed 3D information on numerous ontogenetic stages of a single dinosaur species, from hatchling through juvenile to adult, and to link the various allometric and morphometric deviations from isometry to wider function. In further work, these studies will provide an excellent basis for comparison with more derived neoceratopsians from North America and for exploration of ontogeny-phylogeny links.

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### **Standardising for spatial sampling bias demonstrates constrained diversification of Phanerozoic terrestrial tetrapods**

Richard J. Butler<sup>1</sup>, Roger A. Close<sup>1</sup> and Roger B. J. Benson<sup>2</sup>

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Species richness scales with sampled area, so variation in the geographic extent of fossil localities can profoundly distort fossil diversity curves. However, conventional approaches for estimating palaeodiversity do not correct for spatial biases. In fact, spatial biases explain up to 80% of the variation in diversity estimates for terrestrial tetrapods, even when using sampling-standardisation methods such as shareholder quorum subsampling to control for other forms of bias. We have previously corrected for this by standardising the palaeogeographic spread of fossil localities prior to subsampling. Here, we modify and extend this approach to the entire Phanerozoic record of terrestrial tetrapods, using a dataset of unprecedented size (~40,000 occurrences from ~10,500 collections) from the Paleobiology Database. Patterns of spatially-standardised diversity are robust across a range of geographic scales, and suggest that diversity increased by a factor of ~1.5 from the Palaeozoic into the Mesozoic. Spatially-standardised terrestrial tetrapod diversity exhibits stasis during the Mesozoic, with no statistically significant increase, but rises 2–3-fold across the Cretaceous–Palaeogene boundary, driven by the radiation of Cenozoic mammals. However, there is no evidence for further systematic increases in tetrapod diversity during the Cenozoic. In fact, median spatially-standardised diversity may have even declined from the late Palaeogene to the present, perhaps in response to the cooling of global climate. These results strongly contradict face-value ‘global’ diversity curves that have been used to suggest exponential increases over the last ~100 million years, and suggest, instead, that long-term terrestrial tetrapod diversification was largely constrained.

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## **Evaluating the performance and correlation morphological characters in reconstructing avian and squamate evolutionary history**

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Despite increased use of genomic data in phylogenetics, morphological information remains important for resolving evolutionary relationships, in particular for fossil species for which molecular data is unavailable. However, selection and evolutionary lability can make some morphological characters more prone to homoplasy than others. Moreover, when these characters evolve in semi-autonomous modules, they have the potential to overwhelm genuine phylogenetic signal contained within the data. Here we investigate the prevalence and distribution of character correlations in morphological data in birds and squamate reptiles. We assess the fit of 3 models of character evolution (one uncorrelated, two correlated) to each pair of characters in several datasets to uncover the presence of correlated characters which may impact phylogenetic reconstruction. We compare models using AICc weights and calculate the overall percentage of correlated characters pairs both within and between osteological and soft tissue character partitions. We find few correlated character pairs and no significant difference in amount of correlation between partitions. As such, morphological character correlation is unlikely to be undermining our ability to reconstruct accurate phylogenetic relationships.

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### 3D investigation of the head and shoulder of a stensioellid fish reveals Stensioellida to be a valid group of placoderm-grade affinity

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The Early Devonian Hunsrück Slate, Germany, provides some of the oldest examples of articulated placoderms and other early jawed vertebrates. Nevertheless, many of those remains consist of highly flattened, pyritised and slightly metamorphosed fossils, so that the anatomy and phylogenetic relationships of these specimens are still poorly understood. Among these forms are the enigmatic stensioellids. Their anatomy is still poorly understood so that their validity as a natural group is still uncertain as well as their phylogenetic affinity, been variously interpreted as either placoderms or holocephalan chondrichthyans. Here we present a well-preserved braincase and shoulder girdle of a stensioellid from the Hunsrück Slate, investigated using X-ray computed tomography scanning. The braincase shows a combination of rhenanid and 'acanthothoracid' placoderm characters, especially in the morphology of the occipital glenoids and paravagal cavities. The orbital region presents a broad suborbital floor, well-developed transverse otic processes bounding the orbits laterally, and the openings for many cranial nerves. The morphology of the shoulder girdle resembles the peculiar anatomy of rhenanids and helps to clarify the unusual shoulder girdle morphology of *Stensioella*. It also confirms that the Hensrueck stensioellids are affine to each other and thus that Stensioellida represent a natural group. Moreover, all those features confirm a placoderm identity for those specimens, and in particular we suggest that stensioellids are proximate relatives of rhenanids. This work helps settle a long-standing debate about the phylogenetically enigmatic stensioellids as placoderms and establishes that the Stensioellida are a valid group, rejecting an holocephalan affinity for stensioellids.

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### A quantitative analysis of cranial growth and evolution in sea turtles (Testudinata: Cheloniodea)

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Sea turtles are an odd group of reptiles; despite the family's small size (7 species) there is remarkable dietary diversity, with each species having a differing diet. This diversity is made more interesting given that as hatchlings and juveniles they all eat small, soft-bodied, pelagic organisms. How these changes in diet are related to post-hatchling changes in skull shape has not been systematically investigated. We investigated the ontogenetic changes in skull shape using a sample of over 40 skulls representing all 7 species at a variety of growth stages. With the use of X-ray computed tomography we analysed skull shape using 46 equivalent landmarks and 3D geometric morphometrics (analysed using the R package *geomorph*). General ontogenetic trends in skull shape are similar those of other tetrapod groups, with sensory structures showing negative allometry and trophic structures showing positive allometry. Hatchling skull shape better reflected the molecular phylogeny of the group than adult skull shape. The degree of divergence away from the hatchling morphology varies across the species, showing differing patterns of both paedomorphy (*Dermodochelys coriacea*) and peramorphy (*Caretta caretta*) which are themselves associated with particular skull shapes and diet. The most paedomorphic species, *Dermodochelys coriacea*, has a very similar diet to that of hatchling turtles whereas the most peramorphic species *Caretta caretta* has a diet of hard-shelled benthic organisms. These results suggest that the major changes in skull shape during growth appear to be more defined by diet rather than by phylogeny.

## Climatic drivers behind the demise of non-avian dinosaurs at the end Cretaceous mass extinction

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The extinction of the non-avian dinosaurs at the Cretaceous/Paleogene (K/Pg) boundary, 66 million years ago, has been attributed to significant changes in climatic conditions. However, fierce debate surrounds both the tempo of their demise, as well as the mechanism of their extinction. Whereas a gradualistic decline has been suggested based on a literal view of the fossil record, and via birth-death models, results from palaeodiversity analyses that account for fossil record bias point towards a geologically instantaneous extinction. Here we investigated spatiotemporal patterns of extinction processes during the last 15 million years of the Cretaceous. Integrating paleoclimate models with ecological and taphonomic modelling, combined with fossil occurrence data, we find no evidence for a long-term decline of non-avian dinosaurs in the lead up to the K/Pg event. We combined our ecological niche models with palaeoclimate simulations, reproducing the effects of purported drivers of extinction on global climate (i.e. the extraterrestrial Chicxulub impact *versus* Deccan Traps volcanism), to produce further spatiotemporal constraints on extinction patterns. By decoupling the effects of multiple physical agents, we observe a strong signal for the Chicxulub-induced nuclear winter in decimating habitability globally, whereas Deccan-induced warming appears to have actually increased habitability instead. We use these different lines of evidence to argue for the Chicxulub asteroid impact as the main driver of the sudden extinction of the non-avian dinosaurs. In contrast, Deccan volcanism might have produced a buffering effect, allowing some taxa to survive one of the most catastrophic mass extinctions in the history of life.

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## *Acherontiscus*, the earliest durophagous tetrapod redux

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*Acherontiscus caledoniae* is a small limbless tetrapod of unknown provenance, known from a single, Early Carboniferous specimen from Scotland, first described by Carroll in 1969. In 2013 Milner and Ruta showed it to be the earliest heterodont tetrapod, with large crushing teeth at the centre of the dentary row, and large denticles on the pterygoids. Further micro-CT scanning reveals additional details of the dentition, jaws, palate, parasphenoid and sphenethmoid, although the skull roof remains problematic. The dentary tooth row carries three or four small teeth at the back, at least 7 at the front, and four or five centrally placed large robust teeth, two of which have ribbed crowns. In *Acherontiscus* the combination of tooth size and shape is difficult to interpret functionally, but it is paralleled by an actinopterygian of similar age from Loanhead (Scotland). There, a unique faunistic assemblage has been documented, including small durophagous dipnoans, and possible filter feeders among the limbless adelospondyls and the spade-headed *Spathicephalus*. Palynological analysis indicates a late Visean to Pendeian age and a palaeoenvironment of a small body of still water amid herbaceous lycophytes with a more distant forest of larger lycophytes. Phylogenetic

analyses place *Acherontiscus* as sister to adelospondyls and close to colosteids, with that clade remote from microsauria. Among tetrapods, heterodonty is common in mammals, infrequent in reptiles although present in some Late Carboniferous and Early Permian taxa. It is extremely rare in amphibians. *Acherontiscus* casts new light on the morphological and ecological diversity of Carboniferous tetrapods.

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

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Exceptionally preserved fossils are vital for accurately reconstructing ancient organisms. The preservation of soft-tissues is an incredibly rare occurrence, commonly restricted to specific depositional regimes for a brief moments of geological time and these sites offer an important 'window' into the geological past. The Mazon Creek Lagerstätte (Illinois, USA) is one such fossil bed, where a diverse assortment of late Carboniferous marine and terrestrial vertebrate fossils, including lampreys, fish, sharks, amphibians, and reptiles, have been described. Commonly, both recalcitrant (bone, teeth etc.) and soft-tissues (integument, organs and pigments etc.) preserve within siderite concretions, yet the mode of preservation is poorly understood. In order to elucidate the controls on exceptional preservation in siderite concretions, we utilised museum collections, fieldwork and geochemical analyses (SEM-EDX and XRF) to create the first taphonomic model for soft-tissue preservation in the Mazon Creek, identifying that soft-tissues are preserved by clay templating. We also identify, for the first time, that preservation potential of soft-tissues in the Mazon Creek Lagerstätte is not primarily controlled by tissue histology, or salinity as was previously suggested, but by palaeogeography, particularly proximity to the palaeo-coastline. The impact of palaeogeography is an undervalued control on preservation and has important implications for future investigations of exceptionally preserved organisms, especially in geographically vast sites where ambiguous early vertebrates have been described.

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## **Lung evolution in osteichthyans: insights from synchrotron phase-contrast microtomography**

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The water-to-land transition and colonization of terrestrial habitats by vertebrates in the Late Devonian (~360 Myr ago) confronted a series of challenges, namely desiccation, reproduction, osmoregulation, exposure to ultraviolet radiation and air-breathing. Interestingly, the air-breathing specialisation arose in fishes during the Silurian (~438–408 Myr ago), millions of years before the colonisation of the continental realm by the first terrestrial vertebrates, and has probably emerged independently, as various structures known as Air-Breathing Organs (ABO) are involved. Lungs are the main ABO of the respiratory system of all vertebrates, responsible for the gas exchange and, therefore, fundamental for our survival in the

atmosphere. Although lung development is well known in tetrapods, its evolution and development in fossil and extant basal osteichthyans (actinopterygians and sarcopterygians) remain poorly known, particularly whether the lung in osteichthyans was primitively an unpaired or paired organ. The lung of basal lungfishes and coelacanth is unpaired, whereas that of polypterids has been described as paired. Here, we will present, for the first time, unique ontogenetic series (embryos, juveniles and young adults) of basal actinopterygians, derived lungfishes, and basal amphibians studied using synchrotron propagation phase-contrast microtomography. Based on new virtual sections and 3D reconstructions of the lung in different ontogenetic stages of these taxa, we will discuss the primitive state and the evolutionary history of osteichthyans lung.

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## **Do birds have whiskers?**

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The avian sense of touch is still understudied. While the function and properties of the mammalian tactile whiskers have been intensely explored by researchers, the avian counterparts have been almost entirely overlooked. Many nocturnal avian species have whisker-like feathers on their upper beak, called rictal bristles. Mammalian tactile whiskers are thought to be associated with nocturnality, helping navigation and foraging in dark, complex environments, therefore perhaps rictal bristles could carry out a similar function. If they can convey tactile information from the environment, they need to be paired with mechanoreceptors around their follicles, to receive and transmit those cues to the brain. Consequently, this study provides the first understanding of rictal bristle anatomy and function by comparing the follicle anatomy of representative species of the Caprimulgiform order, in which rictal bristles are particularly prominent. Results demonstrated variation between species in term of presence, organisation and number of mechanoreceptors, as well as in tissue density and composition. Nocturnality appeared to be a possible predictor of the presence and organisation of mechanoreceptors around the follicles. Furthermore, this study gives us insights into avian sensory systems, and also helps us to understand more about these species, of which relatively little is known.

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## **Cranial osteology of *Pachycormus*, and relationships and divergence times among pachycormiforms**

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Pachycormiformes is a modestly diverse order of stem teleosts, ranging in age from the Early Jurassic to the Late Cretaceous, and found in marine deposits across the globe. *Pachycormus* is one of the oldest pachycormiforms, and is often used to represent the group in phylogenetic analyses of stem teleosts. While many flattened specimens have been found in deposits such as the Early Jurassic (Toarcian) Posidonia Shale, three dimensionally preserved individuals are known from the coeval Strawberry Bank locality of the Beacon Limestone Formation of Dorset. Previous descriptions of *Pachycormus* from this locality have focussed on the braincase as revealed by mechanical preparation, or are unpublished works targeting acid-prepared material that has lost spatial anatomical context. Here we use CT-scanning to examine the cranium and pectoral girdle of a 3D specimen of *Pachycormus* from Strawberry Bank, highlighting the internal structures, that would previously have been hidden, in their true anatomical context. We confirm major aspects of braincase morphology in earlier descriptions,



and augment earlier accounts of the gill skeleton. We also provide the first detailed interpretation of the pectoral fin endoskeleton, which closely resembles that of better-known Late Cretaceous forms. These and other observations are included in a revised combined evidence phylogenetic analysis which provides insights into pachycormiform interrelationships and divergence times.

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

**Richard Dearden** and Martin Brazeau  
*Imperial College London*

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

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### **Sediments, skulls and squishing – taphonomic investigations of ceratopsian skull deformation**

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The geological setting of a fossil will determine what happens to it and its final state of preservation. The short-frilled ceratopsian *Centrosaurus* is known from a large number of skulls from the 80 square kilometre region known as Dinosaur Provincial Park in Alberta, Canada in rocks spanning approximately two million years. Reliable identification of the possible genera and species of these centrosaurines is complicated by the deformation that they have experienced. These skulls exhibit a range of deformation states from almost pristine to severely flattened and sheared in one or more planes. These skulls occur in either nearly incompressible sandstones or severely compressed mudstones, and the observed deformation of the *Centrosaurus* skulls reflects the strengths of their enclosing sediment. The DPP *Centrosaurus* skulls have not experienced any tectonic deformation, only two levels of compaction – one due to immediate, perimortem burial by several metres of wet sand or mud,

and then a longer term burial under at least one kilometre of younger Paleogene and Neogene sediments. Using three-dimensional digital models of nearly pristine and warped skulls derived from photogrammetry, we investigated the patterns of deformation of the skulls of *Centrosaurus* in an attempt to reliably recover the original anatomy and proportions of the skulls. Accurate reconstructions, via the application of retrodeformation, can improve the morphometric analysis and systematics of this genus.

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## **What is ‘*Steneosaurus*’? evolutionary relationships within Teleosauroidea (Crocodylomorpha, Thalattosuchia)**

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Thalattosuchia was an exceptional group of marine crocodylomorphs that flourished within the Mesozoic Era, evolving an extensive range of environmental adaptations and feeding specializations. One of the two major groups within Thalattosuchia is Teleosauroidea, a distinctive clade superficially resembling modern *Gavialis*. They were morphofunctionally diverse and attained a near-global distribution, frequenting shallow marine/brackish ecosystems throughout the Jurassic. Despite increased anatomical research over the past ten years, the evolutionary relationships within Teleosauroidea are still poorly understood and little studied. One particular problem within teleosauroid taxonomy is the waste-basket genus ‘*Steneosaurus*’, whose validity has recently been called into question. Here we present an in-depth phylogenetic analysis of Teleosauroidea. Approximately 530 specimens from 12 countries were examined, creating the largest, most comprehensive teleosauroid dataset collected to date. We used parsimony methods with a dataset including 152 crocodylomorph taxa (twenty-six of which are teleosauroids). We find the basal-most teleosauroids (e.g. *Steneosaurus gracilirostris*) to share a common morphotype (i.e. longirostrine, laterally-facing orbits) with the basal-most metriorhynchoids (e.g. *Pelagosaurus typus*), and that these two clades were likely similar to one another in terms of habitat and lifestyle. We then define two major subclades within Teleosauroidea: 1) a Sub-Boreal northern European/Tethyan/Eastern Gondwanan ‘*Steneosaurus*’ + *Machimosaurus* radiation, which represented the most successful lineage of teleosauroids in terms of species, feeding specializations and morphofunctional diversity, and 2) a second Laurasian radiation which includes pholidosaurid-like, more terrestrial and bizarre-looking teleosauroids. In addition, we evaluate the validity of the genus ‘*Steneosaurus*’ and restrict it to just one taxon, *Steneosaurus edwardsi*

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## **Brain structure supports interpretations of an active lifestyle in a small, iconic British dinosaur**

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*Hypsilophodon foxii* is a small ornithichian dinosaur known from the Lower Cretaceous of the UK. Named over 140 years ago it has a rich history, iconic status, and is frequently used as a model for the earliest neornithichian dinosaurs and therefore is an important taxon for evolutionary analyses. Substantial material has been recovered from the Isle Wight (mainly from the Wessex Formation of the Wealden Group) comprising several almost complete articulated and associated skeletons that have facilitated extensive study and detailed descriptions. Previous research includes a partial reconstruction of the brain endocast based on external examination of braincase material. To complete and validate this earlier effort, we

X-ray CT scanned the cranial elements of a single individual and segmented the endocast using a combination of thresholding and direct manual delimitation in Avizo. Our new reconstruction reveals features that were previously unknown for *Hypsilophodon foxii* and are often not discernible in fossilised braincases: a midline hypophyseal canal, Dorello's canals (which housed cranial nerve VI: the abducens), the semicircular canals, and the endosseous cochlear ducts (lagena). The cranial nerves exit the braincase along an axis oblique to the horizontal semicircular canal which resembles the arrangement found in juveniles of *Dysalotosaurus* (a close relative of *Hypsilophodon*) whereas the cephalic flexion and shape of the pituitary fossa resembles adults of *Dysalotosaurus*. The relatively large floccular lobes suggest an active lifestyle which is consistent with the large orbits, long legs, and mineralised intercostal plates that supported the ribcage.

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## **Estimating the flight capabilities of fossil birds from extant bird data and aerodynamic theory**

**Carolina Karoullas** and Robert Nudds  
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Understanding fossil avian flight capability is key to understanding their ecology as well as bettering our understanding of the origins of powered flight in vertebrates. Using current aerodynamic theory in the form of aerodynamic power curves as well as extant data has great potential in helping palaeontologists answer questions about fossil avian flight capability. However, the potential error associated with using extant data to extrapolate back to fossil taxa is often ignored. This error must be explored in greater detail to ascertain if aerodynamic power curves can be used in avian palaeontological research. Subsequently, this study explores how the error associated with the regression equations required to calculate the morphological variables needed to produce the aerodynamic power curves translates into the curves for various fossil and extant taxa. It was found that the error associated with creating an aerodynamic power curve in this manner was too large for the resultant curves to be reliable. It was also found that body mass, in particular, plays an important role in creating this error while body frontal area and wing area play a secondary but still significant role. Consequently, aerodynamic power curves cannot be used to reliably infer the flight capabilities and flight styles of fossil taxa. This study highlights the importance of accounting for error in statistical analyses.

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## **Morphological convergence and functional diversification of sabre-toothed vertebrates**

**Stephan Lautenschlager**  
*University of Birmingham*

Sabre-toothed mammals represent one of the most iconic and instantly recognisable vertebrate fossils. Due to their unusual appearance, featuring two extremely elongated canine teeth, taxa such as *Smilodon* have received considerable academic and public interest. However, sabre-tooths were much more diverse and abundant than this individual, well-known species would suggest. Sabre-tooth morphologies have evolved at least seven times independently over the course of 250 million years in Permian mammal-like gorgonopsians, in the marsupial sabre-tooth *Thylacosmilus*, and five different lineages of carnivorous mammals. Due to this overall morphological similarity, it is generally assumed that the cranial function of all sabre-toothed vertebrates was largely comparable. While some differences between taxa exist, it is generally assumed that they used a similar 'canine-shear' bite to drive their canines through their prey. However, this assumption has not been tested in detail from a biomechanical perspective, and it is further unknown, if the same evolutionary trends led to the

convergent emergence of sabre-toothed morphologies in different clades. Using a combination of digital visualisation, biomechanical analyses and evolutionary modelling, functional performance measures were compared across seven sabre-tooth groups (absolute/effective jaw gape, bite force, mandibular stability). The results demonstrate that these performance measures varied considerably between different groups and between different species. Evolutionary pathways leading to the sabre-toothed morphology were further found to be significantly different between groups. This suggests, that functional diversity was much more widespread among sabre-toothed vertebrates than previously assumed and is likely related to differences in ecological niche occupation and phylogenetic constraints.

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## **Meta-analytical integration of fossil and molecular data in phylogenetic inference and the first truly comprehensive phylogeny for Cetacea**

**Graeme T. Lloyd**<sup>1</sup> and Graham J. Slater<sup>2</sup>

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A major challenge in phylogenetic inference is synthesising fossil and extant data to generate total-group phylogenetic hypotheses for macroevolutionary inference. This is especially difficult when focusing on large clades (hundreds or more species) where morphology alone becomes too labour intensive to be feasible. Here our aim was to produce a phylogenetic hypothesis for the cetacean total-group, comprising some 700 species. Initially we applied an existing meta-analytical protocol to estimate relationships that reanalyses multiple published morphological cladistic matrices before synthesising the results into a single “metatree”. However, this approach ignores the additional available molecular evidence and results in topologies that are incongruent with extant relationships. Next we applied a novel approach where a single molecular alignment was inserted into each morphological matrix before applying the same metatree protocol. This resulted in increases in both resolution and congruence with extant relationships. Finally, we generated three different metatrees representing different levels of taxonomic coverage, comprising 439, 582 or 725 species. These are the results (respectively) of: 1) only including species appearing in a source matrix, 2) including all species assigned to a genus sampled in a source matrix, or 3) including all species assigned to Cetacea. These represent a trade-off between coverage and confidence of phylogenetic placement. We conclude by sharing some preliminary macroevolutionary results before discussing the general applicability of our approach.

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## **Odd narial features in *Ichthyosaurus* suggest the presence of salt glands**

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Salt-secreting glands allow marine reptiles to remove salts that accumulate from ingesting seawater and prey that is isosmotic with seawater. The anatomical position of salt glands varies among extant marine reptiles: orbital glands in sea turtles, oral glands in marine crocodiles and snakes, and nasal glands in lizards. We report features of the external naris in several specimens of the Early Jurassic ichthyosaur *Ichthyosaurus* that might be related to salt glands. On some specimens, a small triangular process on the lacrimal protrudes into the external naris, defining a circular region at the posterior end of the naris. Sometimes the lacrimal is thickened, forming a tall edge on the posterior naris. These features might indicate the position of a duct for excreting a concentrated salt solution from salt glands, if not the salt

gland itself. Many specimens of *Ichthyosaurus* preserve stomach contents consisting of dense masses of cephalopod hooklets, evidence that they were ingesting prey with a high salt content. Thus a method to excrete the excess salt was a necessity. The presence of salt glands has been inferred in other extinct marine reptiles from structures in the narial region of mesosaurs and antorbital region of metriorhynchid crocodiles. Additionally, paired casts of lobate structures in the internal nasal region of a Cretaceous polycotyloid plesiosaur have been interpreted as evidence of nasal salt glands. Thus it is likely that ichthyosaurs also possessed salt-secreting glands.

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## Non-random distribution of homoplasy and the definition of actinopterygian clades

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Traditionally, actinopterygian clades have been defined morphologically and morphology is the only data directly available for fossil taxa. It is certainly a powerful tool to find the patterns of phylogenetic relationships. However, the incorporation of fossils in cladistic analyses have shown that unique synapomorphies are extremely rare, and they might often be rendered homoplastic when new evidence comes to light. Our analyses show that the distribution of homoplasy in the two largest published data sets for Paleozoic and Mesozoic actinopterygians, respectively, is not random, but homoplasy tends to concentrate at the base of the major clades, especially at major radiations. We propose that this pattern is the logical consequence of evolutionary experiments leading to mosaic morphotypes on the stem to new lineages and clearly recognizable, apomorphic morphotypes become established only at higher nodes of each lineage. Our hypothesis implies that homoplasy is a real and positive by-product of Evolution that will always be present in our datasets and will not necessarily lead to spurious results. Good taxon sampling at the base of major radiations is important to solve the homoplasy/synapomorphy question; here, fossil data is therefore essential. An operational consequence of this pattern of concentrated homoplasies is the instability of character-based definitions of clades. We argue that the actinopterygian clades themselves are stable and can be clearly defined using stem-based or node-based definitions. Morphological diagnoses are useful and should be based on unique character combinations, including apomorphies, but we should abandon the use of character-based definitions of clades.

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## Walking with unicorns – metacarpal morphology of the Rhinocerotidae

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The Rhinocerotidae represent a geographically widespread family of odd-toed ungulates (Perissodactyla) containing five modern representatives and multiple extinct lineages. The variation in the limb proportions and manus shape of rhinos has never been quantified in relation to size or habitat. Here, we report the first findings from a geometric morphometric assessment of rhinocerotid metacarpal morphology, in relation to size and ecology. 78 third metacarpals (MCIII) from 23 known species of rhinocerotid were laser scanned. Bone shape was quantified using landmark-based geometric morphometrics. Generalised Procrustes analysis removed effects of scale, orientation and location, and variation was assessed using a PCA. Principal component scores were regressed against estimated body mass (size metric)

and habitat data using Ordinary Least Squares regression. Habitats were defined per species based on average carbon and oxygen isotope values, with phylogenetic groups selected *a priori* and tested for differences using perMANOVA. Morphospace results showed a clear axis of robusticity along PC1, albeit skewed with the inclusion of “hippo-like” teleoceratines. PC2 showed variation in the magnum and MCIV joint facets, and was significantly correlated with isotope-defined habitat ( $p=0.02$ ) and estimated body mass ( $p<0.01$ ). Teleoceratines were significantly separate from all other clades ( $p<0.05$ ); dicerorhines (e.g. *Coelodonta*) were not significantly different to rhinocerotines (*Rhinoceros*). Rhinos inhabiting open grassland and steppe (*Ceratotherium*) demonstrated notable differences in their MCIII shapes compared to those in closed environments (*Teleoceras*), with closed-habitat taxa generally exhibiting a less concave proximal joint facet independent of mediolateral robusticity, thus spreading loading forces more evenly over the third metacarpal.

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## **A comprehensive description of *Endothiodon bathystoma* (Anomodontia, Therapsida), a dicynodont from the late Permian of the Karoo Basin of South Africa**

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The dicynodonts are an extinct group of herbivorous non-mammalian synapsids that were abundant from the Middle Permian through to the Early Triassic. The genus *Endothiodon* is well known from late Permian deposits of the Karoo Basin of South Africa. It is characterized by internal tooth rows on the premaxilla and dentary arranged in replacement waves; longitudinal ridges running from the premaxilla to the pineal crest; and a prominent pineal boss with a pineal foramen. Although *Endothiodon* is well represented by cranial material in South African Karoo vertebrate collections, its postcrania is largely poorly known. Recently, an almost complete skeleton of *Endothiodon* (SAM-PK-K011271) was recovered from the uppermost *Pristerognathus* Assemblage Zone of the Karoo Supergroup. The 1.5m-long fossil comprises the skull and most of its postcranial elements preserved in articulation. The research presented here comprehensively describes the skull and postcranial anatomy of this specimen, which permitted its identification as *E. bathystoma*. By comparison of its skull with all the *Endothiodon* specimens in collections in South Africa, SAM-PK-K011271 was found to be the second largest individual. The well-preserved skull and postcranial skeleton of SAM-PK-K011271 makes it an ideal reference specimen for *E. bathystoma*. Thus, the current study provides an ideal foundation for further studies to address the 3D skeletal reconstruction, biomechanical functioning, as well as other aspects of the palaeobiology of *E. bathystoma*.

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## **North Africa's first stegosaur and the armoured dinosaurs of Gondwana**

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Ankylosaurs and stegosaurs, the eurypodan armoured dinosaurs, are known from Middle Jurassic to Late Cretaceous deposits worldwide. Their remains are abundant and diverse from Laurasian continents, but just six genera are known from Gondwana, and most of these are known from a single partial skeleton alone. It is currently unknown whether the paucity of eurypodans in Gondwana represents a sampling bias, or whether they were genuinely rare. A new stegosaur, from the Bathonian El Mers Group of the Middle Atlas Mountains, Morocco, adds to the known diversity of Gondwanan thyreophorans, and is also one of the earliest records of Euryopoda from anywhere in the world. The stegosaur bears a number of unique

characteristics that allow it to be identified as a new taxon. Phylogenetic analysis suggests a closer relationship with European Late Jurassic taxa than with either of the other two stegosaurs currently known from Africa. This new find, and tantalizing but fragmentary evidence from other parts of Gondwana, indicate that perhaps eurypodans were not as rare in Gondwana as previously thought, and the lack of body fossil record is due to sampling biases. However, there is no statistical correlation between Gondwanan eurypodan occurrences, rocks that commonly preserve dinosaur fossils, or sampling efforts as judged by the number of dinosaur collections made, indicating that sampling biases are not to blame for the rarity of eurypodans in Gondwana, and they may well have been a rare constituents of Gondwanan Mesozoic ecosystems.

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## **New insights on the phylogenetic relationships and biogeographic history of eusauropod dinosaurs**

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Eusauropod dinosaurs had a global distribution by the Middle Jurassic, with the first neosauropods known from the Late Jurassic. Significant progress has been made in the last decade in terms of the phylogenetic relationships of the neosauropod clades Diplodocoidea and Macronaria, via increasing taxon and character sampling, as well as revision of existing characters. However, focussing on these clades separately limits our ability to determine the placement of taxa that lie close to the base of Neosauropoda. Here we present a revised and expanded phylogenetic analysis, comprising 117 taxa, including most Late Jurassic to mid-Cretaceous eusauropods, scored for 542 characters. Our topology generally follows the main relationships recovered in recent analyses, but provides support for several novel or previously uncertain placements. *Haplocanthosaurus*, from the Late Jurassic Morrison Formation of the USA, has proven to be one of the most unstable eusauropod taxa: our results support its placement as a basal diplodocoid. The enigmatic *Tendaguria*, from the Late Jurassic Tendaguru Formation of Tanzania, is recovered as a non-neosauropod turiasaur, the first representative of Turiasauria recognised from Gondwana. A caudal vertebral sequence from the Tendaguru Formation displays several features that indicate a close relationship with Middle–Late Jurassic mamenchisaurids, otherwise thought to be endemic to East Asia. Analysis using the Maximum Likelihood R package BioGeoBEARS, incorporating palaeogeographic constraints, indicates that the biogeographic history of eusauropods is best explained by a combination of sympatry, early occurrences of widespread ancestral stocks followed by regional extinction, and founder-event speciation (i.e. long-distance geodispersal).

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## **An everyday tool: how the avian neck has adapted to (almost) every situation**

**Ryan D. Marek**, Peter L. Falkingham and Karl T. Bates

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Acting as a surrogate forelimb, the avian neck allows for the head to perform environmental manipulation tasks usually accompanied by the forelimbs, which are primarily adapted for flight in birds. This additional selection pressure on the cervical system has led to a vast array of neck morphologies in modern avians, yet no systematic study of this variation has occurred, owing to fluctuating cervical counts. *Hox* genes regulate axial regionalisation in vertebrates and the number of cervical regions is fixed within a group of vertebrates. Thus, studying cervical regionalisation overcomes problems associated with varying cervical counts. Using a combination of 3D geometric morphometrics and Phenotypic Trajectory Analysis this study

assesses the number, size and shape of cervical regions amongst a diverse selection of extant birds. Results support 5 cervical regions within all birds. The anterior- and posterior-most regions show little change in region size, yet the middle 3 regions vary enormously in size. However, region size appears unaffected by both neck elongation and ecology (except for birds that forage in water). Phenotypic trajectory analysis was used to investigate shape change across the entire cervical column, and only birds belonging to 'extreme' ecologies (e.g. carnivores) displayed significant differences from other ecological groupings. Using regionalisation as a metric, it appears that one specific factor does not govern neck morphology in birds, and that the avian cervical column is a generalist musculoskeletal system, capable of performing a multitude of tasks on a daily basis, acting as a surrogate arm.

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### **A 3D reconstruction and mass estimation of a well-preserved pterosaur from Brazil**

**Elizabeth Martin-Silverstone**<sup>1,2</sup>

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Pterosaur fossils are frequently incomplete and flattened, making accurate 3D reconstructions difficult, and impeding our understanding of body mass and mass distribution. Further difficulties exist with using skeletal correlates for mass estimation, often hailed as being a less subjective method possible with incomplete specimens, though these methods cannot generally be applied to pterosaurs. Strong correlates in both quadrupedal and bipedal, as well as volant and non-volant animals produce widely variable estimates, suggesting another method is needed. Here, computed tomography imaging of a three-dimensionally (3D) preserved skeleton of *Coloborhynchus robustus* is used to create a 3D skeletal model, and infer soft tissue body outlines and volumes, using muscular reconstructions as a guide. Densities of different regions are assigned based on previous studies, with modifications based on recent research. The result of the 3D volume reconstruction estimation (3D-VRE) for a *C. robustus* with a 5m wingspan is 30.9 kg. Convex hull estimation results in 23.6 kg. A combination of 3D-VRE and convex hull gives a preferred mass of 29.5 kg. This is heavier than estimates from other volumetric studies of similarly-sized, closely-related animals, but similar to those derived from regressions and scaling equations previously used for estimating pterosaur mass. One skeletal correlate — avian humeral circumference — produced a similar mass estimate, though the significant differences in morphology between pterosaurs and birds implore caution. Further tests are needed. Volumetric methods, though subjective and time consuming, may be more accurate for pterosaur mass estimation, given the morphological and phylogenetic distance from modern animals.

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### **The crystallography of the alligatorid eggshell. Insights from the EBSD**

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The crocodylomorph eggshell shares some fundamental characteristics of the archosaurian eggshell, as its calcite composition and shell units growing from amorphous or microcrystalline calcite aggregates, namely the basal knobs. Nevertheless, it remains to be proven that these structures are homologous to those of dinosaurs. Electron backscatter diffraction (EBSD) is here used for the first time to study a non-dinosaur archosaurian eggshell, namely eggshell from *Caiman yacare* and *Alligator mississippiensis*. Inverse pole figure colouring and grain



boundary maps show important differences in the general architecture of the alligatorid eggshell, when compared with avian and non-avian dinosaurs: shell units are formed by large orientation domains. In the inner part of the eggshell the orientation of these large domains is arbitrary, with crystals growing in every direction. The upper part of the eggshell presents, on the contrary, a strong alignment of crystals, with c axis subparallel to the shell unit vertical axis, although this alignment is much less marked than in dinosaur eggshells. The transition between both patterns occurs at the middle of the eggshell. Orientation domains are limited by high degree misorientation boundaries (over 20°). EBSD data shows that the general eggshell architecture of the crocodylomorph and dinosaur eggshell is fundamentally different and suggest that any similarities between crocodylomorph and dinosaur eggshell are convergent. The general aspect of the crocodylomorph eggshell is that of a drusy cement, suggesting that the organic control of the eggshell growth is minimal, when compared with dinosaur eggshells.

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### **Impact of continuous character coding on the reconstruction of the evolutionary history of Basal Sauropodomorpha**

**Omar Regalado**<sup>1</sup>, Paul Upchurch<sup>1</sup>, Paul M. Barrett<sup>2</sup>, Philip Mannion<sup>3</sup> and Susannah Maidment<sup>2</sup>

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Most recent phylogenetic analyses of 'basal' sauropodomorphs have supported a largely paraphyletic array of taxa leading to Sauropoda, implying a step-wise acquisition of the characters that later established the bauplan of sauropods. Continuous characters were first assessed to determine the extent to which they are correlated with size or each other. Strongly positively correlated characters were then removed to avoid unwarranted duplication and up-weighting. After a comprehensive evaluation of the matrices and character lists used in all analyses to date, and personal observations of specimens, we constructed a final revised data set of 75 taxa and 127 characters. Several sets of correlated characters were found, particularly pertaining to the scapula, ilium and femur - these include many characters that have made important contributions to previous phylogenetic data sets for Sauropodomorpha. Continuous characters were then treated as follows: a) continuous format, representing the character data as ratios; b) using the sample mean as a limit for the character states; and c) applying the method of identifying two-standard deviation gaps on the continuous characters when ordered. To evaluate the impact of these different approaches, the resulting phylogenies were compared with topologies produced with only discrete characters, and by assessing their stratigraphic fit. We found that choice of continuous data treatment appears to be introducing a bias on final topologies. Overall, under the different approaches this new data set does not support a pectinate array of 'basal' sauropodomorphs sauropods, but an array of several smaller clades, but not that congruent with the topology obtained from only discrete characters.

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### **The role of soft tissues in a biomechanical model of the rat skull**

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Musculoskeletal soft tissues, such as ligaments, fascia and cartilage, support structures of the body and distribute loads generated by muscles, body weight, feeding and locomotion. However, testing the mechanical function of these biological structures is challenging due to their complex material properties. With the exception of the jaw muscles, most biomechanical models do not take into account the influence of soft tissues, despite their likely impact on the strain regime of the skull. This is even more challenging when modelling fossil taxa with no soft tissue data. Our aim is to clarify and quantify the role played by apparently passive cranial soft tissues, including the sutures, ligaments and fascia, in a rat biomechanical model. Using 3D computer-based mechanical simulations based on micro-CT, *in vivo* data and detailed dissections, we combine multibody dynamics analysis and finite element analysis to compare the strains of the skull with and without soft tissues. The model was validated against bite force and strain gauge data collected *in vivo*. Sutures generally lead to a more uniform distribution of cranial strain and have the most significant effect on both strain magnitude (an overall increase) and distribution compared to other soft tissues. Including the temporal fascia had local effects on strain magnitude, particularly along the zygomatic arch. However, more research is needed to fully understand the significance of these soft tissues, including comparisons with other species and juvenile individuals. In a broader context, these results will serve to determine the relative significance of different soft tissues in reptiles versus mammals.

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## **Reconciling morphology and molecular data in inferring phylogeny for extant crocodylians**

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Phylogenies for extant taxa based on DNA are increasingly reliable, but often disagree with those based on morphology. For fossil taxa, phylogenies must remain based on morphology, and the accuracy of trees for these taxa is thus questionable. Here modern crocodylians were investigated to assess whether different methods of analyzing morphological data may yield trees consistent with DNA. Homoplasy of morphological characters was assessed against a composite DNA-based tree. Cranial characters were significantly less homoplastic than postcranial characters ( $p=0.05$ ). Characters passing two tests – (1) fully accurate scoring; and (2) strongly justifiable state delimitation – were significantly less homoplastic than other characters ( $p=0.01$ ). A maximum parsimony phylogeny from robust characters only with an extant outgroup (*Varanus*) placed the gharial (*Gavialis*) as the sister taxon to the false gharial (*Tomistoma*), agreeing with molecular data. However the tree was less resolved, with *Crocodylus* collapsing. Using a fossil outgroup (*Bernissartia*), *Gavialis* was placed as the sister taxon to *Tomistoma*+*Crocodylidae*. Additionally, phylogeny was inferred using 3D cranial surface scans using distance matrices and phylogenetic morphometrics; trees inferred broadly yielded an overall peramorphic-paedomorphic dichotomy and did not approach phylogeny inferred from DNA, although grouping of species, and separation of *Varanus* and crocodylians, agreed with conventional taxonomy and DNA data. Character composition and scoring, and outgroup choice, may partly explain differences between phylogenies inferred from molecular and morphological datasets. Shape data may be of taxonomic use at very large or small phylogenetic scales.

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## Functional morphology and hydrodynamics of plesiosaur necks: Does size matter?

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Plesiosaurs are extinct marine reptiles well-known for their unique body plan with two pairs of flippers and an elongated neck – the biomechanical implications of the long neck are not well understood. What are the implications for such a long neck during forward swimming? We evaluated hydrodynamics of neck length and thickness in plesiosaurs using computational fluid dynamics simulations. The simulations were performed of flow patterns forming around five distinctive plesiosaur models, three of different lengths (neck/body ratios of 0.2, 0.41, and 0.63) and two of different neck thicknesses (100% and 343% increase compared to cervical vertebrae width). By simulating water flow past the three-dimensional digital plesiosaur models, our results demonstrated neck elongation does not noticeably affect the force of drag experienced by forward swimming plesiosaurs. This is because pressure drag dominates over friction drag, but neck elongation does not alter frontal area. The consistent drag force experienced by the three neck lengths used in this study indicates that, at least for straight forward motion, hydrodynamic implications were not a limiting selective pressure on the evolution of long necks in plesiosaurs. However, thicker-necked models, in which the neck broadens caudally and smoothly blends into the trunk, experienced reduced drag compared to more ‘conventional’ thinner-necked models. Broader necks reduce the surface area normal or near normal to flow direction, thus reducing pressure drag. In conjunction with soft-tissue preservation reported in some plesiosaur necks, our simulations provide support for reconstructing plesiosaurs with more sea lion-like neck morphology, albeit in some cases much longer.

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## A quantitative protocol for assessing the developmental stage of embryos and its implications for pterosaurs

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Evidence for prenatal pterosaurs is rapidly increasing with 19 embryos and several hundred eggs distributed among four genera reported so far. Collectively, these records are contributing to an increasingly detailed model of the reproductive biology and early development of pterosaurs, but its validity hinges upon the accurate identification of the developmental stage of individual finds. Current assignments, which almost invariably posit a ‘near hatching’ stage for embryos, are insecure, relying on anecdotal evidence and untested assumptions. We reassessed all published records using a new approach consisting of four complementary quantitative measures: metric comparisons; egg shape; cross-comparison of ossification sequences within pterosaurs; and calibration against developmental sequences in extant archosaurs. This analysis confirmed that an embryo of *Pterodaustro* and two embryos of an ornithocheirid from the Yixian Formation of China likely belong to late, near-hatching stages of development. By contrast, several embryos of the ornithocheirid *Hamipterus*, from the Lower Cretaceous of Xinjiang, appear to have died mid-term, a stage of development so far unreported in pterosaurs. Poor ossification of these mid-term embryos was previously used to argue for altriciality in hatchlings of *Hamipterus*, but more likely reflects their relatively early stage of development. Elongation and a relatively greater degree of ossification of wing-spar

bones in these embryos is consistent with (and a pre-requisite of) the fully developed flight apparatus of perinatal individuals and a flight ability soon after hatching. The protocols developed for, and applied in, this study are widely applicable for understanding both prenatal and postnatal development of pterosaurs.

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## Community preservation within the Late Jurassic Morrison Formation, Western Interior, USA

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The Late Jurassic Morrison Formation is ideal for palaeoecological studies; it covers over 1,000,000 km<sup>2</sup> and is one of the best sampled Mesozoic terrestrial deposits. However, interpreting the Morrison Formation ecosystem is complex. Habitat interpretations vary from savannah type to a semi arid or tropical wet/dry to conifer forest. A cause of this disagreement is the imbalance of the preserved Morrison Ecosystem. Dinosaurs and other vertebrate fossils are numerous; however other taxa such as plants and invertebrates are uncommon. It is hypothesised that unfavourable taphonomic characteristics are the cause of this imbalance in preservation. Here, we attempt a quantitative approach to the study of taphonomy in the Morrison Formation. Measures of similarity and distance have been applied to a dataset consisting of 1157 genera from 20 environments and 11 lithologies of preservation downloaded from the Paleobiology Database. We do not find any relationship between lithology of preservation and any genera within the dataset. We find a significant relationship between vertebrate genera and their environment of preservation, but this relationship is absent in plant, invertebrate taxa alone. This suggests that plants and invertebrates do not preferentially preserve in any of the Morrison Formation palaeoenvironments, however certain environments were well suited to the preservation of groups of vertebrate taxa. Further investigations of these vertebrate clusters will be undertaken to understand whether the relationships shown with palaeoenvironment are taphonomic or are representative of original communities.

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## *Elephas recki*: the wastebasket?

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*The Elephas recki* complex of Plio-Pleistocene East Africa is an important lineage for understanding the evolutionary relationships of crown elephantid genera, for traditionally this lineage has long been held as an anagenetic transitional series from an *Elephas*-type ancestor to the immediate precursor of Eurasian *Palaeoloxodon*, comprising of five successive chronosubspecies (*E. recki. brumpti*→*E. r. shungurensis*→*E. r. atavus*→*E. r. ileretensis*→*E. r. recki*). However, this model is now under serious contention as recent ancient DNA evidence reveals the phylogenetic closeness of *Palaeoloxodon* to *Loxodonta* (the genus which includes the living African elephant species), rather than to *Elephas* (the genus which includes the modern Asian elephant). Previous cladistic studies have also recovered the “*E. recki*” complex as apparently polyphyletic. Extensive first-hand re-examination of cranial materials from Ethiopia and Kenya reveal that whereas *E. r. recki*, the nominotypical form of this supposed lineage is morphologically consistent with an immediate precursor to *Palaeoloxodon* (thus *Palaeoloxodon recki*), other earlier remains attributed to the lineage exhibit far greater cranial

disparity than can be explained by anagenesis. The skull from the Late Pliocene of Omo, southern Ethiopia attributed to *brumpti* is most morphologically similar to the contemporary *E. planifrons* of the Siwaliks and *Phanagoroloxodon* from the Russian Black Sea region; whereas the Early Pleistocene *atavus* shares substantial similarities with the contemporary Siwalik *E. hysudricus*. Reconciling these morphological observations with a novel cladistic analysis (>120 characters) reveals crucial new insights about the systematics, biogeography, and morphological evolution of early crown elephantids.

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# SVPCA POSTER ABSTRACTS

## **Algorithmically-assisted selection of ratio characters for the phylogenetic placement of fossils of geoemydid turtles**

**Eduardo Ascarrunz** and Walter G Joyce  
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Recent technical developments have spurred interest in the use of continuous phenotypic characters for phylogenetic inference, particularly in the form of three or two-dimensional landmark coordinates. However, fossils are typically preserved with varying degrees of taphonomic alterations such as breaking, disarticulation, cracking, and plastic deformation. These alterations hinder the applicability of landmark approaches that require faithful data about the geometry of phenotypes. Here we present a simple method for determining phylogenetically informative ratio characters that can be selected based upon the available data that is preserved in the fossils. This approach uses landmark data of species sampled in a reference molecular phylogeny. The fit to the phylogeny of candidate ratio characters obtained from the landmarks is evaluated by the criterion of maximum likelihood. Good ratio characters identified in this manner can then be used to place fossils in the reference phylogeny. We evaluate the performance of the method by a cross-validation procedure on empirical landmark data of shells of geoemydid turtles (Cryptodira: Testudinoidea), and use it to estimate the phylogenetic position of fossil specimens from the Eocene Messel pit Lagerstätte in Hesse, Germany.

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## **Sticky fish as an indicator of specific palaeoenvironmental conditions**

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Skeletons of the actinopterygian *Saurichthys*, found in Middle Triassic sediments at Monte San Giorgio, show a series of preservational features that imply a specific combination of conditions and processes in the depositional setting. The features include overall high completeness and often high articulation, the apparent movement of lateral scale rows or axial skeleton relative to the other, and twisting of the posterior end of the body. Crucially, these features can be attributed to the process of stick and peel. High articulation and completeness is the result of carcasses arriving at the substrate and becoming adhered by microbial mats, facilitating the 'sticking' that prevented extensive element movement and removal. Loss of articulation focused in the scale rows and axial skeleton is the result of shortening in surrounding tissues to the point they were ripped away from substrate - the 'peeling' part of the process - best explained by the tissues becoming dehydrated in hypersaline bottom waters. In some cases the peeled parts of the skeleton became twisted and rolled, suggesting intervals of weak current activity. The recognition of such features is therefore crucial for determining conditions and processes in this and other palaeoenvironments. That one process can explain a specific combination of preservational features is also taphonomically important. This study expands the number of examples of the stick and peel process in fossil vertebrates.

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## **Brain morphology and intraspecific variation in the Triassic cynodont *Thrinaxodon liorhinus***

**Charlotte M. Bird<sup>1</sup>**, Emily Rayfield<sup>2</sup> and Stephan Lautenschlager<sup>1</sup>

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Modern studies in palaeoneurology rely upon non-destructive techniques to augment knowledge of the structures that resided within fossil skulls. Such research in mammals provides valuable information on mammalian brain development through the transition from non-mammalian cynodonts to Mammalia, and the impact improvements in sensory capabilities had upon the size and shape of various brain regions. However, palaeoneurological studies are commonly limited to single specimens, making it difficult to decipher the effects of ontogeny, sexual dimorphism and intraspecific variation. Here, four specimens of the basal cynodont *Thrinaxodon liorhinus* were CT-scanned and digital cranial endocasts were reconstructed, permitting the first description of the brain and inner ear anatomy in this species. Quantitative analyses (linear/volumetric measurements, calculations of encephalisation quotients/hearing capabilities) shed light upon the sensory capabilities and possibilities for intraspecific and ontogenetic variation within *Thrinaxodon*. The reconstructed brain consists of clearly defined olfactory bulbs, cerebral hemispheres, cerebellum and cerebral paraflocculi, which show variation in size on a millimetre scale across the specimens, whilst shape changes are confined to the forebrain. Intraspecific variation in the size, rather than shape, of the reconstructed components is observed, indicating that there is some intraspecific variation (between individuals of a similar age) in the brain and inner ear morphology. Results further demonstrate that the sense of olfaction was the most profound in *Thrinaxodon*, whilst hearing and visual acuity were diminished when compared to extant equivalents (e.g. *Monodelphis domestica*). This is consistent with other nocturnal, burrowing organisms, where a keen sense of olfaction enables efficient tracking of prey.

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## **The use of CT in discerning the life habits of the Early Triassic archosauriform, *Proterosuchus fergusi***

**Emily Brown**, Stephan Lautenschlager and Richard Butler

*School of Geography, Earth and Environmental Sciences, University of Birmingham*

Proterosuchids are a group of carnivorous basal archosauriform reptiles characterised by a bizarre enigmatic overhanging premaxilla. While traditionally considered semi-aquatic, recent histological studies suggest that they were likely terrestrial, however there is currently no consensus. By utilising CT data, we virtually reconstruct the brain cavity and endosseous labyrinths from two adult specimens of *Proterosuchus fergusi* from the Early Triassic of South Africa, in an attempt to understand its life habits within the context of basal archosauriform evolution. Endocasts reveal the brain cavity is tubular in shape and the endosseous labyrinths are highly pyramidal. Elliptical Fourier analyses suggests *P. fergusi* brain morphology was analogous to modern adult crocodiles. The angle of the lateral semi-circular canal of the inner ear reveals *P. fergusi* naturally held its head upwards  $\sim 17^\circ$ , while the length of the cochlear duct suggests poor auditory acuity. Furthermore, the rostrum of *P. fergusi* is found to be highly resistant to both mediolateral and dorsoventral bending when compared to modern crocodylians and is likely enhanced by the overhanging premaxilla. We conclude from comparative anatomical analyses that *P. fergusi* was likely a semi-aquatic, generalist apex predator capable of surviving the harsh environmental perturbations of the Early Triassic. With an upwards-tilted rostrum, its laterally-positioned nostrils may have been held above water level, and a highly resistant snout could have enabled it to hunt large prey and withstand

additional hydrodynamic forces. Crocodylians and phytosaurs seem to have retained a primitive basal archosauriform brain morphology, while the avemetatarsalians have diverged.

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### **A three-dimensional virtual reconstruction of the skull of the problematic Early Jurassic theropod *Coelophysis? kayentakatae*, and the importance of evaluating uncertainty in retrodeformation studies**

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Coelophysid neotheropods represent one of the earliest radiations of dinosaurs, and hence are critical to our understanding of the early evolution of the avian stem lineage. Coelophysids are known from Late Triassic and Early Jurassic deposits across the globe, in some cases from large numbers of individuals. Despite this, the heavy post-mortem compression typical of coelophysid skull material hinders our understanding of their cranial anatomy. Consequently, the taxonomy, interrelationships and even monophyly of the clade are unstable, and poor constraints upon 3D cranial architecture frustrate downstream analyses, compromising efforts to unravel the early biogeographical and ecological diversification of Dinosauria. Here, we present the first comprehensive 3D virtual reconstruction of the skull of an early theropod, based upon CT scans of the holotype of the taxonomically problematic *Coelophysis? kayentakatae*. A rigorous retrodeformation protocol was applied to account for post-mortem warpage of the specimen, with sensitivity analyses to evaluate confidence intervals surrounding the resulting reconstruction. Results permit examination of previously poorly-known regions of the early theropod skull, such as the endocranium and palate, and clarify multiple contested character states. Most notably, the observation of a 'nasal fenestra' – a putative *Megapnosaurus* autapomorphy often instead interpreted as a taphonomic artefact – is robust to cranial deformation. These results inform reappraisal of coelophysid taxa and clarify patterns of cranial character acquisition in early theropod evolution. More broadly, they highlight the wide utility of virtual retrodeformation procedures, but also the necessity of adopting a rigorous, explicitly communicated, approach to evaluate the sensitivity of reconstructions to preservational ambiguities.

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### **Synchrotron microtomography analysis of coprolites from the Carboniferous Obrutschew Bjerg formation, East Greenland**

Hannah Byrne, Per Erik Ahlberg and Henning Blom  
*Department of Organismal Biology, Uppsala University*

The Devonian-Carboniferous boundary strata from East Greenland forms one of the best successions of low latitude sediments from that time. The Obrutschew Bjerg Formation represents a deep permanent lake from the earliest Tournasian, and this black shale deposit can be linked to the famous Hangenberg extinction event. The deposit contains an abundance of actinopterygian remains believed to belong solely to the species *Cuneognathus gardineri*, along with a smaller number of acanthodian and chondrichthyan specimens. Although tetrapod body fossils occur in the late Devonian Aina Dal and Britta Dal formations, none have been found in the Obrutschew Bjerg Formation. However, large non-spiral coprolites may be tetrapod in origin, thus placing tetrapods in the vicinity of the lake. The largest coprolite has been investigated using synchrotron microtomography, and here we present some preliminary results showing the presence of partly articulated fish, multiple cleithra and dental elements of



actinopterygian origin, and two acanthodian spines. The actinopterygian components have good 3D preservation, and so similar analysis of the other coprolites could contribute to furthering our understanding of changes in actinopterygians across the D-C boundary.

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## **Compactor storage for vertebrate collections at the NHM**

**Sandra Chapman**, Lil Stevens and Chris Hughes  
*The Natural History Museum, London.*

Three major collections of marine reptiles and amphibians were combined in one collections area at the NHM in London as part of an extensive refurbishment project. We illustrate the considerations, implications and lessons learned in a project that involved a wide variety of people and processes to complete the re-storage of over 4,000 specimens. We developed protocols for handling and packing very large slab specimens to very delicate skulls, rib bones and mounted skeletons. Techniques for the movement and storage of specimens packed in drawers and boxes were developed with external contractors, as well as the temporary transfer of the very large specimens to the NHM out-store. Issues such as collections security and the buildings welfare were considered, for example floor-loading in storage areas and the logistics of moving specimens through the Museum. Compactor cabinet design and layout mapping of each drawer and shelf was done in conjunction with the cabinet designers, with reference to how the collections are used and how the new cabinets would improve the storage conditions of the specimens. A network of curators, assistants, conservators, project managers, contractors, architects and engineers worked to make each part of the project happen within the wider framework of museum policies, concurrent projects and core collections work. The legacy of the project is the improved functionality of the new collection space for storage, access and research.

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## **Taming the cow: how have humans influenced morphological variation in wild and domestic cattle from prehistory to the present?**

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<sup>2</sup>*Hull York Medical School, University of York*

Cattle (*Bos taurus*) were first domesticated around 10,000 years ago from potentially as few as 80 individuals of aurochs (*Bos primigenius*), the extinct ancestor to cows. Following domestication, they spread across Europe, reaching the UK approximately 6000 years ago. This project aims to uncover differences in the form and function of aurochs and cow skulls and to determine how these were affected by domestication and husbandry. Contrary to other studies which claim aurochs and domestic cows were similar in all but size, this study predicts marked differences in the cranial shape of these two species, resulting from differing niches and the effects of human exploitation and selective agriculture. A total of 82 aurochs and cow cranial specimens were collected from 17 UK institutions, and photogrammetry was used to construct 3D models. Due to the fragmentary nature of fossil specimens, three landmark sets were created so that even the most incomplete material could be utilised. Geometric morphometric analyses were conducted in R. Preliminary results strongly indicate that there is a clear separation between aurochs and cow skulls based on shape. It is speculated that morphological divergence will have increased over time, particularly with the defining of breed characteristics in more recent periods. A programme of carbon-14 dating is planned to improve chronological resolution. This study aims to reveal new insights into the effects of past husbandry practices and to answer long-standing questions such as why cows remain part of our modern environment, but aurochs have become extinct.

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## **Inferring Mode of Life for Extinct Avians and Theropod Dinosaurs Using Measurements of Curvature for the Ungual Phalanx**

**Savannah Cobb**

*School of Earth and Environmental Sciences, University of Manchester*

Past workers have observed a relationship between curvature of the keratinous sheath of the claw of pedal digit III as approximated by circular arcs and mode of life for avians and squamates. This has been used to infer mode of life for extinct avians such as *Archaeopteryx* and theropod dinosaurs. However, these studies do not account for fossil specimens with broken or absent keratinous sheaths. This study aims to determine a similar relationship using measurements of curvature taken for the unguis phalanx of pedal digit III for a large and taxonomically diverse sample of modern birds to improve comparative analysis with fossil claws for which only unguis bones have been preserved. Unguis bone data has been acquired by X-ray imaging using the handheld dental imaging device the Nomad Pro Radiography Unit. Measurements of curvature are then taken in a custom-made software DinoLino.exe for ventral and dorsal curvatures of unguis bones and keratinous sheaths. Various statistical analyses including LDA (Linear Discriminate Analysis) have been performed using these measurements in R Statistical Software. The statistical model is then used to infer terrestrial, predatory, perching, or climbing behaviours for fossil avians, avialans, and theropod dinosaurs.

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## **A student-staff-museum collaboration to restore, image and display the skeleton of a Lower Cretaceous ornithomimid dinosaur (*Tenontosaurus tilletti* LL.1227)**

Matthew Dempsey, Natalia Jagielska, Jake Atterby

*School of Earth and Environmental Sciences, University of Manchester*

Originally unearthed from the Lower Cretaceous Cloverly Formation of Montana, the *Tenontosaurus tilletti* specimen LL.1227 was the centrepiece of the Manchester Museum fossil gallery from 1999 to 2004. The skeleton is estimated to be approximately 70% complete, with the most notable missing elements being the hemal arches of the tail and the outer cranial frame. The original mount contained multiple inaccuracies – most notably the tripod tail-dragging stance and the strongly pronated forelimbs. Several incomplete elements (particularly the forelimbs) were artificially extended apparently without reference to the well-documented literature on the species. Many of these elements remain glued to the now-dismantled material currently in the University of Manchester's storage. The skeleton has provided a unique opportunity for student-staff-museum collaboration and community outreach. We present our progress on fully documenting, restoring and remounting the LL.1227 specimen, which is eventually planned to be re-displayed to modern standards in a renovated section of the Manchester Museum. A particular highlight of this student-led project is the high specification 3D imaging of the specimen using photogrammetry via Agisoft Photoscan. This will allow us to create a 3D print of the skeleton for mounting within the University, and provide a high quality open-source model for research purposes.

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## **The Rise of Dinosaurs: Tetrapod diversity and climate during the Late Triassic**

**Emma Dunne<sup>1</sup>**, Alex Farnsworth<sup>2</sup>, Sarah Greene<sup>1</sup>, Dan Lunt<sup>2</sup> and Richard Butler<sup>1</sup>

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The Late Triassic (237–201 million years ago) was a key interval in tetrapod evolution, encompassing the radiations of several major lineages, such as mammals, crocodylomorphs and dinosaurs. Current hypotheses propose climate-driven palaeolatitudinal structuring of Late Triassic tetrapod faunas. For example, sauropodomorph dinosaurs are proposed to have been absent from low latitude regions due to ‘unstable’ climatic conditions (e.g. fluctuating aridity). However, these hypotheses remain largely untested. We investigated patterns of Late Triassic tetrapod diversity using fossil occurrence data from the Paleobiology Database and methods of sampling standardisation and tree-based biogeographic and character-mapping approaches. Then, we utilised, for the first time, the results of a spatially-explicit general circulation climate model (HadCM3L) to explicitly test hypotheses linking dinosaur diversity with climate. We found that Late Triassic tetrapods do not conform to a modern-type latitudinal biodiversity gradient (instead diversity was highest at mid-palaeolatitudes), and that communities were palaeolatitudinally-structured, suggesting that faunas tracked global climate zones. Using climate data extracted from the model, we statistically examined climate across palaeolatitudes and between localities containing major tetrapod groups. At the global level, our results support the previous assumption that palaeolatitude is a good proxy for mean annual surface temperature (MAT). When compared to all tetrapods, dinosaurs preferentially occupied drier and hotter environments, with less seasonal variation in precipitation. However, sauropodomorphs, occupied areas with significantly lower MAT and high seasonal temperature ranges. This work provides the first quantitative support for palaeoclimate as a major control on the distribution of Late Triassic tetrapods, including early dinosaurs.

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### **The biomechanical significance of the palatal fascia and quadratojugal ligament in the skull of the ornate monitor (*Varanus ornatus*)**

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The skull of lepidosaurs (tuatara, lizards and snakes) forms an open framework of bars and openings, which differ radically from the shell-like skull of mammals. These morphological differences have biomechanical implications. In lizards, strains are generally significantly higher than those of mammals, with less variation between anterior and posterior skull regions. The lightly-built, more flexible skulls of lizards are also supported by more extensive soft tissues than the mammalian skull, such as the quadratojugal ligament spanning over the margin of the upper jaw, and thick palatal fascia in the oral cavity. The role of these tissues has been little studied, despite their potential impact on the strain regime of the skull. For instance, the palatal fascia might allow for the strains to be dissipated from the snout through the palate to the postorbital skull, hence reducing peak strains over the thin bones of the palate. Using the lizard species *Varanus ornatus* as a model organism, we explore the biomechanical significance of these structures by employing 3D computer-based mechanical simulations based on detailed muscle dissections, and *in vivo* data. First, we simulated muscle activity and joint-reaction forces during biting using Multibody Dynamics Analysis. Then, the forces calculated from these models were used as an input for Finite Element Analysis, to investigate the strains of the skull bones. Our results show that the inclusion of the palatal fascia and quadratojugal ligament impacts the strain in the bone, and will serve to discuss the relative significance of different soft tissues in lizards.

## Vertebral proportions in plesiosaurs

**Richard Forrest**

*plesiosaur.com*

A detailed study into the variation in proportions for the whole of the vertebral column is in press at the time of this meeting and describes a methodology which generates a large set of characters and demonstrates patterns of variation which can be used in taxonomic and biomechanical analyses. The study is a description of a methodology rather than the presentation of a robust set of results, but nevertheless provides some important insights. Long-necked plesiosaurs are exceptional in their number of cervical vertebrae, over 70 in some taxa. Patterns of variation in the vertebral column may relate to underlying processes driving the evolution of extreme neck lengths. Numerous explanations for this have been suggested over the two centuries since the earliest specimens were found, but none have produced a testable hypothesis. It is suggested that this extreme elongation is driven by biomechanical factors arising from four-flipper propulsion, a mode of locomotion found uniquely in plesiosaurs. This model can be used to make predictions about vertebral proportions in taxa which have not yet been studied in detail, giving it a degree of testability. Some of the patterns of variation appear to be remarkably conservative over a time scale of 100 million years, hinting at underlying genetic mechanisms governing the growth of the plesiosaurian vertebral column.

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## Morphological conservatism and slow evolution under a new porolepiform phylogeny

**Struan Henderson** and Tom Challands

*University of Edinburgh*

The Porolepiformes are an extinct monophyletic group of morphologically conservative sarcopterygian fish, sister to the Dipnoi (lungfish). Along with the problematic genera *Powichthys* and *Youngolepis*, these groups comprise the Dipnomorpha. To date there has been no comprehensive phylogenetic analysis of the Porolepiformes and basal dipnomorphs. *Powichthys* and *Youngolepis* have been variously proposed as stem-porolepiforms, stem-lungfish or their own monophyletic group, albeit in larger-scale studies of sarcopterygians. Here we present a new character dataset in which most porolepiforms have been coded for the first time, composed of characters gathered from previous studies that are applicable to the Dipnomorpha. We find support for *Powichthys* as a stem-porolepiform and *Youngolepis* as a stem-dipnoan, and also resolve the interrelationships of derived porolepiforms for the first time. Furthermore, by plotting our dataset in a phenetic discrete character morphospace we have quantitatively shown extreme clustering of porolepiforms – an indication of their morphological conservatism. This conservatism suggests that porolepiforms will display significantly slow evolutionary rates relative to the Dipnoi, and we present analyses finding this consistently under multiple time-scaling methods.

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## Insular gigantism in Mediterranean dormice

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During the Pleistocene, the rodent fauna of Sicily was characterised by the presence of *Leithia melitensis*, a gigantic dormouse species around the size of a domestic cat. Even though the enlargement of dormice on islands is a common phenomenon in the Mediterranean area, the exceptionally large size of *L. melitensis* is unique within Gliridae. A second species, *L. cartei*, was also present on Sicily. This species was less extremely enlarged, being comparable in size to the extant species *Eliomys* on Formentera. Here, changes in shape associated with body size increases were analysed by comparing the morphology of *Leithia* with that of extant glirids. Cranio-mandibular shape of individuals from one extinct and six extant genera of dormice were quantified using landmark-based techniques. Procrustes superimposition was performed to correct for size changes within the sample data. Principal component analyses showed distinct clustering of certain genera, with the mandibular shape of *L. melitensis* clearly separated from that of extant dormice. As *Eliomys* and *Leithia* are considered to share a common ancestor, this distinction suggests that shape changes within this giant were allometric. The less extremely enlarged species, *L. cartei*, clusters in the same region as the *Eliomys* species, implying a relatively isometric size increase in comparison with that of *L. melitensis*. Geometric morphometrics indicate intergeneric segregation of dormice based on shape, as well as a clear separation of species influenced by insular gigantism within the Gliridae.

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### **A mystery fossil from the Kimmeridge (Upper Jurassic) of Dorset, UK – the oldest urolith on record**

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<sup>4</sup>*The Etches Collection, Kimmeridge*

Uroliths (e.g. bladder stones) are concretions of mineral salts that can form within the urinary tract of a variety of animals. Their occurrence in the fossil record seems somewhat limited, despite what would appear to be a number of factors that would favour preservation (relatively compact, crystalline calcium phosphate or calcium carbonate). The oldest described urolith comes from the Oligocene of northeastern Colorado and is loosely associated with a terrestrial vertebrate fauna. Prior to this, records were confined to antiquity, with a human record dating back to c. 8,500 years ago from cave deposits in Sicily. Specimen K121 in the Etches Collection has remained undescribed since being discovered in the Kimmeridge Clay Formation (Kimmeridgian, Upper Jurassic) by Steve Etches in 1982. Recent detailed examination of this comparatively large (c.10cm in diameter) and spherical specimen comprising calcium phosphate has revealed a mammaliated surface texture, prominent internal laminations (sub mm scale) with crystallites orientated perpendicular to these incremental lines and a primarily open nucleus subsequently infilled with diagenetic quartz. These features are all specific characteristics of previously described uroliths. Significantly, the identification of this specimen as a urolith extends the known range of this type of trace fossil by approximately 112 million years. This is the first time a fossil urolith has been attributed to a marine ecosystem and it is also the first described from the UK. Uroliths have hitherto probably been collected unknowingly and may be curated in museum collections unrecognised and labelled gastroliths or simply nodules.

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## Tests of masticatory convergence within hard-object feeding primates

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Primates that specialise on hard, stress-limited objects are often considered functionally extreme due to the mechanical challenges presented by their diet. Numerous primates spanning a diverse phylogeny feed extensively on such objects, however, whether morphological convergence has occurred is unknown. This study compares the masticatory form of hard and non-hard object feeding primates belonging to the families Atelidae, Cebidae, Pitheciidae, Cercopithecidae and Hominidae. 90 landmarks (3D) representing key masticatory features were taken on a sample of 101 primate specimens spanning 11 species. Landmarks placed on occluded crania and mandibles captured masticatory form. The analysis was carried out using geometric morphometrics and a distance-based test of convergence was carried out on representative males. It was predicted that the masticatory form of the specialist hard object feeding *Cercocebus atys* would converge with the Pitheciidae, relative to its non-hard object feeding relatives. Preliminary results suggest that hard object feeding primates do not converge in the way that was predicted. The tougher feeding *Sapajus apella* showed significant convergence with the hard object feeding Pitheciidae, however, *C. atys* did not converge with the other hard object feeding primates. Results suggest many-to-one-mapping of masticatory form in order to process hard objects, but could reflect differences in food processing behaviour. Tough and hard foods also appear to place similar demands on the masticatory form. Further analyses will explore the functional differences between these masticatory forms to establish if there are many ways to crack a nut.

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## Walking in the shadows of giants: The small dental assemblage of the Early Cretaceous Kem Kem beds of Morocco, North Africa

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The Kem Kem beds of mid Cretaceous age, South East Morocco, are renowned for yielding in abundance, very large vertebrates, leading to the nickname 'River of Giants'. Previous work has focused on the palaeoecology, palaeoenvironment and taxonomy of the larger vertebrates found mainly by local fossil collectors. Much work has centred on the very large theropod dinosaurs, especially the sail-backed *Spinosaurus*. The smaller vertebrates, represented mostly by teeth, have been largely overlooked, resulting in an unbalanced view of the ecosystem. This study focuses on samples of teeth of 10 mm or less in overall size, sieved from mine spoil by the fossil diggers. The teeth were identified using standard comparative anatomical and morphometric methods and using the macro fauna for comparison. The results show that the small dental assemblage displays a low herbivore / high carnivore ratio, which is also reflected in the macro fauna. The overall vertebrate percentage abundance follows a similar trend, with fish and sharks being most dominant, which is expected due to the fluvial setting, while herbivorous sauropods are extremely rare. A part of the analysis utilised dental serrations and shape morphometrics to assess theropod diversity. Juveniles of each known taxa were recorded, but examples not fitting any so far described morphology are also present in the sample. The preliminary results suggest that the dinosaurs were most likely nesting and raising their young in close proximity to the river, and that the dominance of large carnivores is likely an artefact of sampling by commercial collectors.

## **Microstructure and mineralogy indental plates of the holocephalan chimaeroid *Harriotta raleaghae*: novel dentine and conserved patterning combine to create a unique chondrichthyan dentition**

**Zerina Johanson**<sup>1</sup>, Charlie Underwood<sup>1,2</sup>, Richard Twitchett<sup>1</sup>, Tomasz Goral<sup>1</sup>, Christopher Healy<sup>3</sup> and Moya Smith<sup>1,3</sup>

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Among the cartilaginous fishes (Chondrichthyes), Holocephali is the sister group to the Elasmobranchii (sharks, rays). Crown group holocephalans lack teeth and instead have dental plates in the upper and lower jaws. In the Chimaeridae and Rhinochimaeridae adult plates include extensive trabecular dentine supporting crushing tritoral pads along with unusual series of dentine ovoids along the lateral plate margins. Instead of ovoids, juveniles have elongate rods of dentine. In *Chimaera*, dentine includes the unusual calcium phosphate mineral whitlockite, containing magnesium. We examined the dentition of the rhinochimaerid *Harriotta*, to determine whether whitlockite occurs more broadly within the Holocephali, and to investigate the development of dental plates in juveniles and adults. In both, plate tissues are continually renewed from pulpal tissues deep to the oral surface. Here, rods, ovoids and tritoral pads develop within patterned and organized spaces in the trabecular dentine framework. Rods are lost in the adult dentition except in the anterior dental plates, where they continue to develop posteriorly. Patterning is reminiscent of other chondrichthyan dentition, but in adults, mineralizing tissue in ovoids and tritors is initially a granular, disorganised cluster of crystals differing in shape and composition ( $\beta$ -tri calcium phosphate) from hydroxyapatite crystals in other mineralized vertebrate tissues. Elemental analysis shows that there is relatively more magnesium in these early-forming tissues, decreasing as mineral density increases towards the oral surface. We propose that Mg in dental plates characterizes at least the Chimaeridae and Rhinochimaeridae, and is related to the Jurassic origins of the Chimaeriformes in Mg-rich, aragonitic seas.

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## **Evolution of functional morphology of the *Suncus etruscus* Corsican shrew's mandible: a story between climate, man and island**

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We live in the Anthropocene, an era of rapid environmental changes driven by humans, that impact all aspects of living organisms worldwide, including their morphology. The study of the human-driven impacts has great importance, that's why we aim to understand how human activity and climatic changes influenced the phenotype of animals of the past, before the start of the Anthropocene. We study the environmental changes that took place during the modern era (14-19th century AD) on the island of Corsica and their impact on the mandible of small mammals, as it's a good indicator of the animal's performance, and we focus specifically on the morphology of the mandible of the shrew *Suncus etruscus*. We detect rapid morphological changes during this short period of time that indicate a strong human impact on the island. These changes have functional consequences as they are correlated to changes of the mechanical potential, an estimation of the bite force of the two principal masticatory muscles, temporalis and masseter. Their negative correlation as well as their correlation with vegetation and anthropisation changes suggest changes in the shrew's diet over time. The integration of the body and ramus of the mandible seem to be related to the mechanical potential of the

temporalis muscle but does not constitute an indicator of rapid environmental changes. Nevertheless, whether these morphological changes are the result of natural selection (genetic processes) or of phenotypic plasticity of the shrew mandible (epigenetic processes) is not yet clear.

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## **Morphology, taxonomy, and phylogenetic relationships of the Monteviale crocodylians (Oligocene, Italy)**

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The crocodylian remains from the Oligocene of Monteviale (NE Italy) were referred to two different genera, *Asiatosuchus* and *Diplocynodon*, but more recently, they were all tentatively assigned to the extinct alligatoroid *Diplocynodon ratelii*. The purpose of the present work is to describe the historic collection of crocodylian remains from Monteviale housed in Padua (Italy) as well as in La Rochelle (France) and Basel (Switzerland). The material can be assigned without any doubt to the genus *Diplocynodon*, but it differs from *D. ratelii* because the nasal bones do not reach the external nares. *Diplocynodon* from Monteviale shares the same general suture pattern of the skull with the two Spanish species *D. tormis* (Eocene) and *D. muelleri* (Oligocene). They are two very similar species, whose validity needs to be reevaluated. Therefore, the specific attribution of the Monteviale *Diplocynodon* remains uncertain: it could belong either to the species *D. muelleri*, *D. tormis*, or to a new species, for which the name *Diplocynodon monsvialensis* (Fabiani, 1914) comb. nov. is available. A phylogenetic analysis was carried out with TNT on the basis of a previously published matrix (98 taxa, 179 characters), resulting in a polytomy involving *D. tormis*, *D. muelleri* and the Monteviale *Diplocynodon*.

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## **A new Antarctic specimen of *Prolacerta cf. broomi*, its biogeographical implications and a revision of the taxon**

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*Prolacerta* is an Early Triassic archosauromorph of particular importance to the early evolution of archosaurs due to its generalized morphology. It is well known from many specimens from South Africa and a few relatively small specimens from Antarctica. Here, a new articulated specimen from the Fremouw Formation of Antarctica is presented which represents the largest specimen of *Prolacerta* described to date. It constitutes a nearly fully articulated and complete postcranium in addition to four skull elements. The study of this specimen and the re-evaluation of other *Prolacerta* specimens from both Antarctica and South Africa reveal several important new insights into the morphology of the genus, most notably regarding the manus, humerus, and premaxilla. Furthermore, comparison of the specimens from Antarctica and South Africa indicates that although no major morphological differences can be found, the lack of cranial characters prevents the confident determination of the Antarctic specimens as belonging to *Prolacerta broomi*. Instead the Antarctic material is identified as *Prolacerta cf. broomi*. The biogeographical implications of these new findings are discussed and an emended diagnosis for *Prolacerta* is provided.

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## **The first Mosasaur (Reptilia: Squamata) remains from the Ulster White Limestone Group, Northern Ireland, and refinements to the Wastebasket taxon, '*Mosasaurus gracilis*'**

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Due largely to the relative scarcity of Mesozoic exposures, marine reptiles remain under-documented in Northern Ireland, and previous reported finds have been almost- entirely confined to scarce and mostly fragmented examples from the Westbury and Lower Jurassic Waterloo mudstone Formations. Here, a historically- old but newly- described set of postcranial remains documents the presence of mosasaurs within the (Upper Santonian-Lower Maastrichtian) Ulster White Limestone Group, Co. Antrim. Although commented on in passing within previous works, the study herein represents the first- systematic description of remains from these marine reptiles in Ireland. Originally relegated to '*Mosasaurus gracilis*', a nomen dubium wastebasket taxon, it cannot be included within the species and its identity is revised. The specimen aids in untangling the historically- complex nomenclature surrounding British mosasaur material, and adds to an increasing body of new literature placing greater constraints on evidence for the genus, *Mosasaurus*. Additionally, it extends the geographical distribution of mosasaurs to Westernmost Europe, with potential implications for mosasaur distribution between western and eastern Europe. The presence of accessible coastal and some inland chalk deposits, alongside remaining active quarrying suggests the possibility of further remains in the future. Such remains could augment the current record of British and European mosasaur diversity, and affect theories over Trans- Atlantic movement of mosasaur taxa during the Late Cretaceous.

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## **Global and regional sea-levels during the Late Cretaceous and the evolution and radiation of megaherbivorous dinosaurs**

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The ornithischian dinosaurs represent an important model for testing the evolution and radiation of large-bodied (>1000 kg) taxa. Numerous lineages are characterised by high species richness, with well-established phylogenetic associations, which are supported by reliable stratigraphic and geographic controls. Here, we examine the shift in global and regional sea-levels and the evolution and radiation of large-bodied herbivorous dinosaurs during the Late Cretaceous. We hypothesize that the diversification of the major ornithischian clades Ceratopsidae and Hadrosauridae in North America follow periods of marine regression of the Western Interior Seaway. The time-calibrated phylogenies were built using an informal supertree approach; source data are selected from recent studies utilising comprehensive taxon and character sampling and excluding taxa based on fragmentary material and ambiguous chronostratigraphic ages. The biogeographic analyses were implemented using the BioGeoBEARS package in R Studio. Each terminal taxon was assigned to one of five palaeogeographic regions. The analyses focus primarily on the evolution of Laramidian taxa with the dispersal of large-bodied forms to neighbouring landmasses given maximum dispersal potentials. Preliminary results indicate that the divergence and radiation of the Ceratopsidae correspond with shifting global and regional sea-levels during Late Cretaceous.

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## Postcranial osteology of a new, juvenile skeleton of *Plateosaurus* (Dinosauria: Sauropodomorpha) from Frick, Switzerland

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The basal sauropodomorph *Plateosaurus* is among the best-represented dinosaurs in the world, largely owing to the bone-beds of Trossingen and Halberstadt, Germany and Frick, Switzerland. Despite this abundance of material, early-stage juveniles have been conspicuously absent from the fossil record. However, such specimens are critical in assessing the ontogenetic development of this taxon, as well as the role of heterochrony in sauropodomorph evolution. A new skeleton from the Gruhalde quarry (Klettgau Formation, Norian) of Frick, nicknamed “Fabian”, represents the first substantially complete juvenile referable to *Plateosaurus*. The specimen includes large portions of the cranium and vertebral column and an almost complete appendicular skeleton. The juvenile ontogenetic stage is confirmed by the lack of neurocentral suture fusion in the axial column. At an estimated total length of 2.3 m and a body mass of 40 kg, “Fabian” is an order of magnitude smaller than any other *Plateosaurus* individual. The morphology of the postcranial bones is remarkably consistent with that of osteologically mature individuals, including laminae and fossae of the axial skeleton that are virtually identical to those of adults. Morphometric comparisons are complicated by varying degrees of compaction, but skeletal proportions mostly appear to follow isometry. Possible exceptions are the proportionately larger manus and the proportionately shorter, more gracile humerus and shorter radius, as compared to adult individuals. The overall state of development suggests that developmental plasticity, previously observed in size variation among adults, may also affect morphology in *Plateosaurus*.

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## A phylogenetic supermatrix of the armoured dinosaurs

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The armoured dinosaurs have been known since the early 1800s and include some of the most recognisable dinosaurs such as *Stegosaurus* and *Ankylosaurus*. The individual lineages, Ankylosauria and Stegosauria, have been studied thoroughly but there has never before been a comprehensive whole-group cladistic analysis of Thyreophora. This has hindered efforts to understand the macroevolution of the group, and has obscured character-state transformations at the base of the lineages, making the identification of basal taxa and clades problematic, and the degree of convergence difficult to assess. Here, the first species-level phylogenetic super-matrix of the whole-group Thyreophora is presented, incorporating all previous known cladistic analyses of ankylosaurs, stegosaurs and basal thyreophorans and including all valid species within Thyreophora, for a total of 89 taxa and 338 characters. Analyses were performed under both parsimony (in TNT) and Bayesian inference (under the Mk model in RevBayes) and the effects of reductive and non-reductive coding were investigated. *Hylaeosaurus* was recovered outside of both Ankylosauridae and Nodosauridae, and *Kunbarrasaurus* was found at the base of Nodosauridae. *Alcovasaurus* was found within Stegosauria for the first-time by a phylogenetic analysis. Potential evidence for a ‘polacanthine’ grouping was also found, with *Polacanthus*, *Hoplitosaurus*, *Mymoorapelta*, *Taohelong* and *Dongyangopelta* at the base of the Nodosauridae, although symmetric resampling showed this to have weak support. Reductive character coding produced a slightly lower resolution strict consensus tree than non-reductive coding, but with a lower tree length, suggesting less homoplasy. The phylogeny presented here will become the framework for macroevolutionary studies of Thyreophora.

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## A macroevolutionary look at the history of fishes in coral reefs

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Fishes play a key role in coral reef habitats: herbivorous fishes control the growth of algae on corals and thereby preventing negative cascading effects on both reef health and community-wide patterns of species diversity, while durophagous fishes can control the density of sea urchins and sea stars. All feeding modes have evolved independently in several groups of coral reef fishes: for example major groups of herbivores include rabbitfishes (Siganidae) and surgeonfishes (Acanthuridae), two unrelated groups of percomorphs, while several lineages of seabreams (Sparidae) have convergently switched to a durophagous diet. Although many groups of reef-associated fishes such as siganids, acanthurids, sparids, and carangids, possess a rich fossil record that potentially makes them ideal groups to study how the evolution of feeding modes has impacted reef fish diversification dynamics, few studies have investigated these clades in detail. Combining molecular and morphological datasets that include both extant and fossil taxa into a total evidence approach, we provide a new timescale for the evolutionary history of these clades. Our results demonstrate much earlier origins of these groups than those indicated by the fossil record, supporting a substantial radiation of reef fishes that began in the Cretaceous, followed by episodes of significant extinction during the late Eocene and Oligocene. Integrating our timetrees with morphometric data collected from over 2000 digitized images for these groups, we further investigate the tempo and mode of phenotypic evolution within these clades, and will discuss our findings.

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## Traquair's lungfish from Loanhead: dipnoan diversity and tooth plate growth in the late Mississippian.

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Ramsay Heatly Traquair, the eminent Victorian palaeichthyologist and museum curator, procured an extensive collection of Palaeozoic fishes from across Scotland. Loanhead near Edinburgh was especially productive. Traquair described numerous fish from this Serpukhovian site, including four lungfish taxa: *Ctenodus interruptus*; *Sagenodus quinquecostatus*; *Uronemus splendens*; and *Ctenodus angustulus*. The first three are now quite well known but the fourth was only briefly described in 1881. It is based entirely on tooth plates. These are unusual both in their very small size and the arrangement of the tooth ridges. A further taxon, *Conchopoma* sp., has recently been identified. Represented by a spade-shaped parasphenoid and denticulated jaw elements, it is the earliest known occurrence of the genus, extending its range into the Mississippian. An isolated parasphenoid bearing an anterior process, previously only seen in Devonian lungfish, may represent a sixth taxon. The presence of up to six lungfish taxa at a single locality is unprecedented in the Carboniferous and adds to the growing evidence that post-Devonian lungfish evolution was not as limited as previously proposed. This may have been due to changes in tooth plate growth enabling greater variation in dentition. In most Devonian taxa, tooth plate growth can be explained by comparison with that in extant forms, but analysis of Carboniferous tooth plates suggest growth was different in many taxa, possibly based on more than one pioneer

tooth, allowing for novel patterns of tooth ridges and different types of teeth to develop on the same plate.

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## **The Late Cretaceous (Santonian) ichthyofauna of Iharkút (Hungary), with a summary on the European Late Cretaceous continental fish faunas**

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The Late Cretaceous (Santonian) Iharkút vertebrate site (Bakony Mts., Hungary) yielded the remains of a large variety of vertebrate taxa, including several fish forms as well. The intensive hand-quarrying and screening of the fluvial deposits of the Csehbánya Formation exposed at the locality resulted in a large variety of skeletal and dental remains of the lepisosteid *Attractosteus*, a pycnodontid identified as cf. *Coelodus* sp., vidalamiin and non-vidalamiin amiiforms, an indeterminate elopiform, two indeterminate ellimmichthyiforms, a possible salmoniform, further indeterminate acanthomorphs, at least one indeterminate teleostean, and numerous indeterminate actinopterygians (represented by various teeth). Most of the Iharkút fish taxa are considered as freshwater forms, however, some taxa (e.g. Elopiformes) presumes the vicinity of a marine-deltaic environment. The overall picture of the Iharkút fish fauna resembles some North American fish faunas. Detailed studies report Late Cretaceous continental fish faunas from the Iberian Peninsula, Western Hungary, Southern France and Romania. Some Iharkút fish taxa (e.g. Vidalamiinae) are first reported from the Late Cretaceous of Europe, suggesting that these European fish faunas could have been far more diverse than previously thought. Other groups, (e.g. Lepisosteiformes), however, were much more common, reported from various other European sites as well, indicating a quite general occurrence throughout the continental habitats of the Late Cretaceous European archipelago. The revision of earlier collected remains attributed to infrequent taxa is, however, required, just like an intensive screen-washing for the localities, where it has not been carried out.

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## **Phylogenetic value of jaw elements of lacertid lizards (Squamata: Lacertoidea): a case study with material from the Oligocene of France**

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The species-rich family of Lacertidae is the dominant reptile group in Europe nowadays. However, due to poor preservation and disarticulation, several fossil species are based on single bones, mostly dentaries or other tooth-bearing elements. Here, we used disarticulated bones of lacertid lizards from four Oligocene localities in France (Coderet, La Colombière, Roqueprune 2, Mas de Got B) and compared the phylogenetic signals of three jaw elements: dentaries, maxillae, and premaxillae. We identified three lacertid morphotypes among the premaxillae, four among the maxillae, and six among the dentaries. These morphotypes were scored as single operational taxonomic units for each locality into three separate character matrices with the same 227 characters. Subsequently, the phylogenetic position of the morphotypes within Lacertoidea was tested using maximum parsimony. The resulting consensus trees with the dentaries and the maxillae both recovered a large polytomy in the lacertids, but all morphotypes were situated within that family. The consensus tree with the premaxillae showed a considerably better resolution but recovered one group outside

Lacertidae. The combination of convergent characters and missing data seem to be the reason for the “outgroup” position of some premaxillary morphotypes. The polytomies found in the trees with maxillae and dentaries are most likely caused by their higher morphological variability. Therefore, those bones only seem to be identifiable at family level. However, together with the premaxillae, a determination down to species level was possible. Hence, species descriptions based on highly variable morphological elements like lacertid maxillae and dentaries should be treated with caution.

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## **Tyrannosaurid theropods: did they ever smile like crocodiles?**

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A relationship between surficial skull textures and craniofacial epidermal tissues has long been recognised among living animals, but the use of skull rugosity profiles as means to make detailed predictions of facial skin types in fossil animals has only occurred in the last decade. Recent work on craniofacial anatomy of tyrannosaurine theropods has proposed a regime of scales, cornified sheaths and armoured skin across the dorsal skull region, as well as lipless jaws covered with crocodylian-like ‘flat scales’. Here, we present an alternative interpretation of tyrannosaurid facial tissues based on studies of nearly 30 tyrannosaurid specimens, cataloguing rugosity profiles and jaw bone foramina frequency. We were unable to locate specifically crocodylian-like rugosity profiles in tyrannosaurids and question the correlation of crocodylian skull textures to epidermal scales: modern crocodylian faces are covered with cracked skin, not squamous epidermis. Moreover, discrepancies in skull rugosity profiles between extinct and living archosaur species show that crocodylian and bird anatomy have limited application in the reconstruction of non-avian dinosaur craniofacial tissues. We find an average of 43.5 neurovascular foramina in tyrannosaurid maxillae but 175.5 in crocodylians: these values give differing expectations for extra-oral tissues, ranking tyrannosaurids among ‘lipped’ taxa. Possible further evidence for differentiated tissue types around tyrannosaurid jaws are morphological distinctions between tyrannosaurid alveolar foramina and those situated elsewhere on the jaw. Hummocky rugosities indicative of scaly integument are present on the maxillae of some tyrannosaurids. We conclude that tyrannosaurids, and probably most extinct theropods, were not overtly crocodylian-like in facial appearance.



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