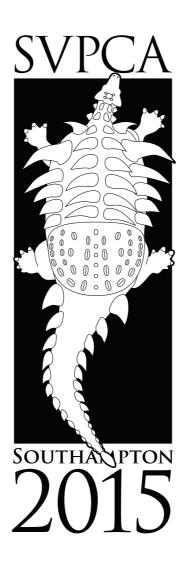
# 63<sup>RD</sup> Symposium for Vertebrate Palaeontology and Comparative Anatomy

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 $24^{\text{TH}}$  Symposium of Palaeontological Preparation and Conservation with the Geological Curators' Group



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#### **ACKNOWLEDGEMENTS**

The organisers would like to thank the Palaeontological Association for their support of this meeting, and also for their continued management of the Jones Fenleigh Memorial Fund. A huge amount of the work putting the meeting together was co-ordinated by Mark Young, including editing this Abstract volume, handling abstract submissions and overall organisation.

We also thank Stu Pond and Jessica Lawrence Wujek for designing this year's SVPCA logo. Liz Martin-Silverstone and Jessica Lawrence Wujek co-ordinated most of the behind-thescenes management for this meeting while Stu Pond designed this year's Conference circulars. Our logo represents a local fossil, *Polacanthus* from the Isle of Wight (based on a fossil collected by Martin Simpson and Lyn Spearpoint). Finally, we thank Richard Forrest for working on the website and providing general information and support.

This year's meetings are supported by the Hampshire Cultural Trust, Dinosaur Isle, Geological Curators Group, Siri Scientific Press, Palaeocast and Frontiers in Earth Science.

#### HOST COMMITTEE

Ocean and Earth Science, University of Southampton, National Oceanography Centre
Gareth Dyke
John Marshall
Darren Naish
Mark Young
Jessica Lawrence Wujek
Liz Martin-Silverstone
Stu Pond
Aubrey Roberts
James Hansford

Hampshire Cultural Trust Christine Taylor

Dinosaur Isle Gary Blackwell

Geological Curator's Group Kathryn Riddington



### MEETING SCHEDULE

Monday 31	st August
9:00-9:45	SPPC/GCG registration at NOC Security desk (4 <sup>th</sup> floor)
	Session — SPPC
	Chair — Mark Young
10:00-10:20	Mark Graham
10.20.10.10	Fossils, Footprints & Fakes
10:20-10:40	Emma Bernard
10 40 11 00	A brief history of the best collection of fossil fish in the world – probably
10:40-11:00	Jeff Liston et al.
11 00 11 20	Leviathan Rising: A new collections curation initiative from the Star Pit dig
11:00-11:20	Luke Hauser
11 20 11 40	Breaking badbone beds: processing the Downton Bone Bed
11:20-11:40	Frank Osbæck
	Preparation of a uniquely preserved turtle from the early Eocene Mo clay formation of northern Denmark
11:40-12:00	Donald Henderson
11.40-12.00	Moulding dinosaur tracks on the banks of the St. Mary River in southwestern
	Alberta, Canada
	Mocrta, Canada
12:00-14:00	Lunch
14:00-18:00	SPPC/GCG trip to Hampshire County Council collections, arriving back at
	NOC before the 18:00 Icebreaker Reception.
19.00 21.00	Joshusakan Dagantian and Dagistustian
18:00-21:00	Icebreaker Reception and Registration
	National Oceanography Centre Seminar Room
Tuesday 1st	Sentember
1 desday 1	<u>September</u>
8:10-8:45	SVPCA registration at NOC Security desk (4 <sup>th</sup> floor)
0.10 0.10	s 11 erring down with a committy wear (1 meer)
8:45-9.00	Welcome by Dr Gareth Dyke
	Session — Pterosaurs & Dinosaurs
	Chair — Manabu Sakamoto
9:00-9:15	Alexander Kellner et al.
	Comments on pterosaur reproduction based on recently found specimens from
	the Jurassic and Cretaceous of China
9:15-9:30	Colin Palmer & Michael Habib
	Giants of the air: how big could they be?
9:30-9:45	David Unwin & D. Charles Deeming
	New evidence for sexual dimorphism in the basal monofenestratan pterosaur
	Darwinopterus
9:45-10:00	Darren Naish et al.

	Romania and the short-necked azhdarchids, flightless avialans and giant lizards of yore
10:00-10:15	Cindy Howells et al.
10:15-10:30	A new Early Jurassic theropod from Wales: geological and discovery context <b>David Martill</b> <i>et al.</i>
10.13-10.30	The oldest Jurassic dinosaur: a basal neotheropod from the Hettangian of Great Britain
10:30-11:00	Morning coffee break
	Session — Dinosaurs
	Chair — David Martill
11:00-11:15	Daniel Vidal et al.
11.15 11.20	The specialized tail of <i>Spinophorosaurus nigerensis</i> (Sauropoda. Middle Jurassic) and the osteological limits on its range of motion
11:15-11:30	Michael Taylor <i>et al.</i> Were the necks of <i>Apatosaurus</i> and <i>Brontosaurus</i> adapted for combat?
11:30-11:45	Craig Fraser
11.00 11.10	The first comprehensive insight into the histology of the basal ornithopod, <i>Hypsilophodon foxii</i> , from the Isle of Wight
11:45-12:00	Stuart Pond et al.
	A critical new <i>Polacanthus</i> specimen from the Wessex Formation of the Isle of Wight
12:00-12:15	David Hone et al.
	Positive allometry in the growth of a ceratopsian frill indicates sexual selection
12:15-12:30	Manabu Sakamoto et al.
	Dinosaurs in decline tens of millions of years prior to the K-Pg boundary
12:30-14:00	Lunch
	Session — Mummies & Birds
	Chair — Ursula Göhlich
14:00-14:15	Diane Johnson et al.
14 15 14 20	Fossils of Qau el-Kebir; an ancient Egyptian funerary fossil collection
14:15-14:30	Niels Bonde On some feethers of Archaeontamy lithegraphics and their preservation
14:30-14:45	On some feathers of <i>Archaeopteryx lithographica</i> and their preservation <b>Eric Buffetaut &amp; Delphine Angst</b>
14.50-14.45	Twenty years of <i>Gargantuavis philoinos</i> : a summing up on an enigmatic Late
	Cretaceous giant bird
14:45-15:00	Vincent Beyrand et al.
	Endocast shape in birds linked with behaviour and flight ability
15:00-15:15	Rachel Frigot
	A geometric morphometric examination of form and function in the avian pelvis
15:15-15:45	Afternoon coffee break
	Session — Birds
	Chair — Eric Buffetaut

15:45-16:00 <b>Estelle Bourdon</b>	et al	l.
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An exquisitely preserved stem roller (Aves: Coracii) from the Early Eocene Fur Formation of Denmark

16:00-16:15 Ursula Göhlich et al.

The penguin with an Albatross-like bill: anatomy of *Spheniscus urbinai* (Aves, Spheniscidae) from the Mio-Pliocene Pisco Formation in Peru

16:15-16:30 Nicholas Chan

Complex evolution of avian leg bones with loss of flight

16:30-16:45 Ryan Felice & Patrick O'Connor

Insights into the evolution of the avian tail apparatus from passeriform comparative anatomy

16:45-17:00 **James Hansford** 

To kill an elephant bird: Diversity and extinction in the Aepyornithidae

Free evening – Space reserved at The Standing Order (Wetherspoons pub) at High Street for those interested

### Wednesday 2<sup>nd</sup> September

8:10-9:00 SVPCA registration at NOC Security desk (4<sup>th</sup> floor)

Session —Basal tetrapods & gnathostome evolution

Chair — John Clarke

9:00-9:15 Marco Castiello & Martin Brazeau

The braincase of the petalichthyid *Shearsbyaspis* revealed by x-ray micro-CT: implications for deep gnathostome phylogeny

9:15-9:30 Timothy Smithson & Jennifer Clack

A wandering entepicondylar foramen and the humeral twist: forelimb evolution in early tetrapods A wandering entepicondylar foramen and the humeral twist: forelimb evolution in early tetrapods

9:30-9:45 **Jennifer Clack** *et al.* 

A new lower jaw from the Late Devonian and its possible relationships

9:45-10:00 Eduardo Ascarrunz et al.

A deeper look into *Triadobatrachus massinoti*: The earliest known lissamphibian (*Vertebrata*: *Tetrapoda*) re-examined by μCT-Scan

10:00-10:15 **Jennifer Hill et al.** 

Evolution of the lower jaw of gnathostomes

10:15-10:30 **Benjamin Otoo** *et al.* 

A taxonomic and palaeoecological investigation of an earliest Carboniferous fauna from Burnmouth, Scotland, UK

10:30-11:00 Morning coffee break

Session — Taphonomy, trackways & ecosystems

Chair — Mark Witton

11:00-11:15 **Donald Henderson** 

Exceptional sets of dinosaur tracks and trackways from the St. Mary River Formation (Campanian-Maastrichtian) in Alberta, Canada

11:15-11:30 Mark Purnell *et al.* 

Experimental taphonomy and the anatomy of Cambrian vertebrates

11:30-11:45	0
11:45-12:00	Difficulties in estimating mass from fossil footprints  Kent Stevens <i>et al.</i>
11.13 12.00	Data-driven analysis and interpretation of fossil trackways
12:00-12:15	Luke Hauser
	The Downton "Tooth Bed": a lost world
12:15-13:30	Lunch
	Session — Crocodylomorphs & Gekkos
10 00 10 15	Chair — Gareth Dyke
13:30-13:45	Mark Young et al.
13:45-14:00	An early origin and diversification of macrophagous metriorhynchid crocodylomorphs, with evidence for multiple instances of parallel evolution <b>Davide Foffa</b> <i>et al.</i>
13.43-14.00	Evidence of macrophagous teleosaurids in the Corallian Group (Oxfordian,
	Late Jurassic) of the UK
14:00-14:15	Thomas Smith & Mark Young
	The phylogenetic implications of re-describing the English crocodyliform
	specimens referred to <i>Pholidosaurus</i>
14:15-14:30	Max Stockdale et al.
	Temperature-driven evolution and evolutionary stasis among the
14:30-14:45	Crocodylomorpha Andrea Villa
14.50-14.45	A review of fossil gekkotans from the Neogene and Quaternary of Italy
14:45-15:45	Afternoon coffee break / Poster Session (I)
	Session — Phylogenetics & palaeoart
	Chair — Darren Naish
15:45-16:00	
16.00.16.15	Positive phenotypic selection inferred from phylogenies
16:00-16:15	Neil Brocklehurst  Pates and mades of body size evalution in early carniveres and barbiveres: a
	Rates and modes of body size evolution in early carnivores and herbivores: a case study from Captorhinidae
16:15-16:30	Maren Jansen et al.
10.15 10.50	The phylogenetic inference of cranial ontogenetic trajectories of basal
	Therapsida
16:30-16:45	Michael Benton et al.
	Key characters and evolutionary rates in the origin of birds
16:45-17:00	Mark Witton et al.
	Trends and patterns in modern palaeoartistry: a call for change
18:00-21:00	Annual Auction and Reception
	SeaCity Museum, Southampton
Thursday 31	rd September

	Session — Mammals (I) Chair — Christine Janis
9:00-9:15	Elsa Panciroli <i>et al.</i>
7.00-7.13	Correlates between calcaneal morphology and locomotion in extant and
	extinct carnivorous mammals
9:15-9:30	Jamie MacLaren & Sandra Nauwelaerts
	Locomotor morphology of a 'living fossil' - 3D GMM assessment of forelimb anatomy in tapirs
9:30-9:45	Marcela Randau <i>et al</i> .
	Vertebral column shape evolution in felids
9:45-10:00	Chris Basu et al.
	Estimating body mass of the extinct giraffid Sivatherium giganteum, using a
	skeletal reconstruction and the minimum convex hull method
10:00-10:15	Gertrud Rössner et al.
	Evolutionary evaluation of fundamental processes in the antler cycle as
	revealed by internal bone structure
10:15-10:30	Roger Close et al.
	Evidence for a mid-Jurassic adaptive radiation in mammals
10:30-11:00	Morning coffee break
	Session — Mammals (II)
	Chair — Roger Close
11:00-11:15	Andrew McIntosh & Philip Cox
11.00 11.10	Musculoskeletal correlates of digging behaviour in African mole-rats
11:15-11:30	Philip Morris et al.
	Morphological convergence of the rodent-like masticatory apparatus in extant
	rodents and non-rodent diprotodonts
11:30-11:45	Christine Janis et al.
	On the probable predatory behaviour of the "marsupial lion", <i>Thylacoleo</i>
	carnifex
11:45-12:00	v
	Cementum histology reveals physiology at the root of the mammalian
	phylogeny
12:00-12:15	Ian Corfe et al.
	Tooth ultrastructure and development of a 200 million year old mammal
	revealed with synchroton nanotomography
12:15-13:30	Lunch
	Session — Teeth & Fish
	Chair — Ian Corfe
13:30-13:45	Robert Goodall & Mark Purnell
13.30-13.43	How the whale became: 3D tooth microtextures shed light on the complex
	dietary transition in archaeocete whale evolution (Cetacea: Archaeoceti)
13:45-14:00	Robert Asher
10.10 11.00	Pearly white & full of information: why we should all love teeth
14:00-14:15	Hermione Beckett & Matt Friedman
	Revisiting <i>Landanichthys</i> , the oldest fossil mackerel?
14.15-14.30	John Clarka & Matt Friedman

14:30-14:45	The 100 million year struggle to teleost supremacy <b>Jeff Liston</b> <i>et al.</i>
	Back from Purgatory: Three Rakers for Fishes at the Base of a Diversification
14:45-15:45	Afternoon coffee break / Poster Session (II)
	Session — Mesozoic reptiles
	Chair — David Unwin
15:45-16:00	Saulo Limaverde <i>et al</i> .
	Preliminary information on a new specimen of <i>Araripemys</i> (Pleurodira:
	Pelomedusoides) from the Early Cretaceous Crato Formation, Brazil
16:00-16:15	Tom Stubbs
	The ecomorphological diversifications of Mesozoic marine reptiles
16:15-16:30	Jessica Lawrence Wujek et al.
	Mary Anning's marine reptiles: taxonomy, systematics, morphometrics and
	evolution of the iconic <i>Ichthyosaurus</i>
16:30-16:45	Luke Muscutt et al.
	The hydrodynamics of plesiosaurs
16:45-17:00	
	Tetrapodophis amplectus, a four-legged snake from the Early Cretaceous of
	Gondwana, and implications for the origins of snakes
19:00-22:00	Conference Dinner
	Royal Thai Pier, Southampton

#### SPPC TALK ABSTRACTS

#### A brief history of the best collection of fossil fish in the world - probably...

Emma L. Bernard<sup>1</sup>

It has been said by many academic visitors and staff at the Natural History Museum, London (NHM), that the fossil fish collection is one of the best in the world.

The collection contains approximately 90,000 specimens from all corners of the globe spanning from the Ordovician to the Pleistocene. Between 1836 to 1884 the Museum acquired thirty eight major collections containing fossil fish. Two of the most important fossil fish collections were purchased by the Museum in the 1880's; William Willoughby Cole, the 3<sup>rd</sup> Earl of Enniskillen and Sir Philip de Malpas Grey Egerton. These collections comprised about 17,000 specimens.

In 1882 Arthur Smith Woodward joined the Museum and recognised the significance of the Fossil Fish Collection and almost immediately devoted all of his time and efforts into the study of fossil fish, culminating in the four part *Catalogue of the Fossil Fishes in the British Museum (Natural History)* published between 1989 and 1901. This is still used by many researchers today. Woodward went onto describe nearly 320 type specimens, the majority held in the NHM. Over the next 115 years the collections have continued to be added to and worked on. With many staff members undertaking expeditions to enhance the collections and developing techniques to expose fossils, such as Harry Toombs.

The collections are still heavily used by researchers from around the world today and we are still actively adding to the collection. Current curatorial projects involve digitising and making publically available the British Mesozoic holdings.

#### Fossils, Footprints & Fakes

Mark Graham<sup>1</sup>

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

The Natural History Museum has undertaken a series of annual field trips to Morocco for collections enhancement purposes. Specimens are collected directly from various locations and also obtained from local collectors and dealers, introduced to the group by trusted local contacts with whom the museum has built a relationship.

The 2015 fieldtrip in late February/early March was very eventful, with sudden snowfall and floods encountered, hidden mountainside quarries visited, little publicised dinosaur trackways discovered and fossil fakery by skilled preparators witnessed at first hand!

This presentation highlights the scientific value and potential pitfalls of such collaborations.

<sup>&</sup>lt;sup>1</sup>Department of Earth Science, Natural History Museum, London, UK

#### Breaking bad...bone beds: processing the Downton Bone Bed

Luke M. Hauser<sup>1</sup>

Bone beds have often been a focus for micropalaeontological study as the high concentration of fossil material allows vertebrate palaeontologists the returns normally experienced only by nannofossil workers and palynologists. It is not always straightforward to release the fossil material within bone beds and the extraction of microfossils from the Downton Bone Bed of the upper Silurian is particularly challenging. Outlined here is an integrated method for processing this bone bed using liquid paraffin and a microwave oven and a comparison in terms of quality and quantity with material recovered using other techniques. This method has also been used on other bone beds to test its effectiveness. This integrated method allows for the recovery of microvertebrates such as thelodonts, and also internal moulds of ostracodes, brachiopods and early plant material. This integrated method is enabling for the first time study of the Downton Bone Bed's fossil content.

### Moulding dinosaur tracks on the banks of the St. Mary River in southwestern Alberta, Canada

Donald M. Henderson <sup>1</sup>

During river survey work in2014, following the extensive 2013 flooding that affected almost all southern Alberta rivers, a new dinosaur tracksite was discovered. Investigation of the site in the spring of 2015 resulted in the discovery of another, even better set of tracks and trackways, and while working on these first two more sets of tracks were found. The blocks of sandstone hosting the tracks are immense, and it was felt that cutting out the tracks was too risky- both for safety of the people involved and the survival of the tracks. Instead, large latex rubber peels, reinforced with an open weave cloth, were made of the tracks. The very hot field conditions – full sun exposure all day with temperatures of 32-36C every day made for challenging moulding conditions. The large peels were successfully returned to the museum where a very thin layer of the very strong, fibre glass reinforced plaster will be used to make a cast. The intention is to display these thin casts by hanging them on walls with low angle lighting from the edge of the cast, along with a map illustrating the various.

<sup>&</sup>lt;sup>1</sup> School of Earth & Environmental Sciences, University of Portsmouth, Portsmouth, UK

<sup>&</sup>lt;sup>1</sup> Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada

#### Leviathan Rising: A new collections curation initiative from the Star Pit dig

Jeff Liston<sup>1,2</sup> & Nigel R. Larkin<sup>3,4</sup>

<sup>1</sup> National Museums Scotland, Edinburgh, UK

<sup>3</sup> Cambridge University Museum of Zoology, Cambridge, UK

Over field seasons 2002 and 2003, the most complete specimen of the large suspension-feeding fish *Leedsichthys* was excavated from the Star Pit, just outside Whittlesey, one of the last clay brick pits that Alfred Leeds collected from. Consisting of over 2,300 parts, the specimen became known as 'Ariston' because it went on and on, rather like the old utility advertisement. It took over 3,100 staff hours to excavate this prodigious quantity of material, achieving the record of the longest single dig for a vertebrate specimen in Europe.

In July 2015, the Esmée Fairbairn Foundation awarded a grant to Vivacity-Peterborough Museum & Art Gallery through the Museums Association's Collections Fund, to complete the work on this specimen. The funds for the Leviathan Project will be used for the specimen to be fully curated, with all associated field documentation including excavation maps, field photographs, video dig diaries and specimen registration books. As well as being used for school activities and events, photography will be employed to help create an online exhibition and website, linking to other collections with stores of this animal's remains around the world. Staff development will occur to ensure the necessary understanding is in place institutionally for long-term access and the global significance of the specimen. As a further part of the legacy from this project, it will provide training for individuals to complete the final stages of preparation, conservation and long-term storage of the final excavated elements of the specimen, completing the work started by Alan Dawn in 2002.

<sup>&</sup>lt;sup>2</sup> Peterborough Museum & Art Gallery, Peterborough, UK

<sup>&</sup>lt;sup>4</sup> Freelance conservator and curator at natural-history-conservation.com

### Preparation of a uniquely preserved turtle from the early Eocene Mo clay formation of northern Denmark

Frank Osbæck<sup>1</sup>

In the spring of 2014 a big block of cement stone concretion was found in Ejerslev Mo clay quarry on the island of Mors situated in the Limfjord, Northern Jutland.

It was from the start obvious that it contained parts of the Carapace and limb bones from a turtle. Once in the lab of Museernes Bevaringscenter I Skive, our "normal" procedure of preparing vertebrate fossils was used.

First Hammer and chisel, diamond rotating tools and heavy pneumatic tools was used, switching to finer tools when coming closer to the fossil surface, then, normally Acetic acid preparation buffered with Calcium orthophosphate would be used. This was changed when the first traces of a thin carbon layer was discovered. This layer represents preserved skin and is as thin as a pencil line and just as fragile, in itself acid resistant but when on top of soluble carbon carbonate concretion, disappears in a few moments when acid is applied. The skin is finely preserved on parts of the carapace, totally on one of the carapace horn plates and sensationally for this location between the toes of one of the hind legs.

The preparation was after this discovery mostly mechanical: scalpel, needles scrapers and pneumatic tools. When finished after a year we have half of the carapace, parts of the pelvis with complete Sacrum, the complete tail and both hind legs almost completely prepared so you see the preserved skin between the toes. It was also possible to collect parts of counter plate with skin impression during the preparation and this is presently being studied by Johan Lindgreen, University of Lund.

This specimen will undoubtedly add new understanding to the early Eocene Turtles.

<sup>&</sup>lt;sup>1</sup> Museernes Bevaringscenter I Skive, Denmark

#### SVPCA TALK ABSTRACTS

### A deeper look into *Triadobatrachus massinoti*: The earliest known lissamphibian (*Vertebrata*: *Tetrapoda*) re-examined by μCT-Scan

Eduardo Ascarrunz <sup>1,2</sup>, Michel Laurin <sup>1</sup>, Pierre Legreneur <sup>3</sup> & Jean-Claude Rage <sup>1</sup>

<sup>2</sup> Department of Geosciences, University of Freiburg, Freiburg, Switzerland

*Triadobatrachus massinoti* is a batrachian known from a single fossil from the Early Triassic of Madagascar that presents a combination of apomorphic salientian and plesiomorphic batrachian characters. It is also the oldest articulated fossil known to date that can be uncontroversially attributed to the *Lissamphibia*. Herein we offer a revised description of the specimen based on X-ray microtomography data. We report previously unknown caudal vertebrae, the possible presence of an angular and mentomeckelians, and hidden parts of other structures, and we confirm the presence of a ventrolateral ledge on the opisthotic. We also rectify some previous interpretations. There are no identifiable quadratojugals, and the identification of cervical ribs is not supported. The presacral region is composed of 15 vertebrae with a unique atlas-axis complex, instead of 14 vertebrae with a bipartite atlas. The configuration of the pelvic girdle is not very clear, although it is likely more plesiomorphic than the anuran-like condition previously assumed.

<sup>&</sup>lt;sup>1</sup> Sorbonne Universités CR2P, CNRS-MNHN-UPMC, Muséum National d'Histoire Naturelle, Paris, France

<sup>&</sup>lt;sup>3</sup> Centre de Recherche et d'Innovation sur le Sport, Université de Lyon, Villeurbane, France

#### Pearly white & full of information: why we should all love teeth

Robert Asher 1

The dentition is among the most durable (and therefore frequently preserved) tissues among vertebrate fossils. Mammals in particular have highly varied occlusal and developmental patterns which enable genus and even species level identification for long-extinct taxa. Thus, mammalian palaeontologists frequently use dental characters in their phylogenetic assessments, sometimes employing hyper-atomized details of dental morphology as seemingly heritable characters to decipher where a group belongs in the Tree of Life. Here, I discuss the extent to which distinct anatomical character partitions (e.g., teeth, skull, postcranium), alone and in combination, succeed in contributing positive information towards known phylogenetic trees. For primates, I find that even very incomplete character sets consisting entirely of dental data often (but not always) succeed in placing taxa with known affinities successfully on the Mammalian Tree of Life, and generally perform significantly better compared to partitions with randomly generated character states. One or few phenotypic character partitions (e.g., the dentition) can indeed be more susceptible to a given selective pressure than many partitions (e.g., dentition, basicranium, postcranium), particularly when one is dominated by interdependent, overly-atomized traits. Nonetheless, the performance of such partitions needs to be evaluated on a case-by-case basis, and even when one partition is uninformative at one level, it may still provide worthwhile phylogenetic information at others. Overall, I argue that the mammalian fossil record is enhanced, not diminished, by the abundance of teeth, the absence of which would render many questions about (for example) adaptation, radiation, and palaeogeography intractable.

<sup>&</sup>lt;sup>1</sup> Department of Zoology, University of Cambridge, Cambridge, UK

#### Positive phenotypic selection inferred from phylogenies

Joanna Baker <sup>1</sup>, Andrew Meade <sup>1</sup>, Mark Pagel <sup>1,2</sup> & Chris Venditti <sup>1</sup>

<sup>1</sup> School of Biological Sciences, University of Reading, Reading, UK

<sup>2</sup> Santa Fe Institute. Santa Fe. NM 87501. USA

It is possible to detect positive genetic selection across phylogenetic trees using the wellknown dN/dS ratio. In this context, positive selection is identified where dN/dS >1: nonsynonymous substitutions contribute over half of all genetic changes along a branch. However, no such method exists for detecting positive phenotypic selection in the same way. Here we outline a method for detecting driven directional changes in morphology by identifying exceptional shifts in the rate of phenotypic evolution. Rates of phenotypic evolution vary widely in nature and these rates may often reflect the intensity of natural selection. With this in mind, we identify branches undergoing positive phenotypic selection by drawing parallels to the genetic dN/dS ratio – where the phenotypic variance attributed to accelerations in the rate of evolution contributes more than half the total phenotypic variance occurring along that branch. We apply our approach to a number of vertebrate datasets, finding positive selection in each. Our results support the growing appreciation that the traditional gradual view of phenotypic evolution is rarely upheld, with a more episodic view taking its place. This moves focus away from viewing phenotypic evolution as a simple homogeneous process and facilitates reconciliation with macroevolutionary interpretations from a genetic perspective, paving the way to novel insights into the link between genotype and phenotype. The ability to detect positive selection where genetic data are unavailable or unobtainable represents an attractive prospect: specifically, when applied to fossil data it can reveal natural selection in deep time that would otherwise be impossible to detect.

### Estimating body mass of the extinct giraffid *Sivatherium giganteum*, using a skeletal reconstruction and the minimum convex hull method

Chris Basu <sup>1</sup>, Peter Falkingham <sup>2</sup> & John R Hutchinson <sup>1</sup>

The Giraffidae clade is dominated by genera with elongated cervical vertebrae and distal limb elements, notably the extant Giraffa camelopardalis. The extinct, 'giant' genus Sivatherium is an unusual giraffid, as it possessed relatively short stout limbs, a short neck, and ornate ossicones. Sivatherium spp. are anecdotally the heaviest of the giraffids, having been historically compared to the size of African elephants. We set out to estimate the body mass of a representative adult of the type species Sivatherium giganteum, using the minimum convex hull method. The reconstructed composite skeleton was based on fossil material (including the type specimen) from the Natural History Museum, London. Missing elements were replaced with those from a previously digitised *Giraffa camelopardalis* skeleton, or estimated from interspecific scaling equations. The giraffe elements were scaled to known Sivatherium skeletal dimensions. The validity of the resulting model was then tested against a different interspecific scaling equation for other artiodactyls. Using a previously published volumetric scaling method, the convex hull volume yields an estimated minimum body mass of 1786 kg (1500 - 2000 kg). Due to the uncertainty surrounding the missing skeletal segments, a sensitivity analysis was performed, where the linear dimensions of the scaled Giraffa elements were increased and decreased by a factor of 10%. This resulted in modest changes to the estimated body mass. The volumetric mass estimates were then compared with those calculated from 'single bone' bivariate interspecific scaling equations. The resulting discrepancies (for example humeral circumference) highlight parts of the skeletal anatomy of Sivatherium which may be morphologically and functionally unusual.

<sup>&</sup>lt;sup>1</sup> Structure & Motion Laboratory, Royal Veterinary College, Hatfield, UK

<sup>&</sup>lt;sup>2</sup> School of Natural Sciences, Liverpool John Moores University, Liverpool, UK

#### Revisiting *Landanichthys*, the oldest fossil mackerel?

Hermione Beckett <sup>1</sup> & Matt Friedman <sup>1</sup>

Scombrids (tunas and mackerels) are among the most studied of living fishes thanks to their remarkable physiological specializations and major economic significance. Although scombrids have a rich fossil record, aspects of their early evolutionary history are unclear. The oldest fossil scombrids that are known in any detail are early Eocene (Ypresian) in age, from the UK and Turkmenistan. Apparently older deposits in Angola have yielded several skulls attributed to scombrids and assigned to two species within the genus *Landanichthys*. Known for more than half a century, Landanichthys has been a side note in subsequent studies of scombrid evolution despite its potential significance. This marginalization stems from ambiguities surrounding its age, and poor documentation of its anatomy. Biostratigraphic evidence strongly supports a Danian age for *Landanichthys*, corroborating initial interpretations and cementing its status as the oldest fossil scombrid. Anatomical study of Landanichthys is complicated by the loss of both specific holotypes. However, examination of material referred to the genus using computed tomography indicates that Landanichthys contains fishes belonging to different scombrid subfamilies. Significantly, these two different forms differ strongly in dentition and jaw morphology, suggesting high degrees of trophic differentiation among scombrids by the early Paleocene. This raises obvious questions about the evolutionary history of scombroids: did they radiate rapidly after the K-Pg as apparently suggested by the fossil record and some genetic studies, or do they have more ancient roots like those suggested by other molecular clocks?

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#### Key characters and evolutionary rates in the origin of birds

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Discovery of new bird and theropod fossils has shown that the list of some thirty characters formerly identified as unique to Archaeoptervx and birds now spread back down the phylogenetic tree to the root of Theropoda. Comparative phylogenetic analyses of character evolution across the theropod tree show how these avian characters emerged, and their relative evolutionary significance. For example, the earlier discovery that one key avian character - reduction in body size – was a sustained trend along the stem of theropods, with a further statistically highly significant change of rate associated with wing length-body size decoupling at the origin of Paraves. Comparative analyses, carried out independently by several author teams, have shown that both features stand out as unusual character shifts, indicated by remarkably high evolutionary rates. Forelimb elongation, against the trend for reduction in other theropod lineages, marked a time of experimentation with various flight modes within several paravian lineages. It is well known that other avian characteristics such as the furcula, feathers, semilunate carpal, hind limb posture and centre of mass, and enlargement of orbits and optic regions of the brain also occurred before the divergence of Archaeopteryx and other birds. Continuing through the Mesozoic, further avian characters are also assessed for their importance, such as the loss of the bony tail in Pygostylia, and further modifications to the limbs associated with flight at higher points in the cladogram. The array of new numerical comparative phylogenetic approaches allows these anatomical novelties to be assessed in sequence across the phylogeny of Theropoda to determine which were associated with pulses of rapid evolution (diversification shifts), and which are associated with models of directional or driven evolution. Such approaches provide a means of testing functional-evolutionary hypotheses.

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#### Endocast shape in birds linked with behaviour and flight ability

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Birds have been evolving for about 120 million years, and have adapted to variety of ecological conditions. The most fascinating of all these traits is the ability to fly. Controlled flight requires a great deal of cognitive abilities, as it requires the capacity to handle the large amount of information needed for complex motor skills and controlling processes. Differences in these abilities are reflected in the sizes of the associated brain compartments, affecting the size and shape of the brain.

Consequently, studying the evolution of brains in bird lineages should provide an insight into how their ability to fly evolved. Understanding how brain shape and behaviour are linked in extant species provides a good approximation of that correlation in fossils; however, brains are not preserved in extinct birds. The solution is to reconstruct the endocasts of fossils, and use that data to study how bird brains changed over time.

We studied a sample of 70 bird species with a great diversity of behaviours, and then applied geometric morphometric methods on the endocasts of those animals in order to see the link between behavior and endocast shape.

Our results show some relationship between behaviour and brain shape, with discrimination mostly by ecology instead of phylogeny. What was particularly apparent was the relation between brain shape and dietary/locomotive behaviours. In some groups there is still also a tiny phylogenetic signal, which could be explained by the fact that the divergence between families happened too suddenly for any ecological factors to affect their evolution.

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#### On some feathers of Archaeopteryx lithographica and their preservation

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'Archaeopteryx, iconic fossils', 11 described specimens and the vast literature about them is clearly full of misunderstandings and paradoxes.

Until most recently it was always claimed, that in 'Archaeopteryx', including also later finds, the feathers were only preserved as imprints (implying no material left apart from the black of the single feather). Early this century when scrutinizing the London specimen a second time, I discovered that in the counterpart some tiny patches of some yellowish material from the flight feathers was preserved included in whitish secondary calcite (really not surprising, as most 'Archaeopteryx' preserve the keratinous claws of the toes). I suggested analysing a few mm of these remains of feathers for a joint publication, but the 'authority' said "No – nothing to be removed!" (recall the entire skull had long ago been taken completely out – and is now scanned). I also found a small (never reported) feather at the thumb that might be an alula, also preserved with material intact, but that has been denied publication in high profile journals by reviewers stating "I don't believe it" and similar unsubstantial remarks (e.g. misunderstanding simple cladistic arguments). In 2010 Bergmann et al. published their analysis of the same kind of 'feather material' from the 10<sup>th</sup> specimen. Almost certainly most specimens (not Berlin) must have had such preservation, and probably most material fell out when the limestone was split (may even have been brushed away!). This is a cautionary tale: prejudicial and censorious attitude by 'authorities' and referees prevented scientific advance.

### An exquisitely preserved stem roller (Aves: Coracii) from the Early Eocene Fur Formation of Denmark

Estelle Bourdon <sup>1</sup>, Niels Bonde <sup>1</sup> & Anette Kristoffersen <sup>1</sup>

A new genus and species of stem roller (Aves: Coracii) from the Fur Formation of Denmark (marine Early Ypresian diatomite, 'mo-clay', ca. 55 MA) is presented here. It is a nearly complete skeleton preserved in 3-D in a calcareous concretion ('cementstone'). The new fossil was a small bird the size of the Northern carmine bee-eater (Merops nubicus). Its appearance is typically 'coraciiform': proportionately large skull; long, strong bill; short and wide pelvis; short tarsometatarsi; anisodactyl toes with indication of syndactyly. This is the earliest evidence of syndactyly in birds. Concentration of fish remains in the stomach region and bill shape indicate that this species was piscivorous. These remains of a small argentinoid (the most common fish in the 'mo-clay', reaching 10 cm) are clearly part of the bird's last meal, rather than a result of animals fossilized on top of each other. Within the 'traditional coraciiform assemblage', there is solid evidence that the Coracii form a clade comprising the two extant families Coraciidae (rollers) and Brachypteraciidae (ground rollers) plus several Eocene taxa from Europe and North America, including the Early Eocene Primobucco. The new species is the earliest known member of the Coracii and is placed as a stem group representative of this clade. With preservation in 3-D, last fish meal and even a few feathers, this may well be 'the World's best fossil bird'.

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# Rates and modes of body size evolution in early carnivores and herbivores: a case study from Captorhinidae

Neil Brocklehurst <sup>1</sup>

Body size is an extremely important characteristic, impacting on a variety of ecological and life-history traits. It is therefore important to understand the factors which may affect its evolution, and diet has attracted much interest in this context. A recent study, examining the evolution of the earliest terrestrial herbivores in the Late Carboniferous and Early Permian, concluded that in the four herbivorous clades examined there was a trend towards increased body size, and that this increase was more substantial than that observed in closely related carnivorous clades. However, this hypothesis was not based on quantitative examination, and phylogenetic comparative methods provide a more robust means of testing such theories. Here, the evolution of body size within different dietary regimes is examined in Captorhinidae, the most diverse and longest lived of these earliest high fibre herbivores. Evolutionary models were fit to their phylogeny to test for variation in rate and mode of evolution between the carnivorous and herbivorous members of this clade, and an analysis of rate variation throughout the tree was carried out. Estimates of ancestral body sizes were calculated in order to compare the rates and direction of evolution of lineages with different dietary regimes. Support for the idea that the high fibre herbivores within captorhinids are being drawn to a higher adaptive peak in body size than the carnivorous members of this clade is weak. A shift in rates of body size evolution is identified, but this does not coincide with the evolution of high-fibre herbivory, instead occurring earlier in time and at a more basal node. Herbivorous lineages which show an increase in size are not found to evolve at a faster rate than those which show a decrease; in fact it is those which experience a size decrease which evolve at significantly higher rates. The opposite is true of the carnivorous lineages, suggesting that in captorhinids it is the carnivores which show the greater trend towards increased body size. It is possible the shift in rates of evolution is related to the improved food processing ability of the more derived captorhinids rather than a shift in diet, but the evidence for this is circumstantial.

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# Twenty years of *Gargantuavis philoinos*: a summing up on an enigmatic Late Cretaceous giant bird

Eric Buffetaut <sup>1</sup> & Delphine Angst <sup>2</sup>

In 1995, a synsacrum fragment from Fox-Amphoux (Var), was the first evidence to be reported of a giant bird from the Late Cretaceous of southern France. The taxon Gargantuavis philoinos was erected in 1998 on the basis of a partial pelvis from Campagnesur-Aude (Aude); a femur from Villespassans (Hérault) was also referred to that species. Since then, a few additional specimens have been discovered, including two pelves from Fox-Amphoux and a cervical vertebra and yet undescribed pelvic elements from Cruzy (Hérault). A synsacrum from the Late Cretaceous of Laño (Spain) is referrable to Gargantuavis. The avian nature of *Gargantuavis* is supported by various anatomical and histological features. including the extremely advanced fusion of the synsacral vertebrae and the distinctly heterocoelous condition of the cervical vertebrae. The advanced pneumatisation of the synsacrum and ilia is also worth noting. Archaic characters include the relatively small number of synsacral vertebrae and the lack of dorsal contact between the ilia. Many aspects of the anatomy and palaeobiology of *Gargantuavis philoinos* remain obscure. No skull elements have yet been found, and very little can be said about its possible diet. Its broad pelvis does not suggest a fast-running bird. Gargantuavis philoinos lived on the Ibero-Armorican island, and histological features indicating protracted cyclical growth, similar to the condition in some moas (*Megalapteryx*), may be linked to insularity. However, unlike ancient New Zealand, the fauna of the Ibero-Armorican island included large terrestrial carnivores (notably dinosaurs) and the place of *Gargantuavis* within this ecosystem remains unclear.

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# The braincase of the petalichthyid *Shearsbyaspis* revealed by x-ray micro-CT: implications for deep gnathostome phylogeny

Marco Castiello <sup>1</sup> & Martin D. Brazeau <sup>1</sup>

Fossil stem-gnathostomes offer the potential to fill the morphological gap between extant jawless and jawed vertebrates, allowing us to reconstruct the stepwise evolution of the gnathostome body plan. The petalichthyids are placoderm-grade stem gnathostomes thought to possess jaws, but also display a combination of neurocranial features otherwise found only in jawless vertebrates, particularly osteostracans. Because of this, they have become central to the debate on the relationships of placoderms and the primitive cranial architecture of gnathostomes. Nevertheless, only the braincase of the petalichthyid *Macropetalichthys* has been studied in detail and the diversity of neurocranial morphology in this group remains poorly documented. Using x-ray computed microtomography, we investigate the endocranial morphology of *Shearsbyaspis oepiki*. Young 1980, a petalichthyid from the Early Devonian of Taemas-Wee Jasper, Australia. We generated virtual three-dimensional reconstructions of the external endocranial surfaces, orbital walls, and cranial endocavity, including canals for major nerves and blood vessels. The neurocranium of *Shearsbyaspis* resembles Macropetalichthys in particular in the course of nerves and blood vessels. Additionally, we reveal phylogenetically informative features previously unrecognized among petalichthyids, including the presence of a denticulated parasphenoid. The presence of a parasphenoid might corroborate traditional placements of petalichthyids as close relatives of arthrodires, raising some questions about current proposals of placoderm paraphyly. We reinvestigate the phylogenetic significance of petalichthyid cranial morphology, comparing the strengths and weaknesses of competing scenarios of placoderm relationships.

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#### Complex evolution of avian leg bones with loss of flight

Nicholas Chan 1

The loss of flight in birds is associated with relative reduction of the wing bones and a decrease in the size of pectoral muscle attachments. However, the changes that occur in the leg bones are less intensively studied. These may be related to changes in size, the need for more efficient terrestrial locomotion, or the amount of time since the loss of flight occurred.

These hypotheses were tested in a dataset of leg bone lengths and diameters for 38 species of flightless birds including 23 extinct taxa. Nineteen volant relatives were measured to provide ancestral models. Measurements were size-corrected and input into a factor analysis. Differences ( $\Delta$ ) in scores between flightless species and ancestral models were input into multiple regressions. Independent variables for regressions were:  $\Delta$  femoral circumference, estimated time since the loss of flight, and whether the species was present on an island or continent. One-sample Wilcoxon Signed Rank tests were carried out on  $\Delta$  factor scores and femoral circumferences to test for directionality in the evolution of limb bone proportions and body size.

No evidence for directionality was found in these analyses with few relationships between the changes in proportions and predictor variables. One pattern found was that ratites outside of New Zealand have longer, narrower distal limb bones than those species found in New Zealand. The trajectories of change in leg bone proportions are far more complex than those seen in the wings and likely reflect variation in ecology rather than any universal selection pressure.

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#### A new lower jaw from the Late Devonian and its possible relationships

Jennifer Clack <sup>1</sup>, Keturah Smithson <sup>1</sup> & Timothy Smithson <sup>1</sup>

One of the specimens discovered on the 1987 Cambridge-Copenhagen expedition to East Greenland was a very small (about 50mm) lower jaw. It was prepared mechanically as far as possible, but given the lack of key information, was never described. Recent micro-CT studies have now allowed further features to be visualized, especially of the adsymphysial and coronoid dentitions. The prearticular is robust and thickened below the adductor fossa for about half the length of the jaw, but only contacts the angular and postsplenial at a few points, leaving Meckelian spaces between. Although the dermal ornament is low-profile, the robust bone and tight sutures suggest that the animal was an adult. The dentary carries approximately 28 teeth and spaces, alternately placed. The adsymphysial carries at least two and possibly more larger teeth, the anterior coronoid at least one, the middle and posterior coronoids at least two each. These teeth are larger than the dentary teeth, but the scan resolution does not allow us to distinguish smaller coronoid teeth or denticle shagreen. The closest approximation to this formula is the Late Devonian *Ymeria denticulata*, although the new specimen is much smaller. It also resembles a more recently investigated specimen from the Tournaisian of the Borders Region. In a cladistic analysis, *Ymeria* appeared as a sister taxon to the Borders specimen. As with recently described limb elements, this finding contributes to the impression that for tetrapods, the Devonian-Carboniferous boundary is beginning to blur.

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#### The 100 million year struggle to teleost supremacy

John Clarke<sup>1,2</sup> & Matt Friedman<sup>2</sup>

Teleosts are the dominant living group of aquatic vertebrates; they comprise approximately 29,000 species, assume a bewildering array of morphologies, and have come to occupy nearly every environment imaginable. In extreme contrast, their holostean sister group comprises a mere 8 living species restricted to the freshwaters of eastern North America. Given this stark contrast, one might assume that teleosts have always reigned supreme regarding morphological and functional variety, yet the 250 million year fossil history of neopterygians has not yet been quantified in sufficient detail to examine this claim. We quantified disparity for >350 neopterygian species across 150 million years of the Mesozoic. The analyses reveal that holosteans were far more diverse in the past, showing greater disparity than teleosts across the Triassic and Early Jurassic. Sustained teleost diversification from the Early Jurassic onwards led them to approach holostean levels of disparity in the Middle Jurassic, before achieving greater disparity than holosteans from the Late Jurassic onwards, over 100 million years after the unequivocal origin of neopterygians in the fossil record. Surprisingly, although the Late Jurassic teleost takeover coincides with the arrival of crown group teleosts – taxa previously shown to display exceptional phenotypic rates and innovation – they are not responsible for the Late Jurassic rise in teleost disparity. Instead, it is the presence of disparate, early diverging teleost clades, such as Pachycormids, Aspidorhynchids and Pycnodonts, that drive the initial teleost takeover. Nevertheless, as the Cretaceous wore on, crown teleosts became an increasingly important contributor to overall teleost disparity.

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#### Evidence for a mid-Jurassic adaptive radiation in mammals

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A series of spectacular discoveries have transformed our understanding of Mesozoic mammals in recent years. These finds reveal hitherto-unsuspected ecomorphological diversity that suggest mammals experienced a major adaptive radiation during the Middle to Late Jurassic. Patterns of mammalian macroevolution must be reinterpreted in light of these new discoveries, but only taxonomic diversity and limited aspects of morphological disparity have been quantified. We assess rates of morphological evolution and temporal patterns of disparity using large datasets of discrete characters. Rates of morphological evolution were significantly elevated prior to the Late Jurassic, with a pronounced peak occurring during the Early–Middle Jurassic. This intense burst of phenotypic innovation coincided with a stepwise increase in apparent long-term standing diversity, and with the attainment of maximum disparity, supporting a "short-fuse" model of early mammalian diversification. Rates then declined sharply, and remained significantly low until the end of the Mesozoic, even among therians. This supports the "long fuse" model of diversification in Mesozoic therians. Our findings demonstrate that sustained morphological innovation in Triassic stem-group mammals culminated in a global adaptive radiation of crown-group members during the Early-Middle Jurassic.

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### Tooth ultrastructure and development of a 200 million year old mammal revealed with synchroton nanotomography

Ian Corfe <sup>1</sup>, Aki Kallonen <sup>1</sup>, Pamela Gill <sup>2</sup>, Elis Newham <sup>3</sup>, Jackie Moustakas <sup>1</sup> & Jukka Jernyall <sup>1</sup>

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Three-dimensional relationships between tooth dentine tubules, enamel tubules and enamel prisms are not fully understood. Previous visualisation methods have been in two dimensions or concern only limited tooth regions. We utilised non-destructive synchrotron nanotomography, producing 3D models of dental ultrastructure with voxel resolutions down to 25 nanometers, and quantified the number, shape and 3D spatial relationships of tubules and prisms of lower molars of mouse Mus musculus, shrew Sorex minutissimus, vole Myodes glareolus and the Early Jurassic mammaliaform Morganucodon watsoni. Dentine tubule densities follow similar patterns, increasing with distance from cusp tips in all taxa, but were twice as dense in the shrew. In all species, dentine tubules split to form more but smaller diameter tubules traversing the enamel-dentine junction (EDJ), and continuous with equal sized enamel tubules. Mus enamel tubules merge and terminate close to the EDJ, whereas in Sorex enamel tubules run throughout the enamel; Myodes and Morganucodon are intermediate in enamel tubule length and density. Enamel tubules of *Sorex* are often but not always associated with an enamel prism sheath. In extant species, there is a sharp angle change of enamel and dentine tubules close to the EDJ, with tubules crossing the EDJ perpendicularly before bending towards the pulp cavity. In *Morganucodon* however, this angle change is considerably less pronounced, with tubules following a near straight line from EDJ to pulp cavity. These results suggest the overall developmental and mineralization ontogeny of *Morganucodon* molars was similar to those of extant mammals, but differed in the finer details.

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#### Difficulties in estimating mass from fossil footprints

Peter L. Falkingham <sup>1</sup>

Fossilized footprints offer exciting glimpses into the palaeobiology of extinct taxa. A common question that has arisen during my work is whether the weight of a dinosaur can be estimated from its tracks. Indeed, in recent years a small number of studies have attempted to do just that based on the depths of fossil footprints. Such studies require reconstructing the mechanical properties of the substrate, and then using force-displacement relationships to determine the range of possible loads. However, the interaction between the foot and the substrate is highly complex, and treating the track-forming process as a simple vertical indentation accomplished with a single load is likely to be extremely inadequate. The track forming process is dynamic, and the load applied, expressed as underfoot pressure, changes throughout the step cycle, meaning there is no 'one' load to reconstruct. There is also rarely a single depth with which to measure vertical displacement. Compounding matters further, if there is a flat base to a track, the likelihood based on experimental data is that the foot was supported by a firmer substrate beneath. This means that even if conditions are accurately assumed for the surface track-bearing sediment, ultimately that layer has not resisted the weight of the animal, and it is a deeper, mechanically different substrate that has supported the animal's weight. Based on the data and inferences gained through experimentation and theory, it is unlikely that footprints can be used as an adequate means of estimating mass in extinct taxa.

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### Insights into the evolution of the avian tail apparatus from passeriform comparative anatomy

Ryan N. Felice <sup>1</sup> & Patrick M. O'Connor <sup>1</sup>

The avian tail is considered a key innovation in bird evolution due to its crucial role in aerial locomotion. The aerodynamic function of the tail is facilitated by its derived structure, composed of an articulated fan of feathers (rectrices), unique soft tissues, and, critically, a specialized caudal skeleton. Recent paleontological and neontological comparative research support the hypothesis that these elements have evolved in a coordinated manner throughout early avialan and modern neornithine history. Here, we explore several lines of evidence to understand how interactions among the elements of the tail apparatus have shaped the evolution of skeletal variation in this system. We test two predictions: (A) that the evolution of costly, sexually dimorphic tail feathers necessitates concomitant phenotypic changes in the underlying caudal skeleton that supports the tail fan and (B) that the free caudal vertebrae and the terminal pygostyle exhibit phenotypic integration and can be predicted to evolve in a coordinated manner. Caudal skeletal morphology was quantified in several passeriform taxa and permutational MANOVA was used to test whether males and females of dimorphic species exhibit sex differences in key caudal traits. Skeletal dimorphism was not consistently detected; suggesting caudal skeletal morphology in these taxa is likely influenced more by phylogeny and locomotor function than by its relationship with tail fan shape. Using a phylogentic implementation of integration analysis, we recover evidence of significant integration between the pygostyle and other caudal skeletal elements. This supports the hypothesis that the tail skeleton evolves as a whole despite its structural and functional regionalization. Together, these findings shed new light on the processes that have shaped morphological variation in this system and can guide future work at the interface of avian origins, comparative anatomy, and developmental biology.

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### Evidence of macrophagous teleosaurids in the Corallian Group (Oxfordian, Late Jurassic) of the UK

Davide Foffa <sup>1</sup>, Mark T. Young <sup>1,2</sup> & Stephen L. Brusatte <sup>1,3</sup>

Teleosaurids were a semi-aquatic group of crocodylomorphs with a fossil record that spanned the Jurassic Period. Abundant specimens are known from Oxford Clay (OCF, Callovian to lower Oxfordian) and Kimmeridge Clay (KCF, Kimmeridgian to lower Tithonian) Formations of the UK, and contemporaneous deposits in northern France. Unfortunately, due to the paucity of material from the intermediate 'Corallian Gap' (middle to upper Oxfordian), we lack an understanding of how and why teleosaurid taxic abundance and diversity declined from the OCF to the KCF. Our discovery of an incomplete teleosaurid lower jaw from the Corallian of Weymouth (Dorset, UK) begins to help rectify this. The vertically oriented dentition, blunt tooth apices, and intense enamel ornamentation that shifts apical to an anastomosed pattern, and deep reception pits on dentary unambiguously demonstrates the affinity of this specimen with a sub-clade of macrophagous/durophagous teleosaurids ('Steneosaurus' obtusidens + Machimosaurus). The high symphyseal tooth count allows us to exclude the specimen from M. hugii and M. mosae, but in absence of more diagnostic material we cannot unambiguously assign the specimen to a more specific level. Nevertheless, this specimen represents the first UK mandibular material referable to Teleosauridae from this poorly known time-span.

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### The first comprehensive insight into the histology of the basal ornithopod, *Hypsilophodon foxii*, from the Isle of Wight

Craig Fraser <sup>1</sup>

The fossilised remains of the basal ornithischian *Hypsilophodon foxii*, have been unearthed from Cretaceous deposits on the Isle of Wight since the early days of vertebrate palaeontology, specifically from the Wessex Formation. Distinguished by its small size and interpreted as a fast bipedal runner, Hypsilophodon is currently regarded as the only known phylogenetic representation of its kind anywhere in the world. In the past, many dinosaur species including a number of basal ornithischians, have been subjected to histological analysis in order to determine specimen age, growth and maturity rates. To date however, there appears to be no data regarding *Hypsilophodon* in this particular field. Here, we present the first definitive histological analysis of *Hypsilophodon* long bone specimens. The fossil resources featured in this data set, were collected from the Isle of Wight, United Kingdom. These particular fossils are part of a larger collection of disarticulated material, interpreted as belonging to multiple individuals. The results were then compared to other dinosaur species to establish possible correlations and distinctive characteristics. The woven texture of cortical bone, represents accelerated growth rates early in the ontogeny of *Hypsilophodon*. There is also extensive vascularisation towards the central cavity, which becomes less frequent towards the outer edge of the bone, suggesting a marked reduction in the growth rate as the individual matured. There is also a noticeable absence of lines of arrested growth, which could be correlated to specimen immaturity, or sustained growth rates through early ontogenv.

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(This abstract is the same for the poster given by Craig Fraser, under the same title.)

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#### A geometric morphometric examination of form and function in the avian pelvis

Rachel Frigot 1

Modern birds represent a large portion of earth's modern diversity and are a unique and diverse clade. Much attention has been dedicated to the mechanics of their flight, but they also exhibit diversity in the hind-limb, often providing adaptations essential to the exploitation of their niche. Some work has attempted to quantify the relationship between the form of the hind-limb skeleton and the function of the hind-limb, but large gaps in knowledge remain.

This study uses landmark geometric morphometrics to analyse the shape of a phylogenetically and functionally diverse sample of avian pelves. The pelvis and synsacrum is the most complex structure in the skeleton of the hind-limb of birds and searching for correlations between shape and function require shape-based, multivariate analyses. Landmarks were collected from complete pelves of adult birds for which the sex of the individual was known and a hind-limb functional group was assigned. These landmarks attempted to capture the shape of regions of the pelvis available for muscular attachment. Subsequently, the shape configurations were aligned and a principal components analysis (PCA) performed.

The results of the PCA show a significant difference and excellent separation between the shapes of pelvis found in different functional groups, demonstrating that shape of the pelvis is correlated to function of the hind-limb. This finding suggests many fruitful avenues of research are possible, including the prediction of life habit from pelvic shape and biomechanical analysis tailored to each functional group.

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### The penguin with an Albatross-like bill: anatomy of *Spheniscus urbinai* (Aves, Spheniscidae) from the Mio-Pliocene Pisco Formation in Peru

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Three species of extinct penguins are described so far from the Miocene-Pliocene marine Pisco Formation in Peru, which all belong to the extant genus Spheniscus. Spheniscus urbinai is the most abundant one in the fossil record of the Pisco Formation. S. urbinai and the second species S. megaramphus are quite large sized of about the size of an extant Royal Penguin (Aptenodytes patagonicus). The third species, S. muizoni, is small sized, closest in size to extant Jackass Penguin (S. demersus) and Magellanic Penguin (S. magellanicus). The investigation on the anatomy and variability of S. urbinai is based on several more or less complete skeletons and several hundreds of disarticulated bones, including skulls and postcranials. The fossils come from five different Peruvian localities (El Jahuay, Aguada de Lomas, Montemar, Sud-Sacaco, Sacaco) covering the age period from the Late Miocene to Early Pliocene, from about 9 Ma up to ca. 3.5 Ma. The overall cranial and postcranial anatomy of S. urbinai corresponds in general well to that of extant penguins of the genus Spheniscus. However, it distinguishes from all extant Spheniscus species by a much more robust and longer beak terminating in a hooked tip, which resembles in size and shape more that of an albatross than that of any extant penguin. It thus might reflect a slightly deviant or more diverse diet.

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### How the whale became: 3D tooth microtextures shed light on the complex dietary transition in archaeocete whale evolution (Cetacea: Archaeoceti)

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The origin of whales is associated with a significant dietary transition: from terrestrial omnivory/herbivory to aquatic piscivory/carnivory. This occurred between the evolution of the earliest Pakicetidae (early Eocene ca. 52.5 Ma) and the emergence of crown group whales near the Eocene/Oligocene boundary (ca. 33.7 Ma). Morphological and isotope analyses suggest an extensive mid-late Eocene semi-aquatic stem lineage, preceding obligate aquatic lifestyles in later stem clades, and transition to the marine realm within protocetids. However, neither morphological nor isotope data reveal direct evidence of trophic ecology. We have employed a novel approach - quantitative 3D-microtextural analysis - to provide new tests of hypotheses of ecological transitions in whale evolution. This technique, developed from engineering approaches to surface metrology, uses quantification of tooth surface textures to provide direct evidence of tooth-food interactions and diet. It is a well-established technique for dietary analysis in terrestrial mammals, but has not previously been applied to aquatic mammals. Our statistical comparison and multivariate analysis of microtextures in extant pinnipeds and odontocetes provides the first evidence that tooth microtextures vary with diet in modern aquatic mammals. Applying this relationship to archaeocetes, we find evidence of clear differences in diet which are not correlated with phylogenetic position. These results paint a more complex picture of dietary evolution in archaeocete whales than previously hypothesised.

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#### To kill an elephant bird: Diversity and extinction in the Aepyornithidae

James Hansford 1

The elephant birds (Aepyornithidae) of Pleistocene-Holocene Madagascar are amongst the largest birds ever (circa 400 Kg). Despite large amounts of interest from the European scientific community following their discovery in the 1850's, serious attempts at reviewing all available museum collections of aepyornithid material have never been made and the last review of recognised taxa was undertaken nearly 100 years ago. Current taxonomy of the aepyornoithids remains confused and literature commonly refers to two broad genera differentiated by differences in size.

The most common post-cranial elements have scrutinized through multiple linear measurements and their diversity are currently being reviewed through multivariate methods as part of this study. Preliminary evidence now demonstrates a quantified explanation of species diversity and patterns of allopatric/sympatric divergence.

Survival of elephant birds into the late Holocene has been documented by a small number of radiometric carbon dates with the latest presence date indicated at circa 1000AD and an unverified second-hand visual account from Etienne Flacourt (French governor of Madagascar in the 1600's). Several questions remain over their extirpation and extinction, timing and drivers.

Humanity is often cited as the extinction driver of these giant ratites due to dated specimens falling after human colonisation of Madagascar. There remains no documented, verifiable evidence relating to human impact. Following the review of European collections, several specimens with potential evidence of direct human impact have been identified for closer investigation. The validity and implications of these specimens will be discussed.

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#### The Downton "Tooth Bed": a lost world

Luke M. Hauser <sup>1</sup>

The Downton Bone Bed is a vertebrate-rich (fish microremains) deposit from the middle Ludfordian (Ludlow Series) within the Downton Sandstone Formation (Platyschisma Shale Member). The Silurian bone beds of the Welsh borders have been well documented over the past 175 years, except the Downton Bone Bed which seems to have been largely overlooked. This is probably for a number of reasons but two of the most likely are 1) its proximity to the Ludlow Bone Bed and 2) the preservational colour of the denticles.

The Downton Bone Bed contains not only vertebrates, but also a wide range of other fossils including bivalves, gastropods, ostracodes, arthropods, brachiopods and plants. This gives a snapshot into the Ludlow area during the late Silurian, a time of tremendous change, as the Downton Bone Bed was deposited on a near shore sand bar during the Lau Event, which is associated with the largest carbon isotope excursion in the Phanerozoic. Results suggest that the "Downton Sea" was a restricted environment indicated by the low diversity assemblages. The most common vertebrate in the Downton Bone Bed is the thelodont *Paralogania ludlowiensis* which makes up 81% of the total identified vertebrate fauna.

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### Exceptional sets of dinosaur tracks and trackways from the St. Mary River Formation (Campanian-Maastrichtian) in Alberta, Canada

Donald M. Henderson <sup>1</sup>

During river survey work in2014, following the extensive 2013 flooding that affected almost all southern Alberta rivers, a new dinosaur tracksite was discovered. Investigation of the site in the spring of 2015 resulted in the discovery of another, even better set of tracks and trackways, and while working on these first two more sets of tracks were found. Dinosaur tracks and trackways are very rare in the Late Cretaceous of Alberta, so to find multiple sets of trackways made by several different families of dinosaurs is newsworthy. The tracks were made by small ornithopods, large ornithopods, ornithomimids - both adults and juveniles, tyrannosaurs, and possibly birds as well. The tracks are hosted on single, large bedding planes on the surfaces of large boulders that fell from high, steep cliffs. There are two possible, mutually compatible explanations for the rarity of dinosaur tracks in this part of the world - 1) the flat, well-watered coastal plain environment, with its shifting, meandering rivers was not good for the preservation of tracks, and 2) the degree of lithification of most of the sediments was too low to allow tracks to resist the rapid erosion they experience with the modern climate.

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#### **Evolution of the lower jaw of gnathostomes**

Jennifer Hill <sup>1</sup>, Philip C.J. Donoghue <sup>1</sup> & Emily J. Rayfield <sup>1</sup>

The origin of the lower jaw is a key innovation that underpins the adaptive radiation of gnathostomes. The jaw has undergone fundamental changes to its composition and has endured major ecological changes including the transitions from water to land, from land to air, and from land back to water. Changes in jaw shape and structure may have facilitated the emergence of different feeding behaviors. We achieve this via an exploration of lower jaw morphospace. Outline analysis and extended eigenshape analysis were used to quantify variation in lower jaw morphology for 500 lower jaw specimens spanning 3 major evolutionary transitions: the origin of Osteichthyes, Amniota, and Mammalia. Principal Component Analysis shows that 28.1% of lower jaw shape variation is attributable to overall length of the dentary and/or the configuration of the postdentary bones. 15.5% of variation is attributable to the robustness of the lower jaw, while the relative thickness of the dentary and the angle of the postdentary bones account for 11.4% of variation. Initial taxonomic group patterns illustrate that fish (including chondrichthyans and osteichthyans) are the most disparate group; birds show little variance in comparison to mammals except for the overall curvature of the mandible and thickness of the (fused) dentary bone. Squamates have lower morphological diversity than mammals, but comparable disparity to birds. Snakes have restricted morphospace occupation. From these results, it is most likely that both ecological and functional consequences affect lower jaw shape variation and that transformation in lower jaw shape allowed different feeding behaviors to emerge.

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#### Positive allometry in the growth of a ceratopsian frill indicates sexual selection

David Hone <sup>1</sup>, Dylan Wood <sup>1</sup> & Robert Knell <sup>1</sup>

Sexual selection is a major evolutionary driver in numerous extant lineages of animal and presumably also operated in the past. Various exaggerated structures and ornaments have been hypothesised to be linked to sexual selection and social dominance but testing remains difficult owing to the limited available data. Sexually selected traits very often show positive allometry as these are condition dependent. Assessment of 37 specimens of the small ceratopsian *Protoceratops andrewsi* encompassing four distinct body sizes and spanning over an order of magnitude in size (basal skull length 24 – 360 mm) shows positive allometry in the length and width of the cranial frill. Both adults and juveniles of *P. andrewsi* form size segregated groups suggesting that herd coherency or dominance within groups was not the primary function of the frill. This is the largest analysis of crest allometry in Mesozoic reptiles to date and uses the largest size range of specimens thus providing a major case for sexual selection in the fossil record.

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#### A new Early Jurassic theropod from Wales: geological and discovery context

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In March 2014, two of us (NH and RH) collectors made the discovery of a lifetime on a beach at Lavernock, near Cardiff. Recently fallen blocks from a cliff were found to contain the partial skeleton of a new juvenile theropod dinosaur. Comparison of lithology and bed thickness enabled fairly precise placing of the new dinosaur within the *in situ* Blue Lias (Jurassic, Hettangian) adjacent to the find. Strata exposed at Lavernock range from the Mercia Mudstone Group (Triassic, Norian) to the lower portion of the Porthkerry Formation (Jurassic, Blue Lias, *angulata* zone). The dinosaur-bearing horizon occurs above the last Triassic conodont, but below the first appearance of *Psiloceras planorbis*, traditionally regarded as marking the base of the Jurassic. We have correlated the Lavernock section with the Austrian GSSP for the Jurassic System on the basis of known carbon isotope excursions, which place the dinosaur-bearing horizon around 1.5m above the T/J boundary. Rhaetic dinosaur remains are very rare in south Wales, and none have previously been found within the marine Jurassic strata.

A second cliff fall in summer 2015 at the same site yielded two more blocks of bone with remains of the same dinosaur to University of Portsmouth Palaeontology student Samuel Davies who was undertaking his 2<sup>nd</sup> level project at the site. Some remains are still missing, but the material collected so far makes this specimen the most complete theropod dinosaur ever discovered in the Lower Jurassic of Europe.

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#### On the probable predatory behaviour of the "marsupial lion", Thylacoleo carnifex

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How does one determine the behaviour of an extinct animal, especially one lacking living relatives? Extinct mammals are often shoehorned into modes of life occupied by extant forms: but were some past forms unique, with no precise extant analogs? A case in point is *Thylacoleo carnifex*, whose behaviour and ecology have been a matter of debate since Richard Owen's 1871 description. Dubbed the "marsupial lion", *Thylacoleo* is assumed to have had felid-like behaviour. *Thylacoleo*'s head is superficially cat-like, and large "carnassial" teeth indicate a carnivorous diet: but *Thylacoleo* lacks canines, and the proposed "caniniform" incisors are blunt rather than sharp. *Thylacoleo* is also unique amongst predatory mammals in its greatly enlarged claw on an apparently mobile thumb. How, then, did this "lion" kill its prey?

We investigate *Thylacoleo's* probable predatory mode of by statistical analyses of elbow-joint anatomy, comparing this enigmatic extinct marsupial with a large number of extant marsupials and placentals. *Thylacoleo's* elbow morphology is unique, combining the capacity for stability in terrestrial locomotion with maneuverability of the forearm otherwise seen in arboreal mammals. We suggest that this elbow joint morphology, in combination with the large claw on the thumb and the blunt "caniniform" incisors, reflects a unique predatory mode: rather than using the claws to hold the prey and the canines for killing, as in extant large felids, we propose that *Thylacoleo* used its enlarged incisors to subdue the prey and a rapid movement of the forearm around the elbow joint (supination) to kill with its huge claw.

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#### The phylogenetic inference of cranial ontogenetic trajectories of basal Therapsida

Maren Jansen <sup>1</sup>, Christian F. Kammerer <sup>1</sup>, & Jörg Fröbisch <sup>1</sup>

The relationships between ontogeny and phylogeny are controversial but it is expected that closely related organisms will undergo more similar ontogenetic changes than phylogenetically more distant ones. If so, morphological characters obtained from ontogenetic data could enhance our understanding of phylogenetic relationships, especially in fossil groups different ontogenetic stages may have been referred to different taxa. Following comprehensive taxonomic revision we combine cranial ontogenetic studies with phylogenetic methods on a phylogeny including a wide sample of basal therapsids, as well as observing allometric trajectories in the cranial ontogeny of representatives of every major clade. Using Principal Component Analysis (PCA) on pooled Procrustes shape data using 3D geometric morphometrics we constructed a linear model between phylogenetic distance and morphological distance, where morphological distance is indicated by the difference between the allometric shape changes on paired taxa, represented by the regression coefficient of PC (main variance correlated with allometry) against Centroid Size (CS). We assessed numerous randomized tree topologies, and calculated the same linear model as above, in order to test for the significance of the observed. PC1-CS regression coefficients show no phylogenetic correlation. However, using PC2-CS regression coefficients, less than 1% of randomly assorted trees show a higher regression coefficient than the observed tree, indicating ontogenetic trends differ in phylogenetically more distant taxa. When, however, applied to individual clades of the phylogenetic tree, the signal is considerably weaker and ontogenetic trajectories are likely constrained by other factors such as function or ecology.

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#### Fossils of Qau el-Kebir; an ancient Egyptian funerary fossil collection

Diane Johnson <sup>1</sup>, Paul Nicholson <sup>2</sup>, Pip Brewer <sup>3</sup>, Emma Bernard <sup>3</sup>, David Ward <sup>3</sup>, Sandra Chapman <sup>3</sup>, Lorna Steel <sup>3</sup> & Robert Kruszynski <sup>3</sup>

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In 1923 archaeological excavations at Qau el-Kebir, middle Egypt, revealed an ancient burial shaft containing artefacts and "tonnes" of fossil bones. Many were noted as hippopotamus but there were a range of mammals, reptiles, fish and what was considered at excavation to be the earliest Egyptian human remains. Later discoveries nearby included fossil bone fragments in ancient linen wrappings, and a second burial shaft containing more fossil bones.

Since prehistoric times ancient Egyptians considered some animals to be sacred as symbols and expressions of divinity; the fossil bones at Qau maybe a function of this practice. This area of Egypt was a recognised cult centre of the god Seth who was frequently depicted as a hippopotamus. It is possible that the fossils were a form of local offerings to Seth perhaps functioning in a similar fashion to the use of animal mummies.

The excavators Guy Brunton and Flinders Petrie noted the importance of the fossil finds but never published a full account of their interpretation or documentation of species present. With time, records of their storage location became lost and no further research was published. The fossils are currently held at the Natural History Museum and are now the subject of a study to bring a paleontological understanding of these intriguing fossils and a reevaluation their original archaeological context.

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### Comments on pterosaur reproduction based on recently found specimens from the Jurassic and Cretaceous of China

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Among the most spectacular pterosaur finds done in recent years is the bone-bed from the Tugulu Group (Lower Cretaceous) discovered in the Hami area, Xinjiang Uyghur Autonomous Region of China. Among the hundreds of specimens of the sexually dimorphic pteranodontoid *Hamipterus tianshanensis* are five three-dimensionally preserved eggs. They are slightly asymmetric, with the length varying from 59-65mm and the average width around 34mm. The external surface is formed by a thin ( $\sim$ 60 $\mu$ m) layer of calcium carbonate that produces the cracking and crazing of the otherwise smooth external eggshell surface. Below, there is a thin shell membrane ( $\sim$ 11 $\mu$ m), that might have been originally thicker. All eggs show depressions, clearly indicating their overall pliable nature. SEM analysis shows that the eggshell structure is similar to some squamates.

Another important material comes from the Late Jurassic Tiaojishan Formation (Liaoning Province). The counter slab (IVPP V18403) of a previously known wukongopterid specimen shows the presence of two eggs, one preserved inside the body of the animal. SEM analysis of the eggshell did not reveal an external calcareous layer suggesting that it was either removed due to taphonomy or not present at all. Histological section of the femur lacks medullary layer, a bone tissue reported in avian dinosaurs during ovulation and egg-laying phase. Those specimens, associated with experimental taphonomic studies, show that pterosaurs had two functional oviducts and laid eggs even smaller than previously thought, indicating that they have developed a reproductive strategy more similar to basal reptiles than to birds.

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# Preliminary information on a new specimen of *Araripemys* (Pleurodira: Pelomedusoides) from the Early Cretaceous Crato Formation, Brazil

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The Araripe Basin, Northeastern Brazil, comprises two *lagerstätten*, the Crato and Romualdo formations, with very similar vertebrate faunas. Six valid turtle species are recognized for the latter unit, of which only one, *Araripemys barretoi*, is also present in Crato Fm. A second species, "*Araripemys arturi*", was described, based on a very incomplete specimen from Crato Fm.

Subsequently, *A. barretoi* and "*A. arturi*" were synonymised. The latter's diagnostic features were invalidated, those being: 1) ovoid-shaped carapace, whereas *A. barretoi* displays a posterolateral angulation at the carapace lateral margin; 2) peripherals IX and X equally long as wide; and 3) lack of arrow-shaped pedal unguals, present in *A. barretoi*. The first has been proposed to be taphonomical or dubious due to the material incompleteness; while the second could represent ontogenetic, sexual or individual variation; and the third, in turn, has been identified as variable within *A. barretoi* specimens.

We report a new almost complete specimen of *Araripemys*, ventrally preserved on a limestone slab from Crato Fm. It differs from general *A. barretoi* morphology, displaying an ovoid-shaped and elongated carapace; elongated cervical vertebrae; pointed rostrum and slender xiphiplastra.

If further analyses validate these differences in the future (eg. morphometric analyses), we suggest that a new species of *Araripemys* should be erected, based on this new specimen. Because the holotype of "*A. arturi*" would still not be distinguished from *A. barretoi* but neither from this specimen, we suggest it should be regarded as *Araripemys* sp.

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#### Back from Purgatory: Three Rakers for Fishes at the Base of a Diversification

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Pachycormiformes were Mesozoic osteichthyan forerunners of many niches that are today filled by sharks, whales, teleosts, among others. In particular, the pachycormid pioneering of the large (>1 metre length) vertebrate suspension-feeding niche has attracted attention as an indicator of a major change in planktonic populations in the Jurassic. The 19<sup>th</sup> century Jurassic genera of *Leedsichthys* and *Asthenocormus* were recently supplemented by the Callovian *Martillichthys*, and the recognition of the Cretaceous suspension-feeder *Bonnerichthys* (often misidentified as specimens of the pachycormid carnivore *Protosphyraena*) extended this clade to the end of the Mesozoic. New specimens of the suspension-feeding pachycormid genus *Rhinconichthys* (erected on the basis of material collected by Gideon Mantell) from North America and Europe provide information on the development of this edentulous suspension-feeding tribe. In conjunction with re-examination of the type material, this taxon provides new information on oral specialisations utilised by this group in order to dominate suspension-feeding in the Jurassic and Cretaceous.

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# *Tetrapodophis amplectus*, a four-legged snake from the Early Cretaceous of Gondwana, and implications for the origins of snakes

Nicholas R. Longrich <sup>1</sup>, David M. Martill <sup>2</sup> & Helmut Tischlinger <sup>3</sup>

Snakes are a diverse and successful group of squamates, with over 3,000 known species, but the origins of this remarkable diversity are poorly understood. Two-legged snakes have previously been described, but snakes with four limbs have remained unknown—until now. Tetrapodophis amplectus, a new snake from the Early Cretaceous (Aptian) Crato Formation of Brazil, represents the oldest definitive snake and the first known with four limbs. Tetrapodophis shows numerous derived features of snakes, including hooked teeth implanting into sockets, an intramandibular joint, zygosphene-zygantrum articulations between vertebrae, >150 presacral vertebrae, and transverse belly scales. Although snake-like in most features, Tetrapodophis retains short but well-developed arms and legs. Adaptations for aquatic life are not evident. Instead, *Tetrapodophis* exhibits specializations for burrowing, supporting a subterranean, burrowing origin of snakes. Surprisingly, the limbs are not vestigial but are instead specialized for grasping. Along with a highly flexible spine, here interpreted as an adaptation for constriction, recurved teeth, and perhaps most striking, the presence of a vertebrate in the gut, this suggests that early snakes preyed on vertebrates. Finally, *Tetrapodophis* provides new insights into the geographic origin of the snakes. Tetrapodophis, along with a high diversity of basal lineages from Africa and South America, both extinct an extant, provides strong evidence that crown Serpentes originated and radiated in Gondwana during the Early Cretaceous. They were part of a unique herpetofauna, dominated by snakes, sphenodonts, and notosuchians, that evolved following the isolation of Gondwana and Laurasia in the Jurassic.

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# Locomotor morphology of a 'living fossil' - 3D GMM assessment of forelimb anatomy in tapirs

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Quantitative comparisons of the appendicular skeleton are an essential first step to increasing the understanding of locomotor morphology in both extant and fossil organisms. The locomotion of extinct species can be elucidated from skeletal material, coupled with comparisons to modern relatives or analogues. The enigmatic tapir (Perissodactyla: *Tapirus*) has been widely regarded as a 'living fossil' and has potential to be a modern locomotor analogue for basal perissodactyls, including palaeotheres and tetradactyl equids. However, modern tapir limb morphology has been generally overlooked and has not been quantitatively described. Here, we present the first quantitative assessment of the skeletal morphology of the tapir forelimb. Scapulae, humeri, radii, ulnae and metacarpals from multiple specimens from four extant species of *Tapirus* were laser scanned, and scans subjected to 3D landmark analysis. Results show significant morphological differences between T. indicus and the extant American species in most skeletal elements. The mountain tapir (*T. pinchaque*) shows significant or near significant separation from its closest relative *T. terrestris* in the proximal limb (scapula, humerus) and the medial hand bones (Mc2, Mc3). Our preliminary results support previous qualitative works comparing *T. indicus* and *T. terrestris* (lowland tapir): however, they also raise doubt as to the uniformity of the locomotor skeleton of American tapir species for comparative work with extinct species. The addition of further specimens to this analysis will provide a more complete appraisal of tapir limb anatomy, and the integration of biomechanical data will assist in interpretations of functional morphological changes.

### The oldest Jurassic dinosaur: a basal neotheropod from the Hettangian of Great Britain

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Approximately 40% of a skeleton, including cranial and postcranial remains, and representing a new genus and species of basal neotheropod dinosaur from the Triassic/Jurassic boundary beds of South Wales is presented.

Its occurrence close to the base of the Blue Lias Formation (Lower Jurassic, Hettangian) makes it the oldest known Jurassic dinosaur and it represents the first dinosaur skeleton from the Jurassic of Wales.

The specimen retains plesiomorphic characters which it shares with *Tawa* and *Daemonosaurus*, including three teeth in the premaxilla making its phylogenetic placement problematic. A cladistic analysis of 366 characters for 46 taxa resolved Neotheropoda, with *Tawa hallae* as its sister taxon and placed the new Welsh dinosaur as a basal member of Neotheropoda. The "coelophysoids" *Liliensternus liliensterni* and *Zupaysaurus rougieri* are now successive sister taxa to crown group neotheropods, making Coelophysoidea synonymous with Neotheropoda. The new dinosaur is recovered as the sister taxon to "*Syntarsus*" *kayentakatae* and all other coelophysids. Coelophysidae is supported by 3 synapomorphies (15 in the bootstrap) and Neotheropoda is supported by 23 synapomorphies. The bootstrap results demonstrate that although Neotheropoda is well supported, the basal part of the group is not. In our bootstrap tree the new welsh dinosaur, *Liliensternus liliensterni*, *Zupaysaurus rougieri*, *Dilophosaurus wetherelli* and *Cryolophosaurus ellioti* are found in a polytomy with the remaining clades of Neotheropoda; Coelophysidae and Ceratosauria.

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### Musculoskeletal correlates of digging behaviour in African mole-rats

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African mole-rats are subterranean rodents belonging to the family Bathyergidae. The family comprises six extant genera, five of which are chisel-tooth diggers, meaning they dig underground using procumbent incisors. The remaining genus (*Bathyergus*) is a scratch digger, using its forelimbs to dig. Chisel-tooth digging is thought to have evolved to enable exploitation of harder soils. It was hypothesised that, to dig successfully using incisors, chisel-tooth digging mole-rats will have a craniomandibular complex that is modified to achieve both a larger bite force and a larger gape compared to the scratch digging mole-rats. Linear measurements of morphological characteristics associated with bite force and gape were measured in a number of chisel-tooth digging and scratch digging bathyergids. In addition, the efficiency of the major jaw-closing muscles was estimated from mechanical advantage. Chisel-tooth diggers were found to have longer jaws and condyles relative to their size (characteristics associated with increased gape), as well as relatively wider and taller crania (characteristics associated with a higher bite force). The mechanical advantage of the temporalis was found to be significantly lower in *Bathyergus* than in the chisel-tooth digging mole-rats, but such a difference was not found with regard to the masseter. The results demonstrate that chisel-tooth digging strongly constrains cranial morphology to optimise both bite force and gape, which is achieved, in part, by increasing the efficiency of the temporalis. The phylogenetic position of *Bathyergus* within the Bathyergidae suggests that the craniomandibular morphology of chisel-tooth digging mole-rats is being driven by function rather than phylogeny.

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# Morphological convergence of the rodent-like masticatory apparatus in extant rodents and non-rodent diprotodonts

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Rodents are characterised by a distinctive masticatory apparatus comprising a pair of enlarged and continually growing upper and lower incisors, termed diprotodonty, separated from a highly reduced posterior dentition by a large diastema. While diprotodonty is present in all living and extinct rodents, it has independently evolved in a phylogenetically diverse range of non-rodent therian mammals, including hyraces and lagomorphs as well as individual species of marsupials (the common wombat) and primates (the ave-ave). Here we examine whether the independent evolution of diprotodonty across therian mammals is limited to the dentition, or if it constrains the disparity of the whole masticatory system. Three-dimensional landmarks were collected from virtual models of the cranium and mandible of rodent-like diprotodont specimens and taxa representing the main extant rodent families. Geometric morphometrics methods were used to examine the convergence between the rodent and non-rodent specimens. The taxa in this study samples large phylogenetic distances, however in both the cranium and mandible morphospaces all taxa group very tightly together. Within the rodents, taxa from the main groupings based on masticatory musculature (hystricomorphs, myomorphs, protrogomorphs and scuiromorphs) form discrete groupings in cranial results. Partial least squares (PLS) show a high level of covariation between cranium and mandible in all taxa. The findings of the study clearly demonstrate that convergent evolution of morphology in diprotodont mammals is not restricted to the dentition, but is also found in the cranium and mandible and their pattern of covariation. This indicates that there are strong functional constraints on the masticatory system associated with diprotodonty.

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#### The hydrodynamics of plesiosaurs

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The flipper movement pattern employed by plesiosaurs is still much debated; all previous work has been either descriptive in nature or has employed rudimentary experiments. The hydrodynamics of plesiosaurs is investigated from an engineering point of view using both numerical simulations and full-scale flume tank experiments, with the kinematics and interaction of the flippers being the focus of the study. As plesiosaurs are the only known animals to have ever swum using four big flippers of comparable size, it is interesting both from engineering and palaebiological perspectives to determine the advantages of this propulsion system. Two-dimensional numerical simulations have shown that certain motions of the four-flipper arrangement would have given the plesiosaur 25% more thrust as compared to two flippers. Experiments to investigate the three dimensional performance were conducted using a specially developed multi axis rig running in a large flume tank. The flipper models are based on the Collard specimen which was found recently in Bridgwater Bay on the Somerset coast. The flippers are preserved in articulation, and the provenance in excellent so this specimen is a good choice for accurate reconstruction of the flippers. The reconstructed flippers are used to determine if the same increase in thrust as seen in the numerical simulations is present for three-dimensional flippers at higher Reynolds numbers, and therefore to shed some light on the swimming method and behaviour of pleisosaurs.

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#### Romania and the short-necked azhdarchids, flightless avialans and giant lizards of yore

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An ongoing collaboratory fieldwork programme is revising our view of the shape and complexity of a Maastrichtian island-endemic faunal assemblage from Romania. Our research can be considered focused on dinosaurs and azhdarchid pterosaurs but we have also discovered significant mammal, turtle, lizard and crocodyliform specimens.

Romanian azhdarchids include the long-necked, mid-sized *Eurazhdarcho* as well as a relatively short-necked, mid-sized taxon (estimated wingspan 3.5-4 m). An enormous 7<sup>th</sup> or 8<sup>th</sup> cervical vertebra, giant proximal syncarpal, and section of mandibular symphysis are referable to *Hatzegopteryx*, described from the Densuş-Ciula Formation of the Haţeg Basin. These remains reveal proportions consistent with the other material of this taxon. *Hatzegopteryx* was a short-necked, robust-skulled azhdarchid, likely with an ecology and lifestyle different from that imagined for slender-necked, slender-jawed taxa.

Theropods are rare in these assemblages but the absence of large taxa appears genuine. *Balaur bondoc* was described as a velociraptorine but re-evaluation reveals its unusual features (including a fused carpometacarpus, reduced third finger, long hallux, laterally bowing pubic bones, and backswept pubes and ischia) better support placement within Avialae, specifically within a grade of *Jeholornis*-like avialans. The status of several more poorly known Romanian maniraptorans (*Elopteryx*, *Heptasteornis* and *Bradycneme*) is uncertain.

Several squamates are known from the Romanian Maastrichtian, including borioteiioids and snakes. The partial skull of a large heterodont lizard, estimated to have had a precaudal length of 475 mm, represents a new taxon under description. This animal is significant in being 'intermediate' in body size and ecology between smaller squamates and small dinosaurs.

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#### Cementum histology reveals physiology at the root of the mammalian phylogeny

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The development of all three mineralized dental tissues, cementum, dentine and enamel, is recorded by growth markers of differing periodicity that are frequently used as records of life history in extant mammals. Cementum, the mineralised tissue that anchors the roots of teeth within the jaw, comprises a series of light and dark increments frequently shown to follow a circum-annual rhythm that records growth throughout life. As cementum is virtually never resorbed, counts of these increments are widely used as an absolute estimate of chronological age in extant taxa. Here, we present the results of the first use of cementum increments as an age estimate for Mesozoic fossil mammaliaforms; Morganucodon and Kuehneotherium. Utilising synchrotron tomography for the first time in cementum increment analysis, this study overcame several caveats cited in previous, thin-section based studies, and gained a greater understanding of increment counts and patterns. Tomographic analys is of a population-sized sample of fossil teeth allowed a minimum estimate of maximum lifespan for both taxa. These estimates are considerably longer than known lifespans of extant mammals of comparable body size, a finding that suggests a proportional disparity in metabolic potential between basal mammaliaforms and extant taxa. The implication of this result for our understanding of mammalian metabolic evolution demonstrates the exciting potential of fossil cementum as a record of life history.

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## A taxonomic and palaeoecological investigation of an earliest Carboniferous fauna from Burnmouth, Scotland, UK

Benjamin Otoo <sup>1</sup>, Jennifer Clack <sup>1</sup>, Timothy Smithson <sup>1</sup> & Keturah Smithson <sup>1</sup>

Historically, there has been a paucity of continental (=nonmarine) vertebrate fossils from the early Carboniferous (Tournaisian and Viséan stages, ~359-330 Ma, also known as "Romer's Gap"), and fossil discoveries from that interval have largely been singletons. A Tournaisianaged fauna from "Tim's Bed," a single horizon from Burnmouth, Scotland provides an opportunity to fill in "Romer's Gap" more completely. The fauna includes tetrapods and sarcopterygian and actinopterygian fishes. The environment was a low-energy pond or lake. Rhizodonts are represented by the most material. Much of that is fragments of dermal bone and scales, but there are also many cleithra. These cleithra form the basis for a quantitative size study that finds a single size class different from and smaller than conspecific, stratigraphically higher material, suggesting that "Tim's Bed" may have been a rhizodont nursery. This is supported by the general lack of larg e animals. Substantial lungfish diversity is composed of new toothplate morphotaxa described from other localities from northern Britain, as well as a new taxon represented by a body fossil. Gyracanths are represented by fin spines; actinoptervgian fishes are represented by rare scales and dermal bones. Two new tetrapod taxa can be identified, a possible whatcheeriid and a colosteid-like tetrapod. Quantitative faunal similarity analyses find the "Tim's Bed" fauna to resemble a number of other sacropterygian-dominated Mississippian faunas. A fundamental divide between Devonian and Carboniferous localities is recovered when the whole dataset is analyzed, though this divide begins to break down when only nonmarine sites and further subsets thereof are considered.

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### Giants of the air: how big could they be?

Colin Palmer <sup>1</sup> & Michael Habib <sup>2</sup>

Fundamental allometry dictates that there must be an upper limit to the size of flying vertebrates. The largest extant birds are around 3m in wingspan and 15kg in weight. Fossil birds may have reached 7m wingspan and weighed as much as 70kg, but they are dwarfed by the giant pterosaurs - 250kg late cretaceous azhdarchids with wing spans of more than 10m. What was it about pterosaurs that enabled them to reach these extraordinary sizes and were they up against the limits to size? Most maximum size estimates for birds and pterosaurs have compared power required with power available, making predictions from the cross-over between these variables. This approach is subject to great uncertainty since the trends are only weakly convergent, so small differences in assumptions can have large effects on the results.

There is more to flying than having adequate steady power. An animal must have sufficient power to leave the ground and climb until it can find rising air, then be able to land without injury. Its wing structure must be sufficiently stiff to support the aerodynamic loads of flight and its morphology must remain aerodynamically efficient in the face of allometric dimensional requirements.

Consideration of these different potential limits throws new light on why pterosaurs were truly the "all time giants of the air" and points to take-off and landing as being the most likely limits to their size, rather than power availability or structural strength.

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### Correlates between calcaneal morphology and locomotion in extant and extinct carnivorous mammals

Elsa Panciroli<sup>1</sup>, Christine Janis<sup>1,2</sup> & Max Stockdale<sup>1</sup>

Determining locomotion and ecology in fossil taxa can be challenging, particularly with limited preserved skeletal material. By determining the relationship between form and function in living animals, it is possible to create a model for testing mode of locomotion in extinct forms. The calcaneum is known to be informative in terms of mammalian locomotion, but there is a still a lack of data for many extant carnivorans. Empirical data from extant taxa, for which locomotion can be reliably documented, is necessary to make informed assertions about the locomotion of extinct taxa.

We took linear measurements and 2D landmark data from 69 extant Carnivora to generate a comprehensive morphological dataset. We carried out multivariate analyses to identify locomotor groupings based on calcaneal morphological characteristics. We then added 48 fossil taxa to determine their probable locomotor mode. We explored the influence of phylogeny through phylomorphospace using maximum-likelihood phylogenetic models, and carried out an ancestral state reconstruction using the extant taxa.

We distinguish distinct morphospace occupation for different locomotor groupings in extant taxa, particularly arboreal and semi-fossorial versus terrestrial and cursorial. The length of the calcaneal heel versus calcaneal foot, the width of the calcaneum, and the shape of the calcaneal foot itself reflect the biomechanics of different locomotor modes, and serve as indicators for locomotor grouping among Carnivora. Our analysis supports an arboreal locomotor mode for the early carnivoran *Dormaalocyon latouri*, and a more arboreal mode for Nimravidae, while early canids occupy a distinctly different morphospace from their extant relatives, reflecting their arboreal origins.

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#### A critical new *Polacanthus* specimen from the Wessex Formation of the Isle of Wight

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Ankylosauria, Ankylosauria) have been known from the Lower Cretaceous English Wealden for over 170 years. Three Wealden ankylosaurian species are currently recognised: *Hylaeosaurus armatus* and *Polacanthus rudgwickensis* from the Wealden Subbasin of Sussex, and *Polacanthus foxii* from both the Wessex Sub-basin of the Isle of Wight and the Wealden Sub-basin. Within recent years all have been interpreted as close relatives within the clade Polacanthidae or Polacanthinae, the monophyly of which is controversial. Most views of polacanthines as a whole are based on substantially better remains from North America. Despite the familiarity of *Hylaeosaurus* and *Polacanthus*, many questions remain about their anatomy, taxonomy and relationships and a thorough re-appraisal of the British taxa are needed.

We discuss a new ankylosaur discovered in 1994 in the Wessex Formation at Chilton Chine, Isle of Wight. This partial skeleton (including limb and limb girdle elements, vertebrae and osteoderms) is one of the most complete ankylosaurs ever found in the UK and has the potential to resolve many questions about these dinosaurs. It has been provisionally referred to *P. foxii* but differs in several respects from the holotype and referred specimens of this taxon.

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#### Experimental taphonomy and the anatomy of Cambrian vertebrates

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The Lower Cambrian Chengjiang biota of China contains four genera of early vertebrates: Haikouichthys, Myllokunmingia, Zhongjianichthys and Zhongxiniscus. These are the oldest fossil vertebrates known and they play key roles in calibrating molecular clocks and informing our view of the anatomy of animals close to the chordate-vertebrate transition; some hypotheses even suggest that differences between these four taxa are informative with regard to this transition. Despite the evident importance of these fossils the degree to which taphonomic processes have affected their anatomical completeness has not been investigated: the possibility remains that some or all of them have been affected by the systematic bias of stemward slippage – the hypothesis that preferential decay of synapomorphies and retention of plesiomorphic characters can cause fossil taxa to erroneously appear outside of the crown group to which they really belong. This hypothesis is based on experimental data derived from decay of non-biomineralised chordates under laboratory conditions. We have expanded this analysis to include a broader range of potentially significant environmental variables and. by comparing the results of different experiments, identified general patterns that we have applied to the Chengjiang vertebrates. These investigations indicate that experimentally derived models of phylogenetic bias are applicable to fossils. Anatomical and phylogenetic interpretations of early vertebrates that do not take these biases into account risk overestimating diversity and the evolutionary significance of differences between fossil specimens.

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#### Vertebral column shape evolution in felids

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While several studies have focused on the skull and limbs of felids and carnivorans in general, the vertebral column has been underrepresented in the morphological and biomechanical literature. Moreover, the vertebral column is often treated as one functional unit, with few studies considering the complexity and regionalisation of this structure in detail.

Here we report the results of both linear and 3-dimensional analyses of vertebral column shape using 22 and nine living species of felids, respectively, to assess whether ecological specialisations have significantly influenced the evolution of vertebral morphology.

Principal components analysis (PCA) of all log-transformed linear variables (e.g., centrum length) showed significant separation of species based on locomotory specialisations. Additionally, shape was more strongly influenced by size in the anterior vertebrae (cervicals and thoracics) than in the posterior (lumbar) vertebrae.

16 3-dimensional landmarks representing the full post atlanto-axial pre-sacral vertebral column of ~100 specimens were analysed with both PCA and Phenotypic Trajectory Analysis (PTA). Again, anterior and posterior vertebrae showed different results, with a stronger niche specialisation signal, both for locomotory (explaining 5.4-17% variance) and prey size groups (3.5-17.5%) observed in the posterior region, where the influence of size was also stronger (3-14%). PTA results also demonstrated that shape differences among ecological groups were concentrated in T10, L1, L4, and L7, and that these are not significantly correlated with phylogenetic relatedness.

Lastly, scaling analyses showed that ecological groups exhibit distinct shape-size allometries, with cursorial (cheetah) and scansorial taxa showing similar slopes, distinct from arboreal and generalist terrestrial taxa.

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### Evolutionary evaluation of fundamental processes in the antler cycle as revealed by internal bone structure

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The unique nature of antlers, being apophyseal cranial outgrowths with intrinsically induced cyclic necrosis, sequestration, and regeneration, unites cervid artiodactyls (deer). This process represents the only example of complete organ regeneration in mammals. The physiology behind is known to be complex and synchronized with behavioural and environmental factors. This poses questions on the origin and evolutionary history of antlers.

A good fossil record allows tracing antler diversity back to the early Miocene ( $\approx 20$  mya). These early antlers of stem cervids share the fundamental apophyseal, branched, and deciduous condition with those of extant deer, but differ in morphology by being simpler structured, lacking a beam construction, with a variety of basic architectures (palmate, dichotomous, bi- to multi-pointed plate- and crown-like).

Previous studies used transversal thin-sections to study antler histology in early deer and inferred on their growth modi. The results pointed to substantial physiological differences leading either to autotomy of still living antler-tissue, inverse ossification before antler sequestration, as well as irregular shedding and indicated evolutionary development in fundamental processes of the antler cycle. To test the previous hypotheses we used x-ray  $\mu$ -CT for displaying internal bone structure across the entire antler of a larger selection of early deer and compared them among themselves and with those in living deer.

Our preliminary results include the absence of arrested growth lines, a longitudinally arranged vascularisation and lack of secondary erosional structures, what lead us to conclude on early antlers as quickly growing, short-lived organs. Moreover, we did not find support for sequestration of living antlers. If this then necessarily implies the context of a regular antler cycle comparable to that in extant deer needs further investigation at the histological-physiological level. However, there is evidence for the existence of fundamental processes in antler development (intrinsically induced cyclic necrosis, sequestration, and regeneration) from the earliest record of antler evolution onward.

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#### Dinosaurs in decline tens of millions of years prior to the K-Pg boundary

Manabu Sakamoto <sup>1</sup>, Mike Benton <sup>2</sup> & Chris Venditti <sup>1</sup>

66 million years ago an enormous meteor hit what is now Chicxulub, Mexico, causing one of the most devastating mass extinction events. It is universally accepted that this impact led to the extinction of all non-avian dinosaurs. However, whether dinosaurs were reigning strong right up to the impact, or were on the decline for a long time prior to it, has been the subject of decades of debate. Here for the first time, we explicitly account for shared ancestry as implied by the dinosaurian phylogeny, to answer this long standing question. We study the patterns of speciation and extinction (speciation dynamics) over 170 million years from dinosaur origins to the K-Pg boundary using a Bayesian phylogenetic regression model. We find overwhelming evidence that dinosaurs were in decline - with the rate of extinction higher than the rate of speciation - tens of millions of years prior to the end of the Cretaceous. This pattern remains true in the three main dinosaurian clades, Ornithischia, Sauropodomorpha and Theropoda, and highlights that Mesozoic dinosaurs showed a marked reduction in their ability to replace extinct species with new ones, making them vulnerable to extinction and unable to respond quickly to and recover from the catastrophic event.

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### The phylogenetic implications of re-describing the English crocodyliform specimens referred to *Pholidosaurus*

Thomas J. Smith <sup>1</sup> & Mark T. Young <sup>1,2</sup>

Pholidosauridae was a clade of longirostrine crocodyliforms that radiated across Europe. Asia, Africa and the Americas between the Middle Jurassic to Late Cretaceous. The type genus of this clade, *Pholidosaurus*, is poorly understood and even the number of valid species referable is uncertain. There is considerable instability in this part of the crocodyliform tree, as previous phylogenetic analyses do not agree upon whether Pholidosauridae is monophyletic or not. Preliminary results based on a first-hand re-scoring of the type specimen of *Pholidosaurus purbeckensis* for different phylogenetic analyses (both in preparation modifications of published datasets) unfortunately does not resolve this issue. When P. purbeckensis is treated as separate OTU, a monophyletic Pholidosaurus is not recovered. The first matrix finds P. purbeckensis and P. schaumbergensis to be distantly related (i.e. a polyphyletic *Pholidosaurus*), whereas in the second matrix both *Pholidosaurus* species form a polytomy with Dyrosauridae and a large clade constituting most of Pholidosauridae (in this matrix the inclusion of *P. purbeckensis* greatly decreases the level of resolution). The on-going in-depth re-description and re-scoring of English *Pholidosaurus* specimens will help determine whether the genus is monophyletic. This further descriptive work will provide a platform from which the internal relationships of the Pholidosauridae can be investigated.

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# A wandering entepicondylar foramen and the humeral twist: forelimb evolution in early tetrapods

Timothy Smithson 1 & Jennifer Clack 1

In extant mammals, the entepicondylar foramen carries the medial nerve and brachial artery through the humerus. The foramen is present in stem group mammals and the earliest amniotes. It also occurs in most stem group tetrapods and new material from the early Carboniferous of Nova Scotia reveals that it transmitted two vessels.

The foramen has been identified as a major landmark on the humeri of tetrapodamorphs and its relative position is thought to have changed little during the early evolution of the tetrapod forelimb. In most stem tetrapods the foramen pierces the entepicondyle enabling the artery and nerve to pass through the humerus from the dorsal to the ventral surface. Recent re-examination of the humerus of the Devonian tetrapod *Acanthostega* revealed that it lacks this morphology. Instead, the foramen is restricted to the ventral surface where it passes through the ventral ridge. The origin of the condition seen in most tetrapods appears to be linked to twisting of the humerus. This rotated the distal end relative to the proximal end, and allowed the manus to be placed on the ground during locomotion. Twisting resulted in the artery and nerve now passing through the entepicondyle producing the characteristic foramen. New material from the early Carboniferous of Scotland shows an intermediate condition between *Acanthostega* and typical forms, in which the foramen pierces the medial edge of the condyle and exits on the ventral surface. These observations have led us to re-assess the homologies of the tetrapodomorph forelimb.

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### Data-driven analysis and interpretation of fossil trackways

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Trackway interpretation, the drawing of inferences about a trackmaker and its movements from a pattern of trace impressions, is examined from an information content perspective. While trackways are commonly regarded as direct records of locomotion behavior, their interpretation is in fact less straightforward than often expected. Trackways indeed contain information about the trackmaker and its movements, but more in the form of constraints than direct relationships. For example, trackmaker size (e.g., its proxy gleno-acetabular distance) is constrained by, but not uniquely determined by, track spacing. Moreover, an analysis of the relationship between trackmaker size, stride length, and limb phase (i.e., gait) reveals a previously unappreciated interdependence among these parameters. Hence, without knowing trackmaker size, any observed pattern of manus and pes tracks has arbitrarily-many possible solutions in terms of limb phase and duty factor (the primary components of gait). The interpretation of trackways thus requires more sophisticated techniques than has been appreciated formerly, to cope with this ambiguity of interpretation which is only compounded by measurement uncertainty and the inevitable incompleteness of the fossil record. We introduce to ichnology the explicit association of uncertainty estimates with all quantitative data, to reduce the propagation of error within computations. Our approach involves the creation of a database and the geometric construction of a graph representations for trackways that minimize the introduction of subjective interpretations early in trackway interpretation, such as the presumption of a smooth trackway 'path' as commonly fitted to trackways.

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#### Temperature-driven evolution and evolutionary stasis among the Crocodylomorpha

Max Stockdale <sup>1</sup>, Michael Benton <sup>1</sup>, Mario Bronzati <sup>2</sup>, Marco de Andrade <sup>3</sup> & Gavin Thomas <sup>4</sup>

The Crocodylomorpha present a unique dichotomy in their diversity and morphological disparity through time. The stem-group is limited to the mesozoic, but is represented by a highly disparate range of ecomorphologies. Conversely the crown-group is limited to amphibious ambush predators, but is represented by a much greater species richness than the stem-group. Despite the abundance of the crown-group, the crown-group Crocodylomorpha are represented by just 23 extant species.

Does this pattern represent a true decline in disparity and diversity through time, or a more complex sequence of shifts within the group?

Here is presented a comparison of evolutionary rates among crown- and stem-group Crocodylomorpha in relation to morphospace occupation. The phylogenetic framework of these analyses is a new phylogeny of the Crocodylomorpha assembled using the Matrix Representation Parsimony (MRP) method.

This study finds support for extreme evolutionary stasis in several crocodylomorph clades. Diversity among the Crocodylomorpha appears to be closely linked with temperature, with decreasing diversity in the Cenozoic closely matching global cooling. Additional morphospace occupation by stem-group Crocodylomorpha relative to the crown-group is occupied by taxa originating from two discreet adaptive radiations in the mesozoic, with disparity otherwise remaining constant throughout the Mesozoic and Cenozoic.

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#### The ecomorphological diversifications of Mesozoic marine reptiles

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Mesozoic marine ecosystems were dominated by reptiles, including sauropterygians, ichthyosaurs, crocodylomorphs, turtles and mosasaurs. Marine reptiles represent an excellent model for testing macroevolutionary trends associated with ecological opportunities, resulting from repeated invasions of ocean ecosystems. Previous research has shown that marine reptiles achieved great taxonomic diversity in the Middle Triassic, as they broadly diversified into many feeding modes following the Permo-Triassic mass extinction. However, it is not known whether this initial phase of evolution was exceptional in the context of the entire Mesozoic. Here, I use a diverse suite of disparity, morphospace and comparative phylogenetic analyses to test this. I focus on ecomorphological variables, including functional disparity in the jaws and dentition and skull size diversity. Results show that the Middle to early Late Triassic represented a time of pronounced phenotypic diversification in marine reptile evolution, with rapid attainment of maximum functional disparity in the jaws and dentition, and a disparate range of skull sizes. Following the Late Triassic extinctions, and the associated loss of disparity, it took over 100 million years to recover comparable variation in the Campanian and Maastrichtian. The signatures of adaptive radiation are not seen in all marine reptile groups. Clades that diversified during the Triassic biotic recovery, the sauropterygians and ichthyosauromorphs, do show early diversifications, early high disparity and early burst, while less support for these trends is found in thalattosuchian crocodylomorphs and mosasaurs. Overall, the Triassic represented a special interval in marine reptile evolution, as numerous groups radiated in new adaptive zones.

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#### Were the necks of Apatosaurus and Brontosaurus adapted for combat?

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The apatosaurine sauropods — *Apatosaurus*, *Brontosaurus* and possibly others — resemble their diplodocine relatives, but are generally more robust. Apatosaur necks are much thicker than in other sauropods: cervical ribs and their supports are uniquely robust, and the ribs are strongly displaced ventrally. The diapophyseal and parapophyseal rami therefore project ventrolaterally, so that the neck would have been subtriangular in cross-section, not tubular. Why did apatosaurines evolve necks that were apomorphically expensive to build, maintain, and operate? While sexual selection is not a convincing explanation for the evolution of sauropod necks in general, several features of apatosaurine necks suggest adaptation for combat:

- 1. Ventral displacement of cervical ribs improved the lever arms of the hypaxial muscles, strengthening ventral neck movements.
  - 2. Ventrolaterally directed parapophyseal rami were oriented to resist ventral impacts.
- 3. The ventral trough between the cervical ribs provided soft-tissue protection for the trachea, oesophagus, and major blood vessels.
- 4. The ventrolateral processes on the cervical ribs may have been bony clubs, bearing thickened pads of connective tissue or keratinous knobs or spikes.

These adaptations suggest a style of combat in which the neck itself was crashed down or sideways into the opponent, rather than giraffe-style combat in which the head is the weapon. The closest extant analogue may be the elephant seal *Mirounga*: males fight by crashing their necks and anterior thoraxes together. As with apatosaurs, their cervical vertebrae are more robust than in relatives, and their ventral processes more pronounced; but enormous soft-tissue padding makes the analogy very inexact.

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# New evidence for sexual dimorphism in the basal monofenestratan pterosaur *Darwinopterus*

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Sexual dimorphism is common in extant vertebrates and almost certainly occurred in extinct species as well, but identifying this phenomenon in fossils is difficult. Meeting two key criteria: a large sample size in which all ontogenetic stages are present; and independent evidence of gender, is rarely possible, but has now been achieved for the early Upper Jurassic pterosaur Darwinopterus modularis. This pterosaur is represented by over 20 individuals ranging from hatchlings through juveniles to mature adults (ontogenetic status determined from osteological, histological and morphometric data). One example, 'Mrs T', is preserved with two eggs and thus clearly a female. Approximately half the mature individuals of Darwinopterus exhibit a cranial crest and several of these individuals have a relatively narrow pelvis. The remainder lack a cranial crest and in two cases, including Mrs T, have a relatively broad pelvis. All immature individuals lack a crest, an observation that applies to other species of pterosaur in which immature individuals are known. This pattern of morphological variation shows that the cranial crest and pelvis of *Darwinopterus modularis* are sexually dimorphic. Datasets for other pterosaurs are less complete and/or lack independent evidence of gender, but many species including Ctenochasma gracile, Germanodactylus cristatus and Pteranodon longiceps, exhibit directly, or closely, comparable patterns of anatomical variation to *Darwinopterus* and are likely to have been sexually dimorphic. We conclude that the spectacular variability in the shape and size of pterosaur cranial crests was likely generated by sexual selection rather than processes such as species recognition.

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# The specialized tail of *Spinophorosaurus nigerensis* (Sauropoda. Middle Jurassic) and the osteological limits on its range of motion

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*Spinophorosaurus nigerensis* is one of the most complete and better preserved specimens of a primitive sauropod known from the remains of a single individual. This makes it a great model for studying the early evolutionary stages of sauropod biomechanics. Some of its most noticeable autapomorphies are its overlapping distal chevrons and a putative thagomizer.

We performed a photogrammetric scan of the bones and digitally manipulated the virtual skeleton to find the osteological limits of motion imposed by these chevrons. In the first 20 caudal vertebrae, vertebrae pairs may deflect for up to 20° before osteological stop in extension and 8-10° in lateral flexion, suggesting the *in vivo* dorsal and lateral range of motion was limited rather by soft tissue. Flexion is limited by the rather large chevrons, which contact with less than 5° of deflection. The motion in the distal region is dorsoventrally limited, as in other taxa with overlapping chevrons (dromaeosaurids or ankylosaurids).

Additionally, the hypaxial caudal region of *Spinophorosaurus* is greatly developed: the anteriormost chevrons are very elongated and the anteriormost transverse processes are dorsally elevated and angled, indicating powerful hypaxial muscles. Also, the first twenty caudals become progressively elongated, as in diplodocids.

An analysis in progress of the dermal ossifications originally proposed as a thagomizer suggests they are not osteoderms at all, thus there is no evidence for such thagomizer. However, the limited proximal flexion, powerful hypaxial musculature, elongated caudal vertebrae and the overlapping chevrons appear to be a single, perhaps incomplete, functional complex of unclear function.

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#### A review of fossil gekkotans from the Neogene and Quaternary of Italy

Andrea Villa 1

Six Italian Neogene and Quaternary localities have yielded fossils of geckos: Gargano "terre rosse", Late Miocene; Moncucco Torinese, latest Miocene; Cava 6 near Orosei, Pleistocene; Valdemino Cave, Middle Pleistocene; K 22, Middle-Late Pleistocene; San Teodoro, Late Pleistocene. Remains comprehend maxillae, frontals, dentaries, indeterminate tooth-bearing bones, vertebrae and humeri.

After a comparative analysis of cranial bones of the four extant species of European gekkotans (*Euleptes europaea*, *Hemidactylus turcicus*, *Mediodactylus kotschyi* and *Tarentola mauritanica*), maxillae and frontals turned out to be the most informative among Italian fossil findings, whereas dentaries and tooth-bearing bones are less useful. Such comparative analysis has not been carried out on postcranial skeleton so far.

Using the newly identified diagnostic features, fossils have been referred to *Euleptes* sp. (Gargano), cf. *Euleptes* sp. (Moncucco), *Hemidactylus* cf. *H. turcicus* (Valdemino), *Tarentola mauritanica* (K 22) and Gekkota indet. (San Teodoro). Remains from Cava 6 and a frontal from K 22 have not been studied yet.

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### Trends and patterns in modern palaeoartistry: a call for change

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Palaeoartistry is a 200 year old institution with clear scientific, pedagogic and cultural significance, and a global industry value of many millions of dollars. Production of quality, scientifically-rigorous palaeoartworks is skilled and time-consuming work, each piece reflecting extensive research, knowledge of natural history and anatomy, and the ability to craft compelling artwork. Despite general recognition of this, palaeoartists fight a losing battle for credibility and even moderate commercial success. Documentation of this struggle dates back to at least the 1980s, and we ascribe its ongoing nature to low awareness of three major issues.

Firstly, palaeoart is rife with copying and plagiarism. Many commissioned palaeoartworks replicate elements or entire compositions from existing works to breach copyright law; perpetuate errors and outdated ideas; deny recognition and financial reward to original artists; and drown out new styles and approaches to fossil animal restoration with artistically homogenous work. Secondly, the scientific rigour associated with many palaeoartworks, even those produced in close association with consulting academics, is often low. We ascribe this to laissez-faire attitudes from some consultants, underestimation of the educational value and influence of palaeoartworks, as well as poor utilisation of the existing pool of demonstrably qualified palaeoartists. Thirdly, many palaeoart patrons have unrealistic concepts of financing artwork, often offering little or even no recompense to artists because of financial restrictions associated with their own projects. We hope that bringing these issues to wider attention will raise support from individuals involved with palaeoart production and help bring real change to industry practises.

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# Mary Anning's marine reptiles: taxonomy, systematics, morphometrics and evolution of the iconic *Ichthyosaurus*

Jessica Lawrence Wujek <sup>1</sup>, Gareth Dyke <sup>1</sup> & Darren Naish <sup>1</sup>

Ichthyosaurus is the most famous of all fossil marine reptiles, yet its taxonomy and composition is little studied. Hundreds of *Ichthyosaurus* specimens are known, and at least five species are recognized by recent authors. The autapomorphies and diagnosis of both Ichthyosaurus as a whole and its constituent species are little studied and several specimens reveal a range of intermediate conditions between currently recognized species. We report the most comprehensive analysis of *Ichthyosaurus* ever undertaken, based on a large sample of specimens (>200) from across the Lias. Precise data on the stratigraphic position of specimens is scant; one aim of this study is to use palynomorphs to establish age and provenance. This work has resulted in: (1) Anatomical clarification of the status of *Ichthyosaurus*: (2) Understanding of the likely species composition within *Ichthyosaurus*: (3) Large-scale morphometric, systematic and phylogenetic analyses within the clade, and; (4) A clear understanding of evolutionary trends within *Ichthyosaurus* across the Liassic. Conclusions indicate that the validity of *Ichthyosaurus* is supported by autapomorphies. However, specimen clusters recovered by principal-component (PC) and size-constrained PC morphometric analyses do not correspond to currently recognized species. *Ichthyosaurus* spans a range of body sizes and individuals cluster into several size classes. Some represent ontogenetic stages within species. Other clusters exhibit trends in body size evolution throughout the Lias. This work helps clarify both the true diversity and evolutionary history of this iconic Liassic animal, first brought to scientific attention by Mary Anning over a century ago.

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### An early origin and diversification of macrophagous metriorhynchid crocodylomorphs, with evidence for multiple instances of parallel evolution

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Metriorhynchids were a widely distributed group of marine crocodylomorphs that thrived during the Middle Jurassic–Early Cretaceous. Within this group there is a subclade, Geosaurini, that evolved craniodential characteristics indicative of macrophagy (feeding on large-bodied prev items). When this subclade evolved and began to diversify into the myriad of morphologically distinct lineages is still unclear. Previous phylogenetic analyses suggest this clade evolved during the Late Jurassic, and rapidly diversified into numerous different ecomorphotypes. It was hypothesized that this was in response to the absence of small and medium-sized pliosaurs after the Middle-Late Jurassic Boundary. However, re-examination of poorly preserved fossils from the Callovian of England and France casts doubt on this. Based on our comparative study of these fossils, and new phylogenetic analyses, we conclude that Geosaurini had evolved and diversified by the mid Callovian. Although comparatively rare in the Middle Jurassic, at least four morphofunctionally distinct lineages of macrophages had evolved. Moreover, based on maximum likelihood modelling analyses, numerous macrophagy-linked characters (e.g. contiguous tooth serrations, low tooth count) evolved independently in these different lineages. Thus, the characteristics that previously suggested a Late Jurassic origin of Geosaurini was due to long-branch attraction and incomplete sampling. That these different macrophagous lineages evolved distinct morphofunctional complexes and began niche partitioning early in their evolution, suggests that their diversification was driven by foraging specialisation. We hypothesise that this may be a common driver of rapid diversification in marine tetrapod evolution.

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#### **SVPCA POSTER ABSTRACTS**

#### Complex neurovascular network in the rostrum of Neovenator salerii

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Neovenator salerii is a mid-sized neovenatorid theropod from the Barremian (Early Cretaceous, c. 125 Ma) of the Isle of Wight (UK), principally known from a single, relatively complete specimen. Cranial material from the holotype MIWG (Museum of the Isle of Wight Geology) 6348 was imaged using micro-focus computer tomography (μCT) at the University of Southampton, revealing the presence of a complex network of canals in the premaxilla and maxilla. This is interpreted here as that of the cranial neurovasculature, previously unseen in any theropod bar *Spinosaurus*. The complexity and volume of this network places spinosaurid neurovasculature in a new context, questioning previous hypotheses of its role in predatory ecology.

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#### Temporal and phylogenetic evolution of the sauropod dinosaur body plan

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The colossal size and body plan of sauropod dinosaurs are unparalleled in terrestrial vertebrates. However, despite numerous studies linking changes in biodiversity, ecology and biomechanics to body size and shape, there have been only limited attempts to examine temporal and phylogenetic trends in the sauropod bauplan. Here we combine threedimensional computational models with phylogenetic reconstructions to quantify the evolution of whole-body shape and body segment properties across the sauropod radiation. Our results demonstrate that discrete changes in body shape occur concurrently with major macroevolutionary and biomechanical events in sauropod history. A caudad shift in centreof-mass in Middle Triassic basal dinosauromorphs, associated with the evolution of bipedalism in various dinosaur lineages, was reversed in Late Triassic sauropodomorphs. A craniad centre-of-mass shift coincided with the evolution of quadrupedalism in the Late Triassic, followed by a striking craniad shift in Late Jurassic–Cretaceous titanosauriforms. Craniad CoM shifts are strongly correlated with neck enlargement, which has long been considered the most important key innovation in sauropod evolution and pivotal to their gigantism. By creating a much larger feeding envelope, neck elongation is thought to have increased efficiency and opened up trophic niches that were inaccessible to other herbivores. However, surprisingly we find that relative neck size and center-of-mass position are not strongly correlated to inferred feeding habits. Instead the craniad center-of-mass positions of titanosauriforms appear closely linked with locomotion and environmental distributions, potentially contributing to the continued success of this group until the end-Cretaceous, long after other sauropods became extinct.

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### Changes in mammal disparity across two fossil *Lagerstätten* sites from the Mesozoic and Cenozoic

Gemma Louise Benevento <sup>1</sup> & Matt Friedman <sup>1</sup>

Extant mammals exhibit a remarkable variety of forms and functions. Mammals have not always shown such high levels of ecomorphological disparity. Mesozoic mammals are stereotyped as small 'generalists' or 'insectivores', only evolving novel forms as a result of an adaptive radiation at the K-Pg boundary. Shifts in the disparity of phenotypic traits in mammals from the Mesozoic to Cenozoic are not well quantified. Complicating matters is an emerging picture of surprisingly high levels of morphological disparity in Mesozoic mammals. In an attempt to better constrain patterns of mammal diversification, we quantified ecomorphological disparity in two *Lagerstätten* stratigraphically flanking the  $K \square Pg$  boundary: the Cretaceous Jehol Biota, and the Eocene Messel pit. These sites were selected due to their common lacustrine setting, as well as the relative abundance of specimens yielding information on anatomical systems beyond dentition. Functionally relevant continuous measurements were collected for limbs and jaws to represent locomotion and feeding type respectively. Preliminary results show that mammals from these two sites do not show substantial differences in disparity in traits related to feeding ecology. The Jehol mammals do occupy a marginally smaller amount of functionspace, but overlap almost completely with the Messel mammals. In terms of diversity of locomotor structures, the Jehol mammals again overlap with the Messel mammals but occupy a smaller region of functionspace. The elevated disparity of Messel can be attributed to a handful of groups with locomotor ecologies unknown from the Cretaceous: bats, early horses, and the genus *Leptictidium*, which may have been semi □ bipedal.

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# Update on work from Woodeaton Quarry, Oxford, UK and the use of volunteers in large scale collection projects

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Between 2012 and 2014 the Department of Earth Sciences at the Natural History Museum (NHMUK), London undertook four digs to Woodeaton Quarry, Oxfordshire, a designated SSSI, to collect sediment to sample for microvertebrates.

Woodeaton Quarry is important as it exposes one of the most complete sections of the middle and upper Bathonian in southern England, spanning from the top of the Taynton Limestone Formation (Great Oolite Group) to the lower part of the Forest Marble Formation (Great Oolite Group).

Over the course of our trips approximately 6.5 tonnes of sediment was collected, washed and sieved. The residue was then separated into different size fractions and examined. Due to the amount of material to curate, a team of volunteers were selected to assist with identifying and sorting the material into broad taxonomic groups (fish, mammal, amphibian, reptile and invertebrates) these are then shown to specialists within the Museum for further identification. This occurs behind a window in the collections area viewable from the public galleries with a microphone and monitor, so we can engage the public with current research ongoing within the NHM and discuss the project. To assist with identifications and future work, we are putting together a guide with descriptions and images.

Woodeaton Quarry offers the chance to provide some unique insights into the small vertebrate diversity of the upper Bathonian. Studies are currently underway focusing on the biostratigraphy, palaeoenvironments and taxonomy.

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### A new dinosaur ichnosite from the Early Cretaceous Sousa Formation, northeastern Brazil

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The Sousa Formation contains the richest dinosaur ichnofauna from the Early Cretaceous Rio do Peixe Basin, Northeastern Brazil. A few ornithopod tracks occur, and such are found also in the Antenor Navarro and Piranhas Formations. Together with one trackway from the Botucatu Formation, some isolated tracks from the Cenomanian São Luís Basin, and some trackways from the Early Cretaceous Corda Formation, now these occurrences indicates the only conclusive presence of ornithopods in the Mesozoic of Brazil. In 2015 a fieldwork was held to investigate potential dinosaur tracks in new ichnosites from the Sousa Formation. The Pereiros ichnosite represents such a new occurrence. The dinosaur ichnofauna comprises a medium-sized, bipedal ornithopod trackway, a single ornithopod track and one pair of theropod tracks. The ornithopod trackway is characterized by plantigrade, tridactyl, mesaxonic, subsymmetrical and wider than long pes tracks, with large and rounded heels, and short and wide digit impressions. It is referred to the ichnofamily Iguanodontipodidae, previously reported for the Sousa beds. Two medium-sized theropod tracks assigned to *Irenesauripus* also occurs, representing an expansion of the paleobiogeographical record for this unusual ichnotaxa. The outcrop studied represents the nineteenth dinosaur tracksite in the Sousa Formation and gives further evidence of the rather rare ornithopod dinosaurs in the Cretaceous of Brazil.

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### A new Devonian-Carboniferous boundary shark from the Old Red Sandstone of East Greenland

Gilles Cuny <sup>1</sup>, Sarah Finney <sup>2</sup> & John Marshall <sup>3</sup>

A new shark specimen was discovered on the weathered surface of a loose block of the Obrutschew Bjerg Formation on Celsius Bjerg, Ymer Ø, East Greenland. The Obrutschew Bjerg palaeoenvironment was a deep, wide, long lived and stratified lake and its age is exactly Devonian-Carboniferous boundary. The palaeogeographic location is in the heart of the ORS Continent and, as such, the shark must have accessed the lake via its discharge to the sea. It was probably feeding on the palaeoniscid *Cuneognathus*, which was about the only other fauna within the lake.

The shark (anterior half only) is quite unusual in that it preserves some 50 teeth together with a dorsal fin spine. It can be attributed to *Cladodoides*, a genus hitherto only known from isolated teeth. This means that, on the basis of the spine, *Cladodoides* can now be attributed to the ctenacanths.

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### Getting into their heads: comparative neuroanatomy of the Late Cretaceous sea turtle *Rhinochelys*

Serjoscha W. Evers <sup>1</sup> & Roger B.J. Benson <sup>1</sup>

Sea turtles (Chelonioidea) originated in the Mesozoic, and show many skeletal and sensory adaptations for marine life. Here, we present CT \( \subseteq \text{based reconstructions of the cranial} \) endocast, inner ear, and carotid circulation of the early sea turtle *Rhinochelys*, and offer comparisons to fossil and modern sea turtles. As in other sea turtles, the cranial endocast of Rhinochelys is tubular. The cephalic flexure is poorly marked, and the cerebral region is transversely weakly. Unlike in *Plesiochelys*, but as in modern sea turtles and *Puppigerus*, the medulla oblonga is located beneath the level of the olfactory tract. Olfactory lobes are. similar to modern sea turtles, smaller than in *Plesiochelys* or *Puppigerus*. The sulcus olfactorius is ventrally closed in its anterior part, a feature unknown in other fossil or extant sea turtles. The foramenorbito nasale is small, and the nasal capsule large. A large, oval trigeminal foramen is bordered by the pterygoid, prootic, and parietal. An epipterygoid could not be discerned. The stapes is more strongly curved than in *Plesiochelys*. Instead of being completely surrounded by bone, the fenestra ovalis is ventrally open between the opistothic and prootic. Semicircular canals are thicker than in *Plesiochelys*, and, as in *Puppigerus*, the common crus is dorsally markedly concave. Carotid arteries are discernable as canals largely confined to the basisphenoid. The comparisons presented show that neuroanatomy is disparate in early sea turtles, and needs to be examined further and in a (pending) phylogenetic context to understand the sensory evolution in the group.

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### A new specimen of cf. *Susisuchus* (Crocodylia, Neosuchia) with soft tissue preservation from the Crato Formation (Cretaceous, ?Aptian) of Brazil

Grant Field <sup>1</sup> & David M. Martill <sup>1</sup>

A new specimen provisionally identified as the neosuchian crocodilian *Susisuchus* is described from the ?Aptian Crato Formation (Araripe Basin) of Ceará, North East Brazil. The material comprises of post cranial remains, including an articulated sequence of thoracic vertebrae, a disarticulated pair of sacral vertebrae, partially complete forelimbs and hindlimbs, and several disarticulated osteoderms. This is the first occurrence of the hindlimbs of *Susisuchus* preserved in association with diagnostic material, providing new anatomical details for this mesoeucrocodylian.

Soft tissue preservation is also reported for the specimen. Details of the dorsal shield are preserved as an external mould showing the tetraserial paravertebral arrangement of body scales and a cast of the soft tissue surrounding the left hindlimb. Soft tissue preservation has been reported for *Susisuchus* previously but this is the most extensive and detailed soft tissue reported so far. The scales are preserved as external moulds (impressions of some authors) while soft tissues of the hindlimb appear to have been mineralised.

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### New specimen and revision of the Late Jurassic teleosaurid 'Steneosaurus' megarhinus

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Teleosaurids were a successful group of semi-aquatic crocodylomorphs that were an abundant part of coastal marine/lagoonal faunas during the Jurassic. Their fossil record suggests that the group declined in diversity and abundance during the Late Jurassic. 'Steneosaurus' megarhinus (Hulke, 1871) from the Kimmeridge Clay Formation is a little known gracile longirostrine species of teleosaurid from the Late Jurassic (late Kimmeridgian). The holotype, an incomplete snout NHMUK PV OR43086, was firstly described by Hulke in 1871. Since then only one other specimen, an almost complete skull from the slightly older Aulacostephanus eudoxus Sub-Boreal ammonite Zone of "La Crouzette", Francoulès (Quercy, France), has been referred to this species. Here, we describe, DORCM G.5067i-v, the anterior rostrum of a teleosaurid from the same horizon and locality as the holotype. We demonstrate that DORCM G.5067i-v is referable to 'Steneosaurus' megarhinus based on a unique combination of characters, which include: strongly ventrally deflected anterior margin of the premaxilla; five premaxillary alveoli, the caudal-most being considerably reduced in size; anterodorsally oriented external nares; conical teeth bearing carinae which are only visible on the apical third of the crown. Importantly, the tooth count, shape of external nares and strong premaxillary deflection distinguish 'Steneosaurus' megarhinus from all other Middle and Late Jurassic longirostrine teleosaurids. Some of these characteristics resemble those seen in pholidosaurids, suggesting some convergence between these clades.

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### The first comprehensive insight into the histology of the basal ornithopod, *Hypsilophodon foxii*, from the Isle of Wight

Craig Fraser <sup>1</sup>

The fossilised remains of the basal ornithischian *Hypsilophodon foxii*, have been unearthed from Cretaceous deposits on the Isle of Wight since the early days of vertebrate palaeontology, specifically from the Wessex Formation. Distinguished by its small size and interpreted as a fast bipedal runner, Hypsilophodon is currently regarded as the only known phylogenetic representation of its kind anywhere in the world. In the past, many dinosaur species including a number of basal ornithischians, have been subjected to histological analysis in order to determine specimen age, growth and maturity rates. To date however, there appears to be no data regarding *Hypsilophodon* in this particular field. Here, we present the first definitive histological analysis of *Hypsilophodon* long bone specimens. The fossil resources featured in this data set, were collected from the Isle of Wight, United Kingdom. These particular fossils are part of a larger collection of disarticulated material, interpreted as belonging to multiple individuals. The results were then compared to other dinosaur species to establish possible correlations and distinctive characteristics. The woven texture of cortical bone, represents accelerated growth rates early in the ontogeny of *Hypsilophodon*. There is also extensive vascularisation towards the central cavity, which becomes less frequent towards the outer edge of the bone, suggesting a marked reduction in the growth rate as the individual matured. There is also a noticeable absence of lines of arrested growth, which could be correlated to specimen immaturity, or sustained growth rates through early ontogeny.

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Hypsilophodon long bone specimens. The fossil resources featured in this data set, were collected from the Isle of Wight, United Kingdom. These particular fossils are part of a larger collection of disarticulated material, interpreted as belonging to multiple individuals. The results were then compared to other dinosaur species to establish possible correlations and distinctive characteristics. The woven texture of cortical bone, represents accelerated growth rates early in the ontogeny of Hypsilophodon. There is also extensive vascularisation towards the central cavity, which becomes less frequent towards the outer edge of the bone, suggesting a marked reduction in the growth rate as the individual matured. There is also a noticeable absence of lines of arrested growth, which could be correlated to specimen immaturity, or sustained growth rates through early ontogeny.

(This abstract is the same for the talk given by Craig Fraser, under the same title.)

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# The osteohistology of the Lower Jurassic ichthyosaur *Ichthyosaurus anningae* and *Ichthyosaurus communis* from the Lias of Dorset, UK

Rebecca Groom <sup>1</sup>, Gareth Dyke <sup>1</sup>, Jessica Lawrence Wujek <sup>1</sup> & Darren Naish <sup>1</sup>

The first detailed osteohistological data for the Lower Jurassic ichthyosaur *Ichthyosaurus anningae* is presented and compared with new data for the contemporaneous *Ichthyosaurus communis* and *Ichthyosaurus* sp.. Data for the sub-adult *I. communis* is consistent with published observations. Cancellous bone is observed in both species and is consistent with an active, pelagic lifestyle. The presence of a fibrolamellar bone complex is indicates high metabolic rates and sustained growth throughout life in both species. The presence of periods of slowed bone deposition within *Ichthyosaurus anningae* bone sections is a feature typically found in non-parvipelvians and thought to be absent from post-Triassic forms. Our new data provides additional support for the hypothesis that thunniform parvipelvians had an elevated body temperature and rapid growth rate.

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### An important plesiosaur discovery from the Oxford Clay: how cooperation between science and industry is benefitting palaeontology

Carl Harrington <sup>1</sup>, Mark Wildman <sup>1</sup>, Mark Graham <sup>1</sup>, Cliff Nicklin <sup>1</sup>, Shona Tranter <sup>1</sup>, Heather Middleton <sup>1</sup>, Roger Benson <sup>1</sup>, Hilary Ketchum <sup>1</sup>, Scott Moore-Fay <sup>1</sup> & Simon Wills <sup>1</sup>

The Peterborough Member of the Oxford Clay Formation is renowned for its abundant and well preserved marine reptile fossils. In recent years, however, the primary source of these fossils, the brick making industry, has gone into serious decline – so much so that there is only one remaining working quarry in the Lower Oxford Clay and, with the future of UK brick manufacturing unclear, the importance of this quarry to vertebrate palaeontology should not be underestimated.

The Oxford Clay Working Group (OCWG) was set up in 2011, in collaboration with the quarry owners, to collect, protect and document vertebrate fossils from this very important resource. Despite collecting some fine fossils (particularly teeth and isolated bones) efforts to secure articulated or disarticulated skeletons have been hampered, not only by modern quarrying techniques, but by reluctance of the operators to excavate to the most productive levels.

Here we report on a newly recovered, partially articulated plesiosaur skeleton representing a fully mature individual, which was saved because of the combined efforts of the OCWG in conjunction with both the quarry owners and employees.

The specimen, which has been safely conserved and secured by the group, will be deposited into an accredited institution and so made available for scientific study and, perhaps, public display. It is planned that the skull block is CT scanned which may not only provide hitherto unknown data relative to Plesiosauroidea but may help, together with other skeletal elements, to solve anatomical and taxonomic problems within Cryptoclididae and, perhaps, Elasmosauridae.

<sup>&</sup>lt;sup>1</sup> The Oxford Clay Working Group

### Eocene Tarpons from the North Sea Region, Denmark and UK

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There are very few tarpons (fam. Megalopidae) and other elopiforms (fam. Elopidae) recorded in the Tertiary. The records are mainly from the Eocene, and more abundant in the 'North Sea Region' in Early Eocene, as for instance the large Danish forms. They are also found in late Early Eocene in London Clay, in Late Eocene in Caucasia, and in Miocene of SE-Asia, although none were described from the famous Bolca fauna (early Mid Eocene). However, there is a large, still undescribed 'tarpon-like' fish in the Bolca Museum (obs. MCL & NB 2014). There are even fewer described from the long Cretaceous period, 4-5? genera, including the large *Paraelops* from Romualdo Formation, Araripe Basin, NE-Brazil, and a large undescribed megalopid from Tlayua, Pueblo, Mexico, both 'Mid Cretaceous'. The oldest elopiforms are from Late Jurassic Solnhofen Limestone.

The large Danish 'tarpons' come from 'cementstones' in Fur Formation (earliest Eocene, ca 55 m.y.), and here we report an almost complete specimen which is c. 110 cm long; however, big isolated scales found in this formation indicate fishes at least twice as big (comparable in size with the living *Tarpon atlanticus* - over  $2\frac{1}{2}$  m). This specimen has a heavy skull lacking the lower jaw, and is preserved in 3-D. It was split in the midline and acid prepared, being then CT-scanned in Aarhus and reconstructed in Lab. Biol. Anthropol., Copenhagen University to attempt precise, detailed comparisons with modern skulls and with the 3-D skulls preserved in concretions from the London Clay.

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### Daggers, swords, scythes and sickles: pachycormid fins as ecological predictors

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Pachycormids occupy a key position within Actinopterygii, as part of the Holostei-Teleostei Transition, although their precise position in this hierarchy has been fought over for some years. Discoveries in the last three years have expanded our global knowledge of the diversity, distribution and success of this group, continuing the recent 'Pachycormid Renaissance'. However, clarity over the definitions of pachycormid taxa has been undermined by the number of type specimens destroyed during World War II, introducing a need for neotype material to be identified (e.g. Asthenocormus titanius, Hypsocormus macrodon), and comparative work has revealed how poorly constrained a number of historical genera are. particularly those of the Toarcian (Early Jurassic) Holzmaden shale fauna that were the foundation of Arthur Smith Woodward's family Pachycormidae in 1895. These historical problems with descriptions and material have undermined confidence in recent phylogenetic analyses. The characteristic unusually long pectoral fins appear to have developed in conjunction with otherwise reduced skeletal ossification to counteract buoyancy problems in a group lacking a gas bladder. A sample of over 90 specimens from 16 recognised pachycormid genera was assessed, demonstrating that the ubiquitously stated 'scythe'-like pectoral fin is not a pachycormid synapomorphy: three clear and distinct pectoral fin structural morphotypes emerged, reflecting a diversity of pachycormid lifestyles that changed throughout the Mesozoic, from agile pursuit predator to slow-cruising suspension feeder. Those morphotypes closely mirror modern fuel-saving wingtip designs from today's aerodynamicists, converging on similar solutions to these enigmatic and fascinating fish some 160 million years later.

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### New data on Early Jurassic theropod diversity and feeding behaviour in the Lufeng Formation of Yunnan Province, China

Jeff Liston <sup>1,2</sup>, Darren Naish <sup>3</sup>, David Hone <sup>4</sup>, Pan Tianyang <sup>5</sup> & Liu Jian-Rong <sup>6</sup>

Bite marks and shed teeth from feeding theropods are rare. We describe two new incidences associated with Hettangian (Early Jurassic) prosauropod remains from Lufeng County, Yunnan Province. Both were recovered from the 'Lufeng Formation', now restricted to the unit previously known as the Lower Lufeng Formation or Series. Within this revised nomenclature, the formation consists of two subunits: the older Shawan Member and the younger Zhangjia'ao Member, representing the former 'Dark Purple' and 'Deep Red' Beds, respectively. A prosauropod specimen (three closely associated sequences of articulated vertebrae) was recently recovered from near DaWaShan, one cervical displaying localized brittle deformation. Within 200 mm of this vertebra, parts of five teeth were recovered, one fitting well in one of the brittle deformation recesses, interpreted as a bite mark. A further sauropodomorph referred to Yunnanosaurus was excavated from the Shawan Member at Qingliangshan, three shed theropod teeth being recovered from among its pelvic elements, matching Sinosaurus triassicus and ranging from 25-30 mm in crown height. Morphometric analyses plot these teeth distinctly from those of other theropod taxa, with an unusually low crown angle (50-64°) for the 15 mm crown base length. The teeth also feature an unusually high denticle density on the distal carina, producing a particularly low denticle size difference index (0.62-0.88), supporting the transfer of the material out of *Dilophosaurus*, and suggesting an unusual functionality. The DaWaShan teeth are not as well-preserved, but their form is clearly distinct from Sinosaurus triassicus and all other theropod taxa known from the Lufeng fauna.

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# Exploring the relationship between muscle fascicle length, muscle length change and joint motion in the archosaur hindlimb

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Muscle fascicle length (FL) is a key determinant of a muscle's performance capabilities. FL correlates closely with muscle contraction speed, force generation and, along with volume, it determines physiological cross-sectional area (PCSA), and therefore power output. For example, short FLs in pennate muscles typically generate greater forces, while long FLs in parallel fibred muscles typically exert smaller forces but over larger joint angle ranges. Thus, data on the architecture of individual muscles are essential for analysing and understanding the locomotor behaviours observed in extant species, and in attempts to predict locomotor capabilities in extinct species. However, these data on soft tissue anatomy cannot be obtained directly from the fossil record. Recent biomechanical assessments of extinct animals have highlighted the effect of the current uncertainty surrounding FL values, showing that this has a substantial impact on our ability to predict their locomotor capabilities. We seek to address this issue by testing the hypothesis that a close link exists between a muscle's FL and its in vivo length change. Here, this relationship is explored in the hindlimbs of four extant archosaurs using 3D musculoskeletal models. In our preliminary dataset, two crocodilian and two terrestrial bird species are modelled using previously collected dissection data. All muscles crossing major joints (i.e. hip, knee, ankle and metatarsophalangeal joints) were included. Comparisons are drawn between extant archosaur groups, different muscle architecture (e.g. parallel fibred versus pennate), muscle function (e.g. flexors versus extensors) and muscle location (i.e. proximal versus distal muscles).

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# Ecomorphology of the perissodactyl metacarpal: comparing traditional and geometric morphometric approaches

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The link between anatomical shape and corresponding ecology (ecomorphology) is frequently used in comparative morphological studies, often including extant and extinct taxa. Locomotion is an important function in the ecology of animals, and adaptations to the under-foot substrate are to be expected. Here we present a pilot study testing the ability of morphometric analyses to differentiate between morphologies adapted to different under-foot substrate compliances (dry grassland, compliant wetland and rocky desert/mountain). We hypothesised that species naturally inhabiting areas with firmer substrates will have shorter and thicker distal limb elements to better withstand bending moments. To test this we assessed the 3-dimensional morphology of the third metacarpal (Mc3) of a range of living and extinct perissodactyls (odd toed ungulates: 108 specimens representing 33 species) using both traditional linear metrics and 3D geometric morphometric landmarks. Traditional metrics were corrected for size effect of length measures using regression analysis, and the residuals were used as shape data. All analyses were assessed in a phylogenetic framework. Strong size and phylogenetic effects were found in both analyses. Results suggest that 3D landmark analysis of the Mc3 cannot distinguish between substrate types. Traditional metrics detect significant differences between substrate types along the first principal component; shape changes recorded are heavily influenced by depth measures of the Mc3 shaft, supporting our hypothesis. To explore the link between Mc3 shape and substrate type further, we suggest using a combination of landmark data and traditional metrics on a larger dataset.

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### Initial report of feeding traces on Early Jurassic fissure fill material from St. Bride's Island, South Wales

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During the Rhaetian transgression, areas of Carboniferous limestone in Glamorgan, south Wales, were isolated to form small islands. One of these islands, St. Bride's Island, remained above water until the early Sinemurian. A karst landscape developed and fissure fills with small tetrapod remains were common. These fissures are now exposed by quarrying, and have yielded hundreds of bones and teeth, including those from mammaliaforms, sphenodontians and small archosaurs. While most material is disarticulated and often fragmentary, recent study of some material from Pontalun (Lithalun) and Pant quarries has revealed some unusual traces on a number of specimens. These traces do not appear to be diagenetic in nature, and are interpreted as bite traces from predation and scavenging. The bones in question have a maximum size of approximately 5 mm per fragment, with the traces on the scale of 10s to 100s of µm wide and apart, indicating the presence of small predating/scaven ging animals. Two elements are identifiable: a scapula with bite traces on either side, and a lower jaw with a possible bite - both from the basal mammaliaform Morganucodon. An additional unidentified long bone fragment exhibits traces comparable to those caused by gnawing mammals. The identity of the trace maker is currently unknown, but the small size of the traces suggests a small mammalian scavenger such as *Morganucodon*, the rhynchocephalian Gephyrosaurus, or small archosaurs. Further studies will determine if these initial indications are correct, and if so, they may be the earliest record of mammal on mammal feeding.

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#### **Evaluating the tetrapod diversity from the Late Triassic of Manzanera (Teruel, Spain)**

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Several outcrops providing Upper Triassic vertebrate remains have been identified in the Keuper levels (Carnian) of the locality of Manzanera (Teruel Province, Spain). These fossils belong to different tetrapod clades. The detailed study of abundant material, including numerous unpublished specimens, allows us to modify and extend the previously proposed faunal list of this locality. The remains assigned to nothosauroids consist of several vertebrae and ribs. Their previous attribution to Nothosauria is refuted, based on the presence of infraprezygapophyses and infrapostzygapophyses in the neural arches. Within sauropterygians these characters are only present in the nothosauroid Simosaurus gaillardoti and the pistosauroid *Bobosaurus forojuliensis*. The morphology of the vertebrae and the presence of distally expanded ribs suggest that the remains from Manzanera could belong to Simosaurus, a taxon so far not recognized in the Iberian record. There are placed ont elements that consist of several isolated osteoderms of the carapace of cyamodontoids. Two isolated osteoderms have the same features of those of the placochelyd *Psephoderma*. Another osteoderm similar to those that conform the dorsolateral ridge in *Psephosauriscus mosis* is also identified. Several partial vertebral centra from the caudal region of ichthiosaurs are also recognized. The disc-like shape of the centra is a derived condition that is not present in the basal forms of ichthyopterygians. These elements represent the first record of Ichthyosauria in the Iberian Keuper, constituting the second reference to this group in the Iberian Triassic. The faunal list from Manzanera also includes temnospondyls, represented by fragmentary cranial remains.

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#### Is Spinophorosaurus nigerensis a dinosaur with caudal spike osteoderms?

P. Mocho <sup>1, 2</sup>, A. Aberasturi <sup>3</sup> & F. Ortega <sup>2</sup>

Spinophorosaurus from Middle Jurassic of Niger was firstly referred as a non-eusauropod. The systematic revision of Spinophorosaurus is in progress, and preliminary results place this taxon within Eusauropoda. One of the most peculiar features of this sauropod was to have spike-bearing osteoderms placed in the distal tail region. Indeed, this feature was used to formulate its generic name. However, herein, we provide a detailed description for these structures providing a new anatomical interpretation.

Two spine-shaped elements (HB64M) were found in association with the scapular girdle (two scapula and a coracoids in articulation) and displaced from its anatomical position. These structures present a triangular to "L-"shaped morphology in internal and external view with a convex external and a concave internal faces. The base of the "L" is expanded and bears a D-shaped cross-section. The distal end of "L" short branch has a rough articular surface in the internal side. The long branch is lenticular in cross-section and bears a longitudinal wide crest in both sides. The outer side of the "L" also bears an important rough surface.

This morphology was considered to be similar to caudal spikes found in some Chinese sauropods suggesting that they might correspond to caudal spikes osteoderms. These of elements are scarce in the sauropod record and some authors have discussed the previous interpretation. The bones have been recently prepared. Now, a full description of these elements supports its reinterpretation as clavicles. The *Spinophorosaurus* clavicles are thicker and bear deeper internal surface than in basal neosauropods.

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### Morphological and laminae pattern variation along the neck of the eusauropod Spinophorosaurus nigerensis (Niger, Middle Jurassic)

P. Mocho <sup>1, 2</sup>, A. Páramo <sup>1, 2</sup>, A. Aberasturi <sup>3</sup>, F. Escaso <sup>2</sup> & F. Ortega <sup>2</sup>

Spinophorosaurus (Niger, Middle Jurassic) was considered a non-eusauropod with several similarities with mamenchisaurids. The systematic revision is considering a new phylogenetic position, within Eusauropoda. The exceptionally preserved axial skeleton of Spinophorosaurus is important to understand the variability of several characters along the series and it is important for the establishment of new morphological characters. Some aspects of the cervical vertebrae morphology along the cervical series are discussed as well as the laminae pattern. The laminae pattern is conservative along the cervicals, with well-defined podl, prdl, spol, sprl and short acdl and pcdl. The position and orientation of laminae are mainly controlled by morphological changes in the spine. The presence of a posteriorly projected tpol might be exclusive of Spinophorosaurus and a convergence with some euhelopodids.

Other exclusive features in *Spinophorosaurus* cervicals were proposed: *i)* anterior cervicals with accessory anterior processes on prezygapophyses; ii) triangular posterior processes on diapophyses; and iii) enlarged triangular cervical epipophyses, posteriorly directed. The former feature is more pronounced in mid-posterior cervicals bearing a striated surface for the attachment of the *Mm. ascendens cervicalis* and *Mm. longus colli dorsalis*. Epipophyses is prong-shaped (as in *Jobaria* and *Euhelopus*), and is round and stout on posterior cervicals. The triangular posterior process of diapophyses becomes prominent from middle cervical vertebrae and sometimes bears striated surface probably for *Mm. intertransversarii* attachment. Some of those features are present in a partial neck of a probable juvenile of *Spinophrosaurus*, while the absence of some characters may be attributed due ontogeny.

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# Paleobiogeographical implications of the identification of a new species of basal eusuchian crocodyliform from the Late Cretaceous of Lo Hueco (Cuenca, Spain)

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Crocodyliform remains from the upper Campanian-late Maastrichtian fossil site of Lo Hueco (Cuenca, Spain) are abundant and comprise cranial and postcranial elements, as well as numerous isolated teeth. This material allowe to identify two morphotypes of non-Crocodylia eusuchians, both with features suggesting a close phylogenetic relationship with the genus *Allodaposuchus*. The morphotypes from Lo Hueco show remarkable differences between them, being recognized as belonging to two taxa.

The first taxon was recognized as a new medium sized crocodyliform, with a relatively wide and rounded rostrum. It has large teeth, separated by small interalveolar spaces. The second taxon, presented here, is also a medium size crocodyliform. It can be distinguished from the former taxon by the presence of a more elongated and thinner rostrum. This second crocodyliform from Lo Hueco presents a unique combination of characters within Eusuchia, including a peculiar dental occlusion between maxilla and lower jaw, the presence of lateral projections of the palatines over the suborbital fenestra, a sagittally septated choana, and an exclusive morphology of the anterior palatine process. Therefore, it is recognized as a new form. Its inclusion in a phylogenetic analysis placed it within a monophyletic group that consists of the type species of *Allodaposuchus* and related taxa. Given these results, a new hypothesis about the paleobiogeographical distribution of the representatives of this clade is here proposed.

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# Two types of appendicular bones of titanosaurs (Dinosauria, Sauropoda) from Lo Hueco (Fuentes, Cuenca)

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The Upper Cretaceous fossil site of Lo Hueco (Cuenca, Spain) has yielded several remains attributable to titanosaur sauropods. Among them, a high abundance and morphological disparity of appendicular bones is recognized. Most of this appendicular material is partially or totally disarticulated. In addition, several specimens lack the proximal or distal ends. These features make difficult its association with other bones corresponding to the same titanosaur individuals, and also its taxonomic assessment. The study of a sample composed by several femora and humeri from Lo Hueco, attributable to titanosaur sauropods, is done through 3D geometric morphometric techniques. It allows identifying two main morphotypes of each category of bone. These results are consistent with previous studies on cranial elements, and in a much more reduced set of femora. Principal Components also supports the differences observed in several characters between both morphotypes.

A robust and anteroposteriorly compressed morphotype of femora is recognized. The other one is a more slender type, with a high eccentric diaphysis. Concerning the humeri, a more robust and a slender and elongated morphotypes are identified. The generation of mean shape 3D models from the sample, related to each of the Principal component analysis (PCA), allows to visualize some morphological differences comparing incomplete specimens, related to the two morphotypes. For example, a difference is the presence of a more quadrangular humeral head, with a high deltopectoral crest, in the robust morphotype; but a more rounded humeral head, with a deep-ventrally directed stepwise deltopectoral crest, in the slender morphotype.

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### A brief account of the history of Dinosaur Isle and its' collections (1820-2015)

Alex Peaker 1

The geological collection of the Isle of Wight Council is now displayed at the Dinosaur Isle Museum in Sandown. Prior to the move to Dinosaur Isle in 2001 the collection was housed in a dedicated geology museum, itself established in 1913 above the Sandown Free Library. Before the transfer of the collection to the Islands' local authority the collection was part of several other museums which eventually became amalgamated to become the basis of Museum of Isle of Wight Geology.

The primary base for the collection was that of the former Newport Museum, which was bolstered by the collection of the Ryde Literary Society Museum sometime after its closure (prior to 1913). With the total closure of the Ventnor Museum in 1955 and the transfer of its specimens to the Council, the Museum of Isle of Wight Geology in Sandown became for a long time the only museum dedicated to the geological heritage of the Isle of Wight.

Over 50% of the current collection of Dinosaur Isle can be traced to transfers from one of these museums or from specimens collected by staff, with the rest of the donations being made by numerous collectors.

Although there have been many people who helped shape the museum into what it is today, a few key individuals played major roles in making Dinosaur Isle a success.

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# Identification of a member of the "Palaeochelys s.l. – Mauremys group" (Testudines) in the early Oligocene of Boutersem (Belgium)

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The Belgian early Oligocene locality of Boutersem (Flemish Brabant) has provided a rich collection of fossil vertebrate remains. They have been found in a fluvio-lacustrine complex, the Boutersem Sand Member of the Tongeren Group. The information currently available on this faunal assemblage is relatively good and allows a correlation with the reference level MP 21 of the mammalian biochronological scale for the European Paleogene. However, its turtle fauna is unpublished. Several fossils of turtles from Boutersem are presented here for the first time. Most of them can be assigned to a single form, represented by partial shells and isolated plates, corresponding to several individuals. The only contemporaneous turtle taxon so far recognized near Boutersem is *Ptychogaster laurae*, defined in the associated MP 21 locality of Hoogbutsel. The turtle from Boutersem differs from *Ptychogaster laurae*, as well as from all the representatives of *Ptychogaster*, by numerous characters, including: thinner plastron, absence of long epiplastral lip in the sagittal plane, absence of long overlap of the pectoral scutes on the entoplastron, absence of plastral hinge. This availability of characters is shared with some members of other freshwater clade of Testudinoidea: the "Palaeochelys s.l. – Mauremys group". These and other characters (e.g. absence of lateral keels in the carapace, trapezoidal morphology of the anterior plastral lobe, the observed contact between the gular scutes and the entoplastron) are shared with *Landreatchelys*, a poorly-known and problematic taxa identified in other European localities of the middle and upper Eocene (MP16 to MP18). This systematic attribution is discussed.

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### A potential podocnemidid turtle from the early Eocene of the British Wittering Formation

Adán Pérez-García 1

Pleurodira is one of the two clades of turtles living today. Unlike Cryptodira, Pleurodira is now restricted to relatively warm regions, with a relative limited geographical distribution, not including Europe. However, Pleurodira was a very successful group of turtles in Europe during both the Upper Cretaceous and the Eocene. Two Gondwanan pleurodiran lineages, belonging to Pelomedusoides, are identified in the European record: Bothremydidae and Podocnemididae. The first was very abundant in the Upper Cretaceous of this continent, being very scarce in the Paleogene record. Podocnemididae reached Europe in the Eocene. Its Eocene record is abundant, including the members of the European genus *Neochelys*, as well as several forms hitherto unpublished or poorly-known.

The so far described British Eocene record of turtles includes a valid member of Pleurodira, *Palaeaspis conybearii*, from the lower Eocene of the London Clay (Isle of Sheppey). Its systematic attribution is controversial, having been proposed as a member of Bothremydidae by several authors.

A new shell, including the partial carapace and the almost complete plastron, is presented here. It comes from Bracklesham Bay (Sussex), having being found in the Early Eocene of the Wittering Formation (Bracklesham Group). Several characters (e.g. wider neurals, more elongated plastron, deeper anal notch) do not allow its attribution to *Palaeaspis*. This specimen could correspond to a podocnemidid. If this hypothesis is confirmed, this finding would correspond to the first confirmed reference to Podocnemididae in the British record. Its comparative study will include abundant unpublished information, corresponding to specimens from several European countries.

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### The basal eucryptodiran turtle *Thalassemys* in the British record: systematic and paleobiogeographic implications

Adán Pérez-García 1

The Late Jurassic was a very successful period for the diversification of several European taxa of basal Eucryptodira. One of the worst-known clades is Thalassemydidae, exclusively represented by the members of *Thalassemys*. The type species of *Thalassemys*, *Thalassemys hugii*, has only been recognized in the Kimmeridgian of Solothurn. A second valid species of this genus, *Thalassemys marina*, is exclusively represented by its type specimen, from the Tithonian of Germany. The only known specimen of the genus *Thalassemys* outside Central Europe was recently identified in Dorset (England), in Kimmeridgian levels of the Kimmeridge Clay Formation. It was recognized as *Thalassemys* sp. A new British specimen is studied here. It also comes from the Kimmeridge Clay Formation, but from Abingdon (Oxfordshire). It preserves elements unknown on the British specimen previously assigned to *Thalassemys*. The study of the Abingdon turtle offers new data on the intraspecific variability of this poorly known coastal eucryptodiran member.

The specimen from Abingdon is identified as *Thalassemys hugii*. It shell corresponds to the largest shell of a basal eucryptodiran turtle recognized globally. The identification of *Thalassemys hugii* outside its type locality, and also outside Central Europe, shows that this coastal turtle had a relatively large paleobiogeographical distribution. The specimen from Dorset is recognized as belonging to a different species. The coexistence of two species of *Thalassemys* in the same formation, and in the same country, is recognized for the first time. In fact, only one species of *Thalassemys* had hitherto been identified in the Kimmeridgian record.

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#### **Evolutionary history of the patella in Mammaliaformes**

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The patella (kneecap) is the largest of the sesamoids (bones which develop within tendons over joints), with important biomechanical functional implications (e.g. muscle/knee joint leverage; "tendon protection"). A patella has evolved several times independently in vertebrate tetrapods; at least three times in birds, lizards and mammals respectively. Within mammals, the patellar bone has a variable pattern of distribution, being present in living monotremes and placental mammals, but largely absent in marsupials and many early fossil Mammaliaformes.

Despite the variability in patellar presence, it is generally assumed that the patella arose only once in the mammalian lineage. Until now, no formal scientific analyses have been performed to support this hypothesis. We ask: how many times did the patella evolve within the mammalian clade?

To address this question, we integrated data from literature and first-hand fossil/Recent specimen studies to reconstruct the evolutionary history of the mammalian patella. Instead of one patellar origin, we instead infer that this bone likely evolved around nine times in crown group Mammalia: in monotremes, in multituberculates, in symmetrodonts, in borhyaenoids, up to four times in marsupials, and finally in the ancestor of all eutherian (placental) mammals.

The reconstruction of trait evolution in mammals also allows us to predict the presence of the patella in fossils with incomplete hindlimb material. For example, because our reconstruction suggests the patella in eutherian mammals is very highly conserved, we expect it to be present fossil species like †*Protoungulatum* and †*Miacis*, for which there are currently no known reports of the patella.

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### A fresh look at *Colymbosaurus* (Owen, 1840) with new material from Late Jurassic of Svalbard

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Plesiosaurs were a clade of secondarily aquatic reptiles that inhabited the Mesozoic seas and included a number of diverse morphological forms and clades. Major efforts have been made to increase the resolution in plesiosaurian phylogenetic trees, as the number and classification of plesiosaurian clades has varied dramatically over the past decade. The family Cryptoclididae is well-known from the Middle and Late Jurassic of Europe, but is also documented in the Northern hemisphere to the Early Cretaceous. Defining synapomorphies of the Cryptoclididae is challenging, as many of the described genera and species either lack overlapping material or are juvenile specimens. Within this family, the question of the validity of the genus Colymbosaurus from the Kimmeridge Clay Formation of the UK and the Slottsmøya Member, Agardhfjellet Formation of Svalbard, Norway, has been debated due to the lack of articulated specimens. Here we present a partial adult cryptoclidid specimen PMO 222.663, excavated from the Slottsmøya Member of Svalbard. PMO 222.663 preserves four partially articulated paddles, most of the pectoral girdle, both ilia and series of caudal and dorsal vertebrae. Comparisons with the known species of Colymbosaurus and PMO 222.663, demonstrate that the current definition of the genus needs revision. The morphology of this specimen from the Slottsmøya Member, along with other partially complete specimens held in British museums, yield new morphological information and insights into Colymbosaurus anatomy. Further comparisons and detailed study of these specimens promise to assist in the definition of this enigmatic genus and to clarify the phylogenetic relationships within Cryptoclididae.

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### Around the world in 146 dogs: a new global fossil canid phylogeny and the historical phylobiogeography of Caninae

Laura Säilä <sup>1</sup> & Nicholas J. Matzke <sup>2</sup>

The phylogenetic relationships of North American fossil Canidae have been subject to many recent studies but canids from other continents have received less attention. We present the results of the first ever combined evidence analysis (molecular and morphological characters) of global Canidae, with additional fossil taxa included either a-priori or a-posteriori based on expert opinion. We used the R package BEASTmasteR to conduct a Bayesian total evidence analyses (tip-dating) for a dated phylogeny of 237 extant and extinct Canidae (65 in subfamily Borophaginae, 26 in subfamily Hesperocyoninae, and 146 in subfamily Caninae). Our results are moderately consistent with previous studies but the inclusion over 50 fossil taxa previously excluded resulted in differences both in the clade topology and timings. We also conducted a historical phylobiogeographical analysis of subfamily Caninae and compared the fit of many different models of biogeography using the R package BioGeoBEARS. Models that include "founder-event speciation" gained over 99% of the AIC model weight. Newly developed BioGeoBEARS features also allowed us to estimate whether an absence of a fossil taxon from a certain region is a 'true absence' or just 'absence of evidence' based on the completeness of the fossil record, resulting in more robust biogeographical models.

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### An exceptional fossil lagerstätte – the Fur Formation (lowermost Eocene) of Denmark, a marine diatomite with limestone boulders

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The Fur Formation, a 50-m-thick, oceanic diatomite ('Mo-clay') of earliest Eocene age (55.6c. 54.5 Ma) includes the world's largest volcanic ash series, related to sea floor spreading in the Greenland-Norwegian Sea. There are limestones with all diatomite pores calcite filled, and formed less than one metre below surface, preserving skeletons (dissolved in soft diatomite). It is laminated sediment, deposited under anoxic conditions, below coast-parallel upwelling at depths of around 500 m, rich in macrofossils, particularly well-preserved in the few limestone horizons, with 1-m-thick concretions. Large calcite pseudomorphs after glendonite/ikaite indicate bottom temperatures below 6-8 centigrades. Sedimentation was continuous from PETM laminated black Stolleklint Clay into beige diatomite, with a slightly lower temperature. Fossils range from silicoflagellates to 10-m-long trunks of Sequoia and include biota from oceanic animals to terrestrial plants, insects and birds. Vertebrates comprise 7-8 shark species, 70 teleosts, mainly pelagic (some deep pelagic), with eye pigment showing preservation of original molecules, as well as turtles (large leatherback and juvenile, exquisitely preserved *Tasbacka* with 'soft' parts, skin and keratin, and a freshwater turtle). Marine snakes (Palaeophis) and over 30 species of land-birds, with coloured feathers, including a flying palaeognath (*Lithornis*) in 3-D preservation. The 'World's best-preserved bird', a complete coraciiform in 3-D (cfr. talk by Bourdon et al.), retaining fish in the stomach. Exceptional preservation includes features of soft parts, 3-D documentation of birds, the first Eocene colours, sounds and evidens of mass moth migration. The Fur Formation (Mo-clay) cliffs as Fossil Lagerstätten are obvious candidates as a World Heritage Site.

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#### Microstructure of ankylosaur pelvic shield from the Early Cretaceous, Isle of Wight

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The rarity of fossil specimens has meant that there have been few histological analyses of ankylosaur pelvic shields. Here we report an unusual feature present across the pelvic shield of a well-preserved ankylosaur from the Isle of Wight, southern England, and discuss its structure, functional implications and usefulness in determining phylogeny. Originally thought to be *Polacanthus foxii*, this new ankylosaur specimen has yet to be described and is considered nodosauroid (indet.). The pelvic shield exhibits alternating light and dark layers at the macro-level, revealed by histological analysis as a plywood-like structure, each ply being rotated at approximately 90° to those above and below. Highly organised collagen structural fibre bundles lie parallel to the dorsal surface within individual plies of the bone matrix as well as perpendicular to the dorsal surface. We infer that the pelvic shield would have proved effective as a tough, protective defensive structure. The histology of the pelvic shield of this Isle of Wight ankylosaur is dissimilar to current *Polacanthus* descriptions and may be unique to this taxon.

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# Crocodilian tooth morphology and niche partitioning in the Hell Creek Formation (South Dakota, USA)

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Fossilised crocodilian teeth are relatively common within the Hell Creek Formation (South Dakota, USA) with the three most common crocodilian species being Thoracosaurus neocesariensis, Borealosuchus sternbergii and Brachychampsa montana. This study has identified crocodilian teeth from a large collection made from a new site in the Hell Creek Formation. The aim of this study was to determine if there were any significant differences in the geometry and morphology of teeth that might help diagnose species and establish possible niche partitioning. Ninety-six isolated teeth were collected from a single locality in Northwest South Dakota. The height, labial-lingual depth, proximaldistal width, and curvatures (labial, lingual and curvature at the carina) were measured for each tooth. Linear regressions and ternary diagrams were used to analyse size and curvature measurements between taxa. The teeth from the new site were identified as *Borealosuchus* sp., Thoracosaurus sp. and Brachychampsa sp. The results from this study suggest a relationship between tooth proportion (height, depth and width) and species with regards to Borealosuchus and Brachychampsa but not Thoracosaurus and there is no correlation between curvature and species. However, the general skull and dental morphologies of these taxa suggest different feeding habits and thus potential niche partitioning. Brachychampsa had short, broad and flat teeth towards the posterior end of the dentary, capable of shell crushing. The snout morphology of *Thoracosaurus* and *Borealosuchus* suggest Thoracosaurus was piscivorous whereas Borealosuchus was carnivorous. Dietary resource partitioning enabled the coexistence of these three species.

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#### A new giant species of thresher shark from the Miocene of the United States and Malta

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In the late Early and Middle Miocene there was burst of gigantism in a number of unrelated species of shark. This event corresponded with the warmest interval of the Neogene, the so-called "middle Miocene climatic optimum", giving high oceanic productivity. Miocene deposits along the eastern seaboard of the USA have been known for their rich vertebrate faunas, principally cetacean bones and sharks' teeth for at least one and a half centuries. The giant shark genera included the hexanchiforms (*Hexanchus*), lamniforms (*Alopias*, *Carcharocles*, *Carcharodon*, *Cosmopolitodus*, *Isurus*, *Parotodus*), and carcharhiniforms (*Galeocerdo*, *Hemipristis*). The teeth of these sharks well-known and present in museum collections with the exception of those of the thresher shark, *Alopias*.

In 1942, Leriche described a large species of thresher shark from the Neogene of the USA. He figured two specimens which he named *Alopecias* (= *Alopias*) *grandis*. The holotype, was from the Miocene Calvert Formation of Nomini Cliffs, Virginia. The other was reworked from the Neogene of the Charleston area This species, although not particularly rare, is poorly known and has received little attention in the subsequent literature. An undescribed species, of similar size but with a serrated cutting edge, is present in slightly younger beds within the Calvert Formation of Calvert Cliffs, Maryland USA. Both species are present in the Early and Middle Miocene of Malta. The new serrated species has now been described and is currently in press.

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