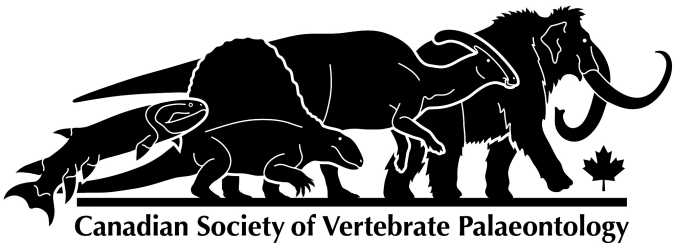
Vertebrate Anatomy Morphology Palaeontology
ISSN 2292-1389

Meeting Logo Design: Our 2021 meeting logo (front cover) is by Matthew Rhodes. He says the design is "a tribute to the 'academic ancestor' of Canadian vertebrate palaeontology, Robert "Bob" Lynn Carroll (1938–2020). Carroll represents Canadian palaeontology not only by his own contributions to the field, but also by the 'academic radiation' of his numerous students, many of whom continue to shape the field today. Much of Carroll's research was dedicated to early tetrapods, particularly from eastern Canada. This led me to his 1969 description of *Paleothyris*, an early reptile often used as a representative of the anapsid skull condition, including in his own book *Vertebrate Paleontology and Evolution*. The *Paleothyris* climbing through the logo was inspired by Figure 12 of Carroll (1969), which cuts off around the base of the tail—the same position at which the logo turns into digital blocks. Carroll's works often have Romerograms (spindle diagrams), so a maple leaf-shaped one materializing from the V seemed appropriate. On a deeper level, the *Paleothyris* sits at the base of the V as if it was the ancestor of the Romerogram's central branch, echoing one of Carroll's lines quoted in Caldwell and Larsson (2020) in *VAMP*: "... if you believe in evolution, you have to believe in ancestors, and I'm going to keep looking for them until I drop". "



Published 21 May, 2021
Editors: Alison M. Murray, Hallie Street and Robert B. Holmes

DOI 10.18435/vamp29374

9th Annual Meeting Canadian Society of Vertebrate Palaeontology

May 26–28, 2021

Online

Abstracts

Message from the Organizing Committee

Greetings to our members across Canada and around the world

What kind of year has it been? Travel restrictions and work-from-home orders have limited our abilities to meet, use lab facilities, and conduct fieldwork. Regardless, vertebrate palaeontology research has adapted and progressed, though maybe in different directions than were anticipated at the beginning of 2020. This year's annual meeting finds us at a sensitive crossroads during the Covid-19 pandemic, balanced between the increasing availability of vaccines and the concerns over the spread of new variants. Staying connected and inspired may be particularly important during these uncertain times, and so the Society felt it was important to have an annual meeting this year. Therefore we are venturing into the realm of digital conferencing.

The CSVP 2021 meeting will be held on May 26–28th with an introductory guest lecture by Dr. Grant Zazula on May 25th. The oral presentations will be given live using Zoom (a video conference software), and digital posters will be available throughout the meeting with a live session for questions and discussions. The Virtual Organizing Committee and the Executive Committee are aware of just how much of our interactions take place via similar media these days, and so the decision was made to limit the conference to a few hours each afternoon/evening. We hope this makes the annual meeting accessible to all our members without being overwhelming. The reduced time did limit the number of presentations we were able to accept, and so we hope that members of the Society understand our choice to prioritize students and early career researchers.

There are, of course, aspects of an in-person conference that we cannot replicate virtually. However, without the need to pay for travel or accommodations, the virtual format of CSVP 2021 has attracted interest from students and researchers across Canada and from as far afield as Europe and Asia. We are grateful for the dedication, patience, and flexibility the members of our community have shown to each other and to the Society over the past fifteen months. We hope members can make the best of the virtual meeting this year, and we look forward to our next opportunity to meet in person,

Your Virtual Organizing Committee,

Bassel Arnaout

Emily Bamforth

Julien Divay

Annie McIntosh

Hallie Street

Yan-Yin Wang

TABLE OF CONTENTS

Lissamphibia: a polyphyletic group within Temnospondyli?

Thomas Arbez

Department of Earth Sciences, Carleton University, Ottawa, ON, Canada; thomasarbez@cunet.carleton.ca

Phylogenetic relationships between lissamphibians (frogs, salamanders and caecilians) and their fossil relatives (i.e., non-amniotic extinct tetrapods) is a century old question, yet still actively debated, and in spite of phylogenetic matrices including more and more taxa and characters.

Several hypotheses about Lissamphibia relationships are still discussed: Lissamphibia as a monophyletic group included among the Temnospondyli (Temnospondyl Hypothesis – "TH"), or among lepospondyls (Lepospondyl Hypothesis - "LH"), or as a polyphyletic group divided among the temnospondyls and lepospondyls (Polyphyletic Hypothesis – "PH").

The absence of consensus regarding the position of lissamphibians is attributed to the lack of specimens displaying a mosaic of characters specific to lissamphibians and to a particular clade of extinct non-amniote tetrapods. The most ancient fossils attributed to lissamphibians are indeed already extremely similar to extant lissamphibians and share few similarities with extinct non-amniote tetrapods. This difference is particularly visible with the great reduction of the number of cranial bones in the extant lissamphibians by comparison with the extinct non-amniote tetrapods.

Here, a cladistic phylogenetic analysis made with PAUP and including all the major groups of extinct non-amniote tetrapods, as well as lissamphibians and amniotes (63 taxa and 213 characters), reveals methodological aspects also have an important influence on the resolution of lissamphibian relationships. The phylogenetic analysis was divided into three variants (when compared to a reference) in order to test different character treatments (e.g., ordered vs unordered characters), as well as the impact of the inclusion or exclusion of some characters (e.g., character coding the presence or absence of a given bone).

Interestingly, different hypotheses of the position of lissamphibians, as well as their monophyly or polyphyly, were recovered based on different tests of the same matrix, allowing comparison of these hypotheses within a constrained framework (i.e., comparing topologies that are not the product of analyses with great differences in taxon or character sampling, as it could be when comparing different studies).

The comparison of the different hypotheses recovered here, in terms of tree length, character support as well as character transformation coherence shows that the lissamphibian's monophyly (TH and LH) is mainly supported by the "absence of bones" without any exclusive synapomorphies.

A hypothesis of a polyphyletic Lissamphibia within Temnospondyli (TH-p), where frog and salamanders are found within the Dissorophoidea and caecilians are found within Brachyopidae, appears to be the most coherent in terms of character transformations despite not being the most parsimonious overall (by a few steps). In addition, the TH-p hypothesis seems to solve several inconsistencies among the TH, LH and PH (e.g., multiple bone reappearances or multiple reversions of morphologically complex character states).

So, the classical view of a monophyletic Lissamphibia is weakly anatomically supported as the synapomorphies would only be the "absence of bones". The resulting similarity appears to be due to a similar cranial simplification process already known to be happen convergently in different extinct non amniotic tetrapod groups (e.g., Lepospondyls) and likely due to paedomorphosis events. The fact that frogs, salamanders and caecilians do not form a monophyletic group when including extinct non-amniote tetrapods would explain why currently all the synapomorphies exclusive to the Lissamphibia are based on soft tissues and not hard tissues, such as bones.

First occurrence of a sea turtle (clade Panchelonioidea, superfamily Chelonioidea) from the Dinosaur Park Formation of Saskatchewan, Canada

Emily L. Bamforth[1,2] and Hallie P. Street[3]

[1]Royal Saskatchewan Museum, *T. rex* Discovery Centre, Eastend, SK, S0N 0T0, Canada; emily.bamforth@gov.sk.ca
[2]University of Saskatchewan, Department of Geological Sciences. Saskatoon, SK, S7N 5E2, Canada
[3]Edmonton, AB, Canada; hallie.street@gmail.com

Though relatively uncommon, sea turtles (clade Panchelonioidea) are an intriguing component of western Canada's Cretaceous marine faunas. Studies of panchelonioid diversity patterns within the Late Cretaceous Western Interior Sea suggest, for reasons not yet fully understood, that these animals favoured southern portions of the Western Interior Sea (Nicholls and Russell 1990), occurring much less frequently in Canada than in the United States. In Saskatchewan, panchelonioids are represented by just two occurrences from the Santonian Niobrara Formation along the Manitoba Escarpment, and one from the upper Campanian Bearpaw Formation of southwest Saskatchewan (Nicholls et al. 1990). The Niobrara Formation specimens, a humerus (RSKM P2077.64) and other fragmentary remains (RSKM P2077.31) were described by Nicholls et al. (1990) as protostegids, largely based on their small size. Protostegidae is an extinct basal panchelonioid group which includes the giant sea turtle *Archelon*. It is the sister taxon to the Chelonioidea, which includes nearly all other known sea turtles (Evers et al., 2019). The Bearpaw Formation specimens, small rib pieces and a badly weathered peripheral fragment (CMN 40660), could not be identified beyond Chelonioidea (Nicholls et al. 1990).

Herein is described the first occurrence of a chelonioid sea turtle from marine strata within the Dinosaur Park Formation of Saskatchewan. RSKM P3197.198 is a left costal plate of the carapace, with a maximal length of 150 mm, maximal width of 90 mm in width, and maximal thickness of 16 mm. While broken along its medial margin, the lateral peripheral edge is reasonably well preserved. The costal plate is broad and slightly convex dorsally, with no noticeable suturing or ornamentation. The specimen was collected in 2016 from a marine bonebed near the hamlet of Herschel, Saskatchewan. Recent studies have placed the Herschel Marine Bonebed (HMB) within a marine interval of the upper Dinosaur Park Formation, in a shallow-marine barrier-island basin environment (Street et al. 2019). The HMB has yielded a high diversity of marine vertebrates, including ichthyodectids, *Enchodus* sp., *Protosphyraena* sp., *Ischyodus rayhaasi*, hybodontids, odontaspidids and other lamniforms, as well as polycotylid and elasmosaurid plesiosaurs, and mosasaurine and plioplatecarpine mosasaurs.

In a review of marine turtles from the Late Cretaceous of Alberta, Brinkman et al. (2015) identified at least three genera of chelonioids from this province: *Nichollsemys*, *Lophochelys* and *Kimurachelys*. *Nichollsemys* is known from open marine sediments of the Bearpaw Formation (Brinkman et al. 2006), while *Kimurachelys* and the specimens ascribed to *Lophochelys* are from the Lethbridge Coal Zone of the uppermost Dinosaur Park Formation (Brinkman et al. 2015). RSM P3197.198 is significantly larger than the Alberta specimens referred to *Lophochelys*, and both *Nichollsemys* and *Kimurachelys* are known only from cranial material. Therefore, more work and more specimens will be required to determine if RSKM P3197.198 can be ascribed to any of these taxa, or if it represents the first occurrence of another taxon in the northern Western Interior Seaway.

Comparison of RSKM P3197.198 from the HMB with the Alberta material raises an intriguing question about the possible paleoenvironmental preference of Canadian chelonioids. Although not necessarily directly contemporaneous with the Lethbridge Coal Zone, the HMB represents a similar shallow-marine, nearshore environment. Brinkman et al. (2015) suggested that chelonioids may have been brackish-water or even freshwater tolerant. This may also apply to RSKM P3197.198, which was found in a similar paleoenviroment. Although the sample size is small, chelonioid diversity appears to be higher in nearshore, shallow-marine or estuarine

deposits. More specimens and more research could help to elucidate is this was a true biological signature, and if chelonioid sea turtles preferred these habitats over the open ocean.

RSM P3197.198 represents the largest and most diagnostic chelonioid specimen known from Saskatchewan. The collection of additional specimens from marine sediments of the Dinosaur Park Formation may reveal important information on the diversity and paleoecology of marine turtles in western Canada.

Literature Cited

Brinkman, D., M. Hart, H. Jamniczky, and M. Colbert. 2006. *Nichollsemys baieri* gen. et sp. nov, a primitive chelonioid turtle from the late Campanian of North America. Paludicola 5:111–124.

Brinkman, D.B., M. Densmore, M. Rabi, M.J. Ryan and D.C. Evans. 2015. Marine turtles from the Late Cretaceous of Alberta, Canada. Canadian Journal of Earth Sciences 52:581–589.

Evers, S.W., P.M. Barrett., and R.B.J. Benson. 2019. Anatomy of *Rhinochelys pulchriceps* (Protostegidae) and marine adaptation during the early evolution of chelonioids. PeerJ 7:6811.

Nicholls, E.L., and A.P. Russell. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79:149–169.

Nicholls, E.L., T.T. Tokaryk, and L.V. Hills. 1990. Cretaceous marine turtles from the Western Interior Seaway of Canada. Canadian Journal of Earth Sciences 27:1288–1298.

Street, H.P., E.L. Bamforth, and M.M. Gilbert. 2019. The formation of a marine bonebed at the Upper Cretaceous Dinosaur Park-Bearpaw transition of west-central Saskatchewan, Canada. Frontiers in Earth Science 7:209.

Potential preservation of keratinous tissues associated with frill ornamentation of an immature *Centrosaurus* (Ornithischia, Ceratopsidae)

Caleb Brown

Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, AB, Canada, T0J 0Y0; caleb.brown@gov.ab.ca

The recognition and description of keratinized epidermal structures in dinosaurs is becoming increasingly common. Within Ornithischia these keratinous structures include bristles/filaments (Psittacosauridae, Heterodontosauridae, Neornithischia), scaly skin (various taxa), keratinous osteoderm scales (Ankylosauria), rhamphothecae (i.e., keratinized beaks) (Hadrosauridae), and hooves (Hadrosauridae/Ankylosauria). The skulls of the Ceratopsidae possess several bony (i.e., osseous) features which were likely capped by robust keratinized tissues including rhamphothecae on the rostral (i.e., rhinotheca) and predentary (i.e., gnathotheca), and keratinous sheaths for the nasal and postorbital horns, and likely the frill and jugal horns (i.e., epiossifications) as well. Despite this high potential for keratinous preservation in ceratopsid skulls, and the abundant fossil record of this group, direct evidence of its preservation is rare to non-existent.

In 2019, a small parietal of *Centrosaurus* (TMP 2019.012.0122) was collected from low in the Dinosaur Park Formation (Campanian) of Alberta. During preparation, the preparator discovered several flat, semi-circular to crescentic structures located under (i.e., stratigraphically beneath) the parietal within the jacket. Importantly, a broken and displaced section of lateral ramus of the parietal was found at the same level as these structures. Due to their shape and association they were initially thought to be unfused frill epiossifications (i.e., epiparietals), however breaks reveal their composition to be entirely ironstone with no bone component. A return to the quarry later in the season located more structures in the spoil pile of the jacket (i.e., matrix removed to lighten the jacket).

In total eight structures are preserved. The specimens vary from semi-circular to crescentic in shape, with the curved/convex margins having a rounded beveled edge, while the flat/concave 'basal' margin often shows a concave facet-like edge. The basal margin of one specimen also shows a bi-lobed facet reminiscent of the epiossification spanning the parietal squamosal contact. The specimens vary in size, with basal widths of 30-80 mm, basal-apical heights of 21–41 mm, and thickness of 6–11 mm, with these three measurements scaling approximately isometrically. The surface texture of the structures is distinctive, bearing parallel ridges and grooves, approximately 1 mm in width. In particular, on the rounded margins these striae form a distinctive braided or ropey appearance with parallel lineation showing a larger-scale sigmoidal pattern along the periphery of the elements. More centrally, one of the flat surfaces of each element shows a radial pattern of striae, while the opposite side has a subtler and more random pattern.

The parietal preserves the midline bar, right lateral ramus and much of the posterior ramus, missing the left side. P1 loci (the medial-most parietal horn positions) are preserved on both left and right sides of the parietal, with a gap in the right P2 (and P3?) area, followed by four right lateral loci (P3–P6 or P4–P7 — lateral parietal horn positions) to the squamosal suture, with all loci expressed as thin, subtle scallops. The parietal is 391 mm long (sagittal length) and 317 mm wide (right half width), one of the smallest known for *Centrosaurus*. The thickness and convex rounded bevel of the posterior and lateral edge of the parietal correlate well with both the thickness and concave facets on the flat edge of the structures.

The size, shape, ornamentation development, and mottled texture of the parietal are consistent with an early subadult stage, comparable to, but smaller and potential earlier than, TMP 1995.175.0064 (470 mm x 335 mm) and CMN 11839 (496 mm x 366 mm). Centrosaurine parietals of similar, or younger, ontogenetic stage are not known to have preserved epiossifications, whereas larger/older specimens show associated and then fused epiossifications.

These structures are tentatively identified as fossils preserving the shape, but not organics, of keratinous sheaths associated with parietal horn loci. If this interpretation is correct, this specimen indicates that that keratinous horns may ontogenetically precede the development of the epiossification at parietal loci. Further, the size of these keratinous horns is larger and more exaggerated than would be expected for a specimen at this ontogenetic stage. Alternate interpretations or identifications of these structures are welcome.

Development and evolution of regionalization within the avian axial column

Hoai-Nam N. Bui and Hans C.E. Larsson

Redpath Museum, McGill University, Montreal, QC, H3A 2K6, Canada; hoai-nam.bui@mail.mcgill.ca; hans.ce.larsson@mcgill.ca

The origin of birds from their terrestrial antecedents was accompanied by a wholesale transformation of their skeleton as they transitioned from a terrestrial to an aerial realm. A significant aspect of this dramatic transformation is the reduction of separate vertebral elements into regional fusions to increase axial rigidity. Specifically, the transition from non-avialian theropods to highly derived birds is accompanied with the loss of an elongate tail, fusion of posterior caudals into a pygostyle, a broadly fused synsacrum and, sometimes, a notarium. This is partially mirrored within the development of the axial column, with the axial column experiencing increasing regionalization and the loss of individual skeletal elements through vertebral fusions. Using a detailed description of the morphological development of the axial column in the model domestic chicken, *Gallus gallus*, we present a map of axial chondrification and ossification based on discrete characters. We find that delays in ossification occur in conjunction with the formation of fusions. Our study shows that the pattern and sequence of fusion and ossification during development may reflect the presence of independent modules, or functional units, as subsets

within the typical regions of the avian axial column. Interestingly, few of these fusion modules correspond to the initial axial Hox expression patterns, suggesting another patterning mechanism is driving axial fusion regionalization. Additionally, two regions of fusion are discovered in the synsacrum. The anterior region of seven fused synsacrals may correspond to the non-ornithuran pygostylian synsacrum of the same number of vertebrae. This work provides further insight into the evolution of modern birds utilizing an integration of anatomical, developmental and evolutionary perspectives that can be used for future applications in paleontology.

First definitive occurrence of Polycotylidae (short-necked plesiosaurians) from non-marine sediments of the Dinosaur Park Formation of Alberta: evidence for a multi-taxic, freshwater plesiosaurian assemblage

James A. Campbell[1] and Caleb M. Brown[2]

[1]Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, AB, T2N 1N4, Canada; james.campbell2@ucalgary.ca

[2]Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, AB, T0J 0Y0, Canada; caleb.brown@gov.ab.ca

Non-marine to paralic sediments of the Dinosaur Park Formation (DPF) have produced a stratigraphically extensive record of plesiosaurian remains (n = 105 individuals). The majority of this material comes from Dinosaur Provincial Park (DPP), where the DPF is approximately 70 m thick. About 42% of this material is diagnostic to the family level, of which the majority (95%) is referable to Elasmosauridae (i.e., long-necked plesiosaurians). About 19% of the elasmosaurid material is referable to the recently named *Fluvionectes sloanae*, whose remains extend from 25 to 56 m above the base of the DPF. In addition to these elasmosaurid occurrences, three isolated teeth (TMP 1987.048.0042, 2001.012.0151, and 2002.012.0051) from the DPF of DPP were tentatively identified as polycotylid (i.e., short-necked plesiosaurians) in 2005. These teeth represent the only published evidence that polycotylids inhabited non-marine to paralic environments of the DPF. Juvenile polycotylid remains are also known from marginal marine sediments of the DPF near Herschel, Saskatchewan.

We re-examined these teeth and found that they are labiolingually compressed and have smooth (i.e., lacking enamel ridges) labial surfaces, as in elasmosaurids but not polycotylids, and are morphologically similar to those of *Fluvionectes*; we therefore identify them as elasmosaurid. Although this would bring the occurrence of polycotylids from the DPF of Alberta into doubt, we also report on two previously undescribed isolated polycotylid centra (TMP 1980.016.0422 and 2020.012.0008) from the DPF in DPP. Both specimens are identified as cervical centra, based on the presence of rib facets, and a ventral keel separating two foramina subcentralia. The neural arch appears to be unfused in both specimens, suggesting that these individuals had not reached full osteological maturity, as is the case for most plesiosaurian remains from the DPF. These centra are nearly circular in articular view and are anteroposteriorly short, both of which are characteristic of polycotylids. These centra would have been slightly longer in life, as the articular rims have been lost to abrasion. Taking this into account, these centra are proportionately shorter than most other polycotylid taxa, so this may represent a diagnostic feature. Both specimens were collected from an interval between 30 and 40 m above the base of the DPF, overlapping with *Fluvionectes*, from palaeochannel sediments that are thought to have been deposited at least 100 km inland from the Western Interior Seaway. It is likely that these centra were transported a considerable distance downriver, given their isolated and moderately abraded conditions.

We believe that the low ratio of polycotylids relative to elasmosaurids (1:21) in non-marine to paralic sediments of the DPF likely represents an ecological signal and not a sampling or taphonomic bias, given the long history of plesiosaurians collected from this unit, and the two clades having similar taphonomic profiles. Elasmosaurid remains are also more abundant than polycotylid remains in marginal marine sediments of the DPF near Herschel, Saskatchewan, and in the marine Bearpaw Formation. Plesiosaurian remains are particularly common in the interval of the DPF that produced these two centra, which may in part explain why polycotylids have not yet been found elsewhere in this unit. The DPF represents one of only five multi-taxic, non-marine plesiosaurian assemblages known, the others being the Late Jurassic Spilsby Sandstone Formation of England, the Berriasian Deister Formation of Germany, and the late Campanian/early Maastrichtian La Colonia and Allen formations of Argentina. The differing diet and feeding strategies between polycotylids and elasmosaurids, as reflected in their tooth and cranial morphologies, may have enabled these two families to co-exist within the non-marine to paralic DPF, as they did in the marine realm.

PalaeoPoems: A digital anthology highlighting a unique form of science communication

Brigid E. Christison[1], Michael G.W. Thompson[2], and Katrin Emery[3]

[1]Biology Department, Carleton University, 1125 Colonel By Drive, Ottawa ON, K1S 5B6, Canada; brigidchristison.cmail.carleton.ca
[2]Museum of Natural Sciences, University of Saskatchewan, 114 Science Place, Saskatoon SK, S7N 5E2, Canada; michael.g.w.thompson@gmail.com
[3]Ottawa, ON, K1Y 2V4, Canada; katremery@gmail.com

Poetry is a form of science communication (SciComm) that is able to express the thoughts and feelings of those who study fossils in a unique way. Poetry can communicate scientific concepts in a language that is accessible to a wider audience than academic writing alone. PalaeoPoems.com is a digital anthology founded in 2018 that aims to compile as many of these poems as possible. Academics have written poetry to discuss complex scientific ideas, feuds, and even morphological descriptions since at least the 1800s and continue to do so. These poems are therefore both educational and historically significant, letting readers understand prevailing ideas about palaeontology from the times they were written.

PalaeoPoems.com aims to make these poems as available as possible to both researchers and the public by presenting them alongside their primary sources. Each month, PalaeoPoems.com features a poem related to the field of palaeontology, accompanied by analyses of the historical and scientific aspects of their written content. These breakdowns allow readers to understand the terminology used within and provide context for certain verses. Featured poems are also accompanied by contemporary artwork from different artists. By including contemporary artwork with each poem, our goal is to show that historical poetry is not merely an outdated curiosity, but still retains value as a genuine form of modern SciComm. Contemporary artwork highlights the scientific message of the poems themselves in ways that are also promotional for each featured poem, allowing the blog to reach a wider audience.

Another major goal of the PalaeoPoems project is to encourage poetry writing among academics and palaeontology enthusiasts. PalaeoPoems.com issues weekly poetry-writing prompts on social media, usually about a relatively broad palaeontological topic. For scientists not used to writing in verse, these poem prompts are an opportunity to think about topics in a less conventional way. Our goal with this challenge is to promote the practice of writing PalaeoPoems so that academics, science communicators, and other people can become more familiar with these ways of writing and thinking and in turn inform them about the value of poetry and other writing styles as SciComm.

Evolution of marine ecosystems, a global view from the Early Cretaceous marine tetrapods of Colombia

Dirley Cortés[1,2,3], Hans C.E. Larsson[1], Erin E. Maxwell[4], Alexandre Demers-Potvin[1], Hoai-Nam Bui[1], Anthony Smith[1], and Mary Luz Parra-Ruge[3]

[1]Redpath Museum, Biology Department, McGill University, 859 Sherbrooke St. W., Montréal QC H3A 0C4, Canada; dirley.cortes@mail.mcgill.ca; hans.ce.larsson@mcgill.ca; alexandre.demers-potvin@mail.mcgill.ca; hoai-nam.bui@mail.mcgill.ca; anthony.smith2@mail.mcgill.ca
[2]Smithsonian Tropical Research Institute, Balboa-Ancón 0843–03092, Panamá, Panamá
[3]Centro de Investigaciones Paleontológicas, Kilómetro 5.2 vía Santa Sofía, Villa de Leyva, Colombia; mlparra@centropaleo.com
[4]Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany; erin.maxwell@smns-bw.de

This research investigates how the ancient marine ecosystems spanning the establishment of the Hispanic Corridor (a seaway linking the eastern Pacific and western Tethyan oceans) evolved, and assembles a comprehensive dataset from multiple diverse fossil localities that temporally and spatially span a time of large-scale global sea level rise, temperature rise, and tectonic rifting that connected the Atlantic and Pacific Oceans during the Early Cretaceous, over 130 million years ago. These data will be used to estimate the aspects of these ecosystems that were most stable and which evolved during this dramatic environmental event. Emphasis is placed on high ecological trophic levels, because as we know from the modern world, predators offer the most robust signals of ecosystem complexity and food web interactions. To address how marine reptiles responded to biogeographic changes (opening of the Hispanic corridor), climate (temperature), and sea-level changes, the marine fauna from the Paja Formation (Hauterivian-Barremian) of Colombia is being used as a model system to investigate evolutionary patterns of top predators (i.e., origination, extinction, anatomical rates) using accurate time-calibrated phylogenies. We propose a hypothesis that biotic factors will show significant signatures to support a hotspot of high origination rates, low extinction rates, high morphological rates of evolution, and high endemism. Preliminary results show remarkable insights. First, the occurrence of a Colombian Barremian teleosauroid demonstrates that the thalattosuchian teleosauroid lineage, thought to be extinct, survived the Jurassic / Cretaceous extinction. With a body length of 9.6 m, this specimen is one of the largest known teleosauroids and the youngest known for the lineage. This finding supports the hypothesis that tropical water temperature played an important role in controlling the diversity and distribution of these large marine predators. Second, the descriptions of ichthyosaur material reveal the first hypercarnivore ichthyosaur from the Cretaceous, which opens up questions about food web structures for Jurassic-Cretaceous ecosystems. Finally, a 3D surface scan of a pliosaur from the Paja Formation reveals numerous cranial autapomorphies, which provide distinguishable information to place this new genus in a taxonomic and systematic context and to evaluate its phylogenetic and paleobiogeographic relevance. While most pliosaurs were certainly extinct by this time, the clade including *Kronosaurus* and *Brachauchenius* survived well into the Late Cretaceous, thus the evaluation of this sauropterygian material from the same rocks suggests the Paja Formation of Colombia may be where some of the last pliosaurs and first elasmosaurs ever known occur. This project will set the stage for continued explorations of large-scale patterns in species diversity for other taxonomic levels for a better understanding of the consequences of the Jurassic-Cretaceous extinction on marine vertebrate faunas, and ultimately of the advent of today´s marine ecosystems.

Morphological analysis of a nectridean lepospondyl, *Diceratosaurus*, from Linton and Five Points, Ohio

Jamey H.M. Creighton[1] and Jason S. Anderson[2]

[1]Department of Biological Sciences, University of Calgary, 2500 University Dr. NW, Calgary, AB, T2N 1N4, Canada; jhcreigh@ucalgary.ca

[2]Department of Comparative Biology & Experimental Medicine, University of Calgary, 3330 Hospital Dr. NW, Calgary, AB, T2N 4N1, Canada; janders@ucalgary.ca

Lepospondyli is a group of small-bodied tetrapods traditionally including five Paleozoic groups: Microsauria, Lysorophia, Nectridea, Aistopoda, and Adelosondyli, united by the presence of elongate trunks and holospondylous vertebrae. However, more recent studies have shown these taxa show few consistent similarities and are likely a polyphyletic assemblage. For example, recent analyses have placed aïstopods deep on the tetrapod stem (with animals showing a progression from 'fish' to terrestrial tetrapod features) and Lysorophia and Microsauria (in part) with amniotes. Nectridea, which is thought to be quite basal in the early tetrapod phylogeny, has not yet been included in some of these studies. More information needs to be collected to test the interrelationships of nectrideans among early tetrapod groups. This study focuses on *Diceratosaurus*, a nectridean solely known from Linton and Five Points, Ohio. Latex peels of the skull roof and the palate are being analyzed and illustrated by using photography and light microscopy. Preliminary results suggest that *Diceratosaurus* comprises two distinct morphs that altogether range from 14–25 cm in skull length: a broad, round-snouted morph, and a small, narrow-snouted morph which has never been seen in nectrideans before. We test several hypotheses to explain this variation including ontogenetic change, polymorphism, and the presence of multiple species. Examining the smallest specimens, which are the narrow-snouted morphs, to the largest specimens which are the broad-snouted morphs, there seems to be no signs of an ontogenetic difference; the dermal ornamentation is organized with distinct pits and ridges, all bones in the skull roof are ossified, and the sutures are tightly closed in the smaller narrow-snouted morphs. This is not what one would expect if this were a juvenile form of *Diceratosaurus*. Although more work remains to be done documenting the anatomy of the palate, there are differences in the bones of the pre-orbital region of the skull and in the ornamentation around the tabular horn region. We believe multiple species to be the most likely explanation. The discovery of a second morph and these results could further support the conclusion that not only nectrideans, but lepospondyls as a group, are more diverse than originally thought.

A morphometric analysis of the turtle manus and its implications for the palaeoecology of extinct turtles

Thomas W. Dudgeon[1,2], Marissa C.H. Livius[3], and Jordan C. Mallon[3,4]

[1]Department of Ecology and Evolutionary Biology, University of Toronto, 27 King's College Circle, Toronto, ON M5S 1A1, Canada; thomas.dudgeon@mail.utoronto.ca
[2]Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, ON, M5S 1C6, Canada
[3]Department of Earth Sciences, Carleton University, 1125 Colonel By Drive, Herzberg Laboratories, Ottawa, ON, K1S 5B6, Canada; marissalivius@cmail.carleton.ca
[4]Beaty Centre for Species Discovery and Paleobiology Section, Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, ON K1P 6P4, Canada; jmallon@nature.ca

Among the most widely used predictors of palaeohabitat in fossil turtles is the skeletal proportions of the forelimb (humerus:ulna:manus), yet its application has been criticized on the grounds that the ternary diagrams used to represent those proportions neither control for phylogenetic effects, nor provide statistical likelihood estimates for palaeohabitat assignment. In this study, we apply linear statistical modeling to investigate the relationship between forelimb proportions and habitat among turtles, and use them to infer the palaeohabitats of problematic fossil species. We performed three morphometric analyses: the first focusing on the major components of the forelimb (humerus, ulna, and manus), the second on the manus proper (metacarpals, phalanges, and unguals), and the third combining these two datasets (humerus, ulna, metacarpals, phalanges, unguals). For each of these datasets, we used phylogenetic generalized least squares regression to extract the residuals for subsequent analysis, which are corrected for both size and the phylogenetic non-independence of taxa. Each set of residuals was subjected to a linear discriminant analysis (LDA) to determine the predictive accuracy of these measurements on habitat, which was divided into the following six bins: 'all bodies of water', 'moving or large bodies of water', 'primarily on land', 'primarily on land often in water', 'primarily on land seldom in water', and 'stagnant or small bodies of water'. We then used the discriminant functions to predict the palaeohabitats of the extinct *Basilemys variolosa, Palaeochersis talampayensis, Proganochelys quenstedti, Eunotosaurus africanus*, and *Odontochelys semitestacea*. The manual dataset and combined forelimb and manual dataset performed similarly well, with classification accuracies of approximately 82% and 83%, respectively. The forelimb dataset performed poorest, with a classification accuracy of just 72%. Based on these analyses, *Basilemys variolosa* is resolved as a fully terrestrial turtle that preferred dry environments with well-drained substrates; *Palaeochersis talampayensis* and *Proganochelys quenstedti* are similarly recovered as highly terrestrial; *Eunotosaurus africanus* was likely primarily terrestrial, occasionally venturing to the water; and *Odontochelys semitestacea* was likely semi-aquatic, spending significant periods of time both on land and in the water. Taken together, these results suggest that manual proportions provide a particularly powerful habitat proxy in turtles, and provides still further evidence that stem turtles were primarily terrestrial in nature.

A new plastomenine trionychid (Testudines: pan-Trionychidae) from the Milk River Formation of Southern Alberta (Cretaceous: Santonian)

Shauna C. Edgar[1], Don B. Brinkman[2], Michael J. Ryan[3], and David C. Evans[1,4]

[1]Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON, M5S 3B2, Canada; shauna.edgar@mail.utoronto.ca
[2]Royal Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, AB T0J 0Y0, Canada; don.brinkman@gov.ab.ca
[3]Department of Earth Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada; michaelj.ryan@carleton.ca
[4]Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, ON, M5S 1C6, Canada; d.evans@utoronto.ca

The pre-Campanian trionychid fossil record in North America comprises highly fragmentary specimens, which are often not identifiable beyond Pan-Trionychidae. Here, we describe a new species of plastomenine soft shell turtle based on a partial carapace and plastron (ROM 56647) from the Santonian Milk River Formation of southern Alberta, dated at approximately 84 Ma. Plastomeninae is characterized by the complete suturing of the plastral bones along the midline, a crescent-shaped entoplastron, and enlarged eighth costals. ROM 56647 has a unique combination of plastomenine characters (i.e., midline contact of posterior plastral elements, dorsoventrally long eighth costal) and apomorphies (emarginate nuchal, enlarged tubercles on the carapace, wide pygal notch with a straight anterior edge, and fused hyo-hypoplastron) that allows us to identify it as a new taxon. Phylogenetic analysis using parsimony places the new taxon within Plastomeninae as the sister taxon to a clade containing *Plastomenus*, *Helopanoplia* and *Hutchemys*. This phylogenetic position implies that *Aspideretoides foveatus*, *Atoposemys*, and *Gilmoremys*, all of which have a more basal position within Plastomeninae, and had ghost lineages extending at least to the Santonian. As the oldest pan-trionychid that can be described to the species level in North America, the new taxon represented by ROM 56647 offers novel insights into both the early evolution of trionychids in North America and the pre-Campanian biodiversity of turtles in what is now southern Alberta.

Life history of an archaic placental mammal, *Pantolambda bathmodon* (Placentalia, Pantodonta)

Gregory F. Funston[1], Paige E. dePolo[1], Sarah L. Shelley[1], John R. Wible[2], Thomas E. Williamson[3], and Stephen L. Brusatte[1]

[1]School of GeoSciences, University of Edinburgh, Edinburgh, UK; Gregory.Funston@ed.ac.uk
[2]Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
[3]New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA

The rise of mammals after the extinction of the dinosaurs remains one of the most enigmatic intervals in the evolution of mammals. A relatively sparse Paleocene fossil record and confusing interrelationships between taxa means that little is known of the evolution, ecology, and biology of these animals. As a result, the life history of these organisms is completely unstudied, despite likely playing a key role in the ability of these clades to rapidly proliferate and increase in body size in recovering ecosystems. However, intensive collection efforts in

the San Juan Basin of New Mexico in the last decade have drastically improved the record of many Paleocene mammals, and offer the first opportunity to address questions about the life history of these animals. Here, we present preliminary results of an in-depth paleohistological analysis of *Pantolambda bathmodon*, an early, possibly gregarious pantodont, using an ontogenetic series of individuals. Pantodonts were bizarre, herbivorous eutherians of unknown phylogenetic affinity, and were among the first mammal lineages to reach large body sizes in the Paleocene. In examining both dental and skeletal records of growth from the same individuals, including a juvenile still bearing deciduous teeth, our study is among the most comprehensive paleohistological analyses of any fossil mammal. This intensive approach allows for unprecedented insights into the life history of this species. Neonatal lines in the teeth indicate that the deciduous premolars and the first upper molar were erupted prior to birth, similar to precocious, nidifugous mammals today. Daily incremental lines in the enamel and dentine suggest rapid crown formation times (~45–70 days) and a gestation period of at least 15 weeks. A stress line in the postcranial bones, recording an anomalous decrease in growth towards the end of this individual's life, may represent the weaning event. In the absence of geochemical evidence, it is unclear which of two stress lines in the teeth corresponds to this event, but these lines occur roughly one and two months after birth, respectively. The weanling perished approximately 2.5 months after birth, weighing about 17 kg. An adult individual exhibiting severe wear on the dentition allows us to estimate maximum longevity in *Pantolambda bathmodon* at about 7 years. In comparison with life history data on living mammals from the PanTheria dataset, *Pantolambda bathmodon* had a gestation length and weaning duration below average for a placental of its adult body size (42 kg), but within the range of known variation. However, its lifespan was exceptionally short, falling outside the bounds of comparable living mammals. Together, these lines of evidence suggest a relatively rapid pace of life in *Pantolambda bathmodon*, despite its relatively large body size. Ongoing sampling of more individuals and geochemical analyses should allow for estimation of time to sexual maturity and help to confirm the identity of the weaning line, completing our picture of the life history of this pioneering species.

Revisiting the sedimentology and depositional evolution of the Cypress Hills Formation (Eocene – Miocene) in southwestern Saskatchewan, Canada: implications for vertebrate microfossil assemblages

Meagan M. Gilbert

Saskatchewan Geological Survey, Box 104, La Ronge, Saskatchewan, S0J 1L0 meagan.gilbert@gov.sk.ca

The Eocene to Miocene Cypress Hills Formation (CHF) spans 28 million years, and forms the conglomeratic caprock of the Cypress Hills plateau in southwestern Saskatchewan. The formation records one of the last major sedimentation events in the western plains of North America at a time when the world was undergoing major climate fluctuations. As well, the CHF contains the only high latitude, non-polar mammalian fossil assemblage known (Uintan to Whitneyan land mammal stages) in North America. Several palaeontologic studies have largely focused on taxa recovered from vertebrate micro and macrofossil sites, which have shed light on diversity and faunal turnover during this critical time. In contrast, the CHF has been the focus of few detailed geologic studies, reflected in the relatively poor constraint on the regional stratigraphy and timing of depositional events. Recently a field program has been underway to establish a depositional model for the CHF immediately north of Eastend, Saskatchewan augmented by fauna recovered from vertebrate microfossil sites. Preliminary results have illustrated a

complex network of multi-episode cut-and-fill braided channel deposits and their associated channel bars and floodplains. This complexity has serious implications for understanding the stratigraphic relationships between fossil sites and the strata they are recovered in, particularly regarding vertebrate microfossil assemblages. This ongoing study highlights the importance of high-level sedimentology and stratigraphy for understanding fossil assemblages in time and space, and will provide invaluable context for future paleontologic work undertaken in the region.

Dinosaur fossil discovery using remotely piloted aircraft systems and spectral mixture analysis

Sean Herridge-Berry[1], Caleb M. Brown[2], Derek R. Peddle[1], Brian J. Pickles[3], and Craig A. Coburn[1]

[1]Department of Geography & Environment, and Alberta Terrestrial Imaging Centre (ATIC), University of Lethbridge, Lethbridge, AB, T1K 3M4, Canada; s.herridgeberry@uleth.ca; derek.peddle@uleth.ca; craig.coburn@uleth.ca
[2]Royal Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, AB, T0J 0Y0, Canada; caleb.brown@gov.ab.ca
[3]School of Biological Sciences, University of Reading, Whiteknights, Reading, RG6 6EX, UK; b.j.pickles@reading.ac.uk

Prospecting for new fossil sites remains an integral part of palaeontological research. Given that fossil discoveries generally rely on exposed bedrock, the most productive areas are often associated with similar geophysical features, including low vegetation cover, high topographic relief, and high rates of erosion, such as badlands, deserts, and/or Arctic outcrop. These regions also tend to have limited transportation infrastructure, are remote and rugged, and can be geographically extensive in area, posing limitations to terrestrial access. Given these limitations, potential fossil-bearing areas may represent prime areas for remote sensing where imagery can be collected in a relatively short amount of time from platforms such as satellites, airplanes, helicopters, or remotely piloted aircraft systems (RPAS, a.k.a. drones). The sensors aboard these platforms measure the amount of solar radiation in different wavelengths as reflected by the ground surface to provide information about the unique reflectance patterns of the target. These technologies have revolutionized the acquisition of large-area georeferenced imagery useful for ecological interpretation and resource exploration. They may have utility in detecting exposed fossil resources that are indicative of a larger area (10–100 m), high-density (10–100 bones/m2) accumulations of large bones, representing monodominant or multi-taxic bonebeds. To date, the use of these aerial platforms in palaeontology has been minimal, and when used, has been restricted to mapping known fossil occurrences – primarily trackways such as in Petti et al. (2018). However, it remains to be tested if, and to what extent, remote sensing can perform in the original detection of these extensive fossil resources.

This research represents a laboratory and field-based proof-of-concept test for the remote sensing of fossil resources, specifically vertebrate bonebeds, using the Campanian-aged Dinosaur Park Formation (DPF), Dinosaur Provincial Park, Alberta, as a case study. The markers used in this study include weathered fossil bones and modern lichen colonies (*Xanthoria* sp.), which may preferentially colonize fossil bone relative to other substrates. Fossil bones can possess diverse microbial communities (Saitta et al. 2019), and a study of Antarctic Eocene fossils revealed colonisation by several lichen species (García et al. 2020). Distinct geological features such as palaeo-channels and point bar deposits may also represent markers to be detected.

Due to the small size of most fossil targets, Spectral Mixture Analysis (SMA), an advanced image processing technique, is being investigated as a sub-pixel scale analytical approach following some of the key SMA protocols developed by Peddle and Smith (2005). To test this, high-resolution spectral measurements of these characteristic fossil targets were collected in a controlled laboratory setting at the Alberta Terrestrial Imaging Centre (ATIC). Fossils, lichen-covered fossils, and geologic samples were loaned from the Royal Tyrrell

Museum of Palaeontology (RTMP) and provided representative examples of targets found from DPP for spectral measurement at ATIC.

Spectral measurements were acquired in the ATIC Remote Sensing Lab at the University of Lethbridge using an Analytical Spectral Devices (ASD) Fieldspec-3 Full-Range Spectroradiometer (350–2500 nm). Spectra to derive reflectance were acquired with reference to a calibrated white Spectralon panel (pressed polytetrafluoroethylene — PTFE). The spectra were post-processed and adjusted to account for multi-detector noise at sensor boundaries of 1000 nm and 1900 nm. Amongst the samples, there were four distinct patterns of reflectance: fossil bone, sediment, modern lichen, and teeth. This shows that these representative targets are sufficiently different spectrally and suitable for input to SMA for spectral separation with pixel-scale targets. These data provide a basis for laboratory spectral analysis and as a planned input for SMA of imagery from RPAS missions (described below). For example, we expect that the unique reflectance signatures of fossil bone and teeth, sediment, and lichen are suitable endmember spectra for input to SMA.

In September 2020, field deployment of a RPAS took place at DPP with ATIC, RTMP and Alberta Parks staff, and following COVID-19 protocols. Five sites were imaged at two altitudes (30 m and 100 m above ground level, or AGL) using two camera systems. Multispectral images were acquired using a MicaSense RedEdge-M five-band camera, with simultaneous RGB images acquired using a DJI X4S gimble-mounted camera. The multispectral camera captured images in five bands allowing data to be collected from the blue, green, red, near-infrared, and red-edge areas of the electromagnetic spectrum while the RGB camera acquired images in the blue, green, and red portions of the spectrum. After images were mosaicked using stitching procedures in Pix4D software, the resulting images had nominal ground sample distances as small as 0.8 cm at 30 m AGL.

Based on analysis of these remote sensing lab and RPAS products to date, the high spatial resolution imagery combined with the spectroradiometer data provides appropriate inputs to SMA. Using these data and algorithms together offers new opportunities for detecting fossil resources in the DPF and may have utility in other similar but more remote, extensive, and challenging fossil-bearing outcrops.

Literature Cited

García, R., G. Márquez, and C. Acosta Hospitaleche. 2020. Richness of lichens growing on Eocene fossil penguin remains from Antarctica. Polar Biology 43:2011-2019. DOI 10.1007/s00300-020-02761-9

Peddle, D.R., and A.M. Smith. 2005. Spectral mixture analysis of agricultural crops: Endmember validation and biophysical estimation in potato plots. International Journal of Remote Sensing 26:4959-4979. DOI 10.1080/01431160500213979

Petti, F.M., M. Petruzzelli, J. Conti, L. Spalluto, A. Wagensommer, M. Lamendola, R. Francioso, G. Montrone, L. Sabato, and M. Tropeano. 2018. The use of aerial and close-range photogrammetry in the study of dinosaur tracksites: Lower Cretaceous (upper Aptian/lower Albian) Molfetta ichnosite (Apulia, southern Italy). Palaeontologia Electronica 21:1-18. DOI 10.26879/845

Saitta, E.T., R. Liang, M.C.Y. Lau, C.M. Brown, N.R. Longrich, T.G. Kaye, B.J. Novak, S.L. Salzberg, M.A. Norell, G.D. Abbott, M.R. Dickinson, J. Vinther, I.D. Bull, R.A. Brooker, P. Martin, P. Donohoe, T.D.J. Knowles, K.E.H. Penkman, and T. Onstott. 2019. Cretaceous dinosaur bone contains recent organic material and provides an environment conducive to microbial communities. Elife 8:e46205. DOI 10.7554/eLife.46205

Feeding ecology of the Bearpaw Formation mosasaur community

Femke M. Holwerda

Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, T0J 0Y0, Canada; f.m.holwerda@gmail.com

The Campanian sediments of the Bearpaw Formation yield a rich marine fauna from the northern exposures of the Western Interior Seaway. Many well-preserved mosasaur skeletons, representing most of the mosasaur taxa from this geological unit in Alberta, including skulls and dentition, are housed at the Royal Tyrrell Museum of Palaeontology.

Good preservation of tooth-bearing bones not only allows for the study of tooth morphology, but also for analysis of dental microwear, or microscopic wear on dental surfaces, generated by tooth-tooth or tooth-food occlusion/abrasion, and geochemical analyses. Microwear is categorized as small scratches, large scratches (gouges) and pits.

The three most common mosasaurs from the collections were sampled for two-dimensional microwear: *Mosasaurus missourensis*, *Prognathodon* sp., and *Plioplatecarpus primaevus*. The most common and large mosasauroids, *Mosasaurus* and *Prognathodon*, show differences in microwear between their upper and lower jaws. *Mosasaurus missourensis* shows a high total and average number of small scratches in the premaxillary and maxillary teeth, and a low number in the dentary. *Prognathodon* sp. shows a large amount of pits in both upper and lower tooth rows, and a high number of gouges in the maxilla. As scratches indicate feeding on softer prey, and gouges show feeding on harder prey items, this could already reveal a difference in feeding ecology between these two large mosasaurs.

Teeth of the less common and smaller *Plioplatecarpus primaevus* also show a high average number of gouges and pits, in contrast to its small piscivorous tooth morphology. This could indicate regular feeding on ammonites and belemnites for this taxon.

Using Energy-Dispersive X-ray Spectroscopy (EDX) analysis as another independent line of evidence of mosasaur feeding in the Alberta Bearpaw Fm., the elements strontium, calcium and barium are measured on isolated teeth. *Mosasaurus missouriensis* plots on the resulting PCA scatterplot together with elasmosaurid plesiosaurs, hybodont and *Cretodus* sharks, indicating mainly piscivory and sarcophagy. *Prognathodon* sp. mainly plots together with sawfish, indicating durophagy. Finally, *Plioplatecarpus* plots away from both of the larger mosasaurs, and overlaps with hybodont sharks, possibly indicating piscivory.

This study hints at an efficient level of niche partitioning amongst the mosasaurs of the northern Western Interior Seaway. A follow-up study using isotopes and three-dimensional microwear analysis will seek to confirm these findings.

Osteohistology of a thescelosaurid (Dinosauria, Ornithischia) fibula from the Wapiti Formation (Campanian) of Northern Alberta: implications for diversity of growth strategies and osteohistological features within Thescelosauridae

Michael Naylor Hudgins[1], Phil R. Bell[2], Nicolás E. Campione[2], Federico Fanti[3], Robin L. Sissons[1], Matthew J. Vavrek[4], Derek W. Larson[5], and Corwin Sullivan[1,6]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; hudgins@ualberta.ca; robin.sissons@gmail.com; corwin1@ualberta.ca
[2]School of Environmental and Rural Science, University of New England, Armidale, NSW, 2351, Australia; pbell23@une.edu.au; campion@une.edu.au
[3]Dipartimento di Scienze della Terra e Geologico-Ambientali, Alma Mater Studiorum, Università di Bologna, 40216 Bologna, Italy; federico.fanti@unibo.it
[4]Cutbank Palaeontological Consulting, Grande Prairie, AB, T8W 0H6, Canada; matthew@matthewvavrek.com
[5]Royal British Columbia Museum, Victoria, BC, V8W 9W2, Canada; dlarson@royalbcmuseum.bc.ca
[6]Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 3S0, Canada

Bone histological studies have provided detailed information about the diversity of, and variation in, growth strategies, life history, and behaviour in non-avian dinosaurs. However, only a few osteohistological (i.e., analyses focusing on the microscopic structure and function of bones) analyses of Thescelosauridae have been conducted. Here we present new histological data from a partial fibula (UALVP 50999) of a thescelosaurid from the late Campanian (~73.5 Ma) Wapiti Formation of northern Alberta. The partial fibula consists of well-vascularized fibrolamellar and parallel-fibred bone with longitudinal and lamellar vasculature, as well as primary and secondary osteons, throughout. Extensive secondary remodeling occurred on the posteromedial margin of the section, likely due to biomechanical stresses from locomotion as the animal grew. Seven lines of arrested growth (LAGs) were deposited, suggesting that the individual was at least seven years old at the time of death. The individual likely reached sexual maturity based on prior growth models of reptilians and dinosaurs, although this is difficult to determine with certainty. The onset of sexual maturity in UALVP 50999 coincides with bone texture changes from the inner to outer cortex, and growth deceleration reflected in narrowing inter-LAG spaces towards the periosteum. However, the individual had not reached skeletal maturity at the time of death, based on extensive secondary remodeling and the absence of an external fundamental system. This inference is consistent with prior research indicating that dinosaurs reached sexual maturity before skeletal maturity. The histology of the partial fibula suggests that the growth rate of the Wapiti thescelosaurid was similar to that of *Haya*, *Jeholosaurus*, and *Oryctodromeus*, and faster than that of *Orodromeus*, but slower than that of *Hypsilophodon* and derived ornithischians. In UALVP 50999, an interval of rapid growth appears to have taken place following deposition of the fifth LAG, although growth abruptly slowed again with deposition of the last two LAGs. Some specimens of *Haya* and *Jeholosaurus* show evidence of a similar growth pattern, involving 'moderate' growth in early life, followed by a period of rapid growth, and then slow growth later in life. However, the increases and decreases in growth rate inferred from UALVP 50999 may also indicate changing environmental conditions, niche partitioning between juveniles and adults, or random variation in the individual's growth rate. The skeletal immaturity

of UALVP 50999 adds to the evidence, from previous histology-based age estimates for other taxa, that most small-bodied ornithischian specimens in the fossil record represent individuals that did not live to reach skeletal maturity. Whether this pattern results from an r-selected reproductive strategy in thescelosaurids, a taphonomic bias, or a random signal is unclear. A larger histological data set is necessary for future research addressing a range of fundamental questions pertaining to thescelosaurid palaeobiology, but the present analysis represents a step towards this goal and provides evidence that should prove useful in future studies of bone tissue variation and diversity of growth strategies among small-bodied ornithischians in general.

Impacts of Miocene tectonism and climate change on diversity dynamics of carnivoran and ungulate mammals in North America

Blue Hunter-Moffatt[1], and Danielle Fraser[2]

[1]Department of Earth Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6; bluehuntermoffatt@cmail.carleton.ca
[2]Palaeobiology, Canadian Museum of Nature, PO Box 3443 Stn "D", Ottawa ON K1P 6P4; dfraser@nature.ca

Across modern landscapes, tectonically active, topographically complex environments (e.g., mountain ranges) support greater mammalian biodiversity than tectonically quiescent lowlands at the same latitude. One possible explanation for topographic diversity gradients is that tectonic processes promote diversification of mammals by increasing habitat heterogeneity. Additionally, climate warming may increase species richness in mountainous regions as lowland taxa track their climatic niche to higher elevations. In this study, we assess the influence of landscape evolution, involving both tectonic and climatic change, on the diversity dynamics of Miocene carnivoran and ungulate faunas in North America. Using Capture-Mark-Recapture (CMR) methods and fossil occurrence data from the MioMap database, we calculated origination and extinction rates of carnivoran and ungulate species in five North American study regions with unique landscape histories.

CMR involves repeatedly sampling, marking, and releasing organisms thus creating an "encounter history" for each individual. In palaeobiology, occurrences of fossil species divided among discrete time bins comprise the encounter histories that are used to estimate the number of species present in each time bin, sampling probabilities, and diversification rates. Three regions, the Columbia Basin, the Rocky Mountains, and the Southwest (i.e., California, Arizona, New Mexico, Nevada), were tectonically active during parts of the Miocene. Two regions, the Great Plains and the Gulf Coast, were tectonically quiescent. We did not detect pulses of origination coincident with tectonic events in any active region, contra to our prediction. However, we found extinction peaks in the Rocky Mountains and Southwest during the Middle Miocene Climate Optimum. This is consistent with extinction of high elevation taxa during global warming, which is predicted for numerous high latitude taxa today. We used biogeographic stochastic mapping to test for rates of dispersal among regions and found that biogeographic processes during the Miocene were dominated by dispersal of species from the Great Plains to other study regions likely reflecting habitat tracking during climate change. Together, these results suggest that interactions between climate change and topographic complexity influence mammalian dispersal and extinction dynamics, but that tectonic activity alone has not promoted speciation of large mammals at least in North America.

New material of the oldest metamorphic salamander (Amphibia, Urodela) from the Middle Jurassic of China yields insights into palaeoecological disparity

Jia Jia[1,2,3], Jason S. Anderson[3], and Ke-Qin Gao[1]

[1]School of Earth and Space Sciences, Peking University, 5 Yiheyuan Road, Beijing 100871, China; jia_jia@pku.edu.cn; kqgao@pku.edu.cn

[2]State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS), 39 East Beijing Road, Nanjing, Jiangsu Province, 210008, China

[3]Department of Comparative Biology and Experimental Medicine, University of Calgary, 3330 Hospital Drive, Calgary, AB, Canada, T2N 4N1; janders@ucalgary.ca

Salamanders (total-group named Caudata; crown-group named Urodela) are a group of extant tailed amphibians that are ecologically diversified with individuals at adult stage living in water (aquatic), on land (terrestrial), in a tree (arboreal) or migrating between water and land (semiaquatic). How and when these ecological preferences differentiated among salamanders remains unclear because of a poor fossil record. The origin of Caudata was estimated by molecular studies to have occurred during the Late Paleozoic, whereas the geologically oldest salamander *Triassurus sixtelae* was documented from the Middle/Late Triassic (~230 Ma) in southwestern Kyrgyzstan. The next oldest known fossil records of salamanders are found from the Middle Jurassic Bathonian (~168–166) in several localities of Eurasia (UK, Russia, Kyrgyzstan and China). Most of these Middle Jurassic, and the only known Triassic, salamanders are stem members of Urodela as evidenced by the absence of the spinal nerve foramina in the atlas that characterize Urodela. Only five contemporary taxa have been found as basalmost urodeles, including *Kiyatriton krasnolutskii* from Siberia, Russia; 'Kirtlington salamander B' from Kirtlington, UK and three taxa (*Chunerpeton, Jeholotriton* and *Liaoxitriton daohugouensis*) from the Daohugou fossil locality in northern China. The morphological evolutionary histories of early salamanders are insufficiently understood because most Middle Jurassic or earlier taxa are represented either by immature specimens (*Triassurus*) or fragmentary/disarticulated bones (e.g., *K. krasnolutskii*), but the three taxa from China are represented by complete and articulated skeletons. Moreover, patterns of palaeoecological disparity among early salamanders remain unclear because all stem-group and most crown-group urodeles are neotenic, except *Liaoxitriton daohugouensis*, which represents the oldest known metamorphic salamander as evidenced by its moderate size, absence of internal and external gills, anterolaterally oriented palatal ramus of pterygoid, and extensively ossified limb structures.

To date, *Liaoxitriton daohugouensis* is known from three specimens from the Middle Jurassic Haifanggou Formation at the Daohugou fossil locality, Inner Mongolia, China. It was originally misclassified as congeneric with the Early Cretaceous *Liaoxitriton zhongjiani* from the Yixian Formation at the Xintaimen fossil locality, Liaoning Province, China, but this attribution raised doubts. Here we report a new, complete, and almost fully-grown specimen from the type locality. Micro-CT scanning and visual examination reveal details of the dermal skull roof, suspensorium, braincase, mandible, autopodium, and tail that were previously unclear. Five autapomorphies of this taxon are identified, including: parietal elongate; palatal process of pterygoid expanded; vomer expanded posteriorly, reaching close to anteroposterior ventral midpoint of cranium; cultriform process of parasphenoid shortened anteroposteriorly; and scapular blade shortened to slightly more than one-half width of coracoid. Our cladistic analyses based on a data matrix of 108 morphological characters (24% newly identified) and 22 taxa find that "*L. daohugouensis*" is crownward of *Linglongtriton* and is not the sister taxon to *L. zhongjiani*, which enable us to transfer "*L. daohugouensis*" into a new genus. Our results further identify "*L. daohugouensis*" and several Mesozoic taxa including *Linglongtriton*, *Liaoxitriton* sensu stricto, *Nuominerpeton* and *Regalerpeton* from northern China as stem members of the Asiatic salamander family Hynobiidae, and therefore predates the origination time of Hynobiidae previously estimated by molecular studies by at least 8 Myr.

The new specimen of "*L. daohugouensis*" has a wrinkled caudal fin and several features commonly seen in extant terrestrial hynobiids, including anteroposteriorly short skull, rounded snout, many vomerine teeth with vomerine teeth rows spanning most of the transverse dimension of the palate, and extensively ossified limb. The combination of these features suggests "*L. daohugouensis*" is a semi-aquatic at adult stage, a previously unknown palaeoecological preference among Mesozoic salamanders. Comparisons with both contemporary taxa (*Chunerpeton* and *Jeholotriton*) and other stem hynobiids, including the metamorphic and terrestrial *Nuominerpeton* and the neotenic *Regalerpeton* suggest that both life history strategies and ecological disparities have taken place by the Middle Jurassic Bathonian stage among urodeles.

This research was supported by National Science Foundation of China grants NSFC 41702002 and 41872008; and the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) 193111.

Vertebrate diversity trends and chrono-, litho-, chemo-, and cyclostratigraphy of the Late Cretaceous Manitoba Escarpment in Saskatchewan and Manitoba, Canada

Aaron A. Kilmury[1], Michelle P.B. Nicolas[2], and Kirstin S. Brink[1]

[1]Department of Geological Sciences, University of Manitoba, Winnipeg, MB, Canada; kilmurya@myumanitoba.ca; Kirstin.Brink@umanitoba.ca
[2]Manitoba Geological Survey, Winnipeg, MB, Canada; michelle.nicolas@gov.mb.ca

Stratigraphic correlations of Late Cretaceous Western Interior Seaway (WIS) deposits of the Manitoba escarpment with coeval deposits across North America have proven historically challenging due to poor surface exposures and the repeating nature of calcareous and non-calcareous, massive mudstone units bound by unconformable contacts. Stratigraphic work over the last two decades, including an improved lithostratigraphic framework, radiometric ages of several horizons, chemostratigraphic profiles of drillcore, and timing and duration estimates of transgressive-regressive mega cycles, have significantly improved the accuracy of regional correlations. A correlation chart consisting of several types of stratigraphic profiles was constructed and correlated with recently estimated trends of vertebrate generic diversity in order to provide insight into potential relationships between changes in relative sea level and vertebrate diversity over a broad temporal range (Cenomanian-Maastrichtian) from a biogeographically important, north-central locality along the WIS eastern margin.

Transgressive-regressive mega cycles are recognized in the litho- and chemostratigraphic profiles of the Upper Cretaceous deposits in Manitoba. Deposition of lithologic units with the highest estimates of vertebrate generic diversity, the Cenomanian Belle Fourche and early Campanian Pembina members, respectively coincide with an unnamed mega cycle referred to here as the Belle Fourche mega cycle and the Claggett mega cycle. A significant change in community structure is also apparent between the shark-dominated communities of the Belle Fourche Mbr and the marine reptile-dominated communities of the lower Pembina Mbr. Differences of average water depth between the mid-Cenomanian and early Campanian WIS could partially explain the apparent change in vertebrate community structure. Other likely contributing factors to the difference in community structure include the feeding habits of apex predators, with mainly piscivorous sharks and pliosaurs dominant in the mid-Cenomanian and mosasaurs with comparatively more diverse feeding habits dominant in the early Campanian. Taken together, these data are helping to elucidate the dynamics of community structure in the WIS through time.

The internal cranial anatomy of *Panoplosaurus mirus* (Dinosauria: Nodosauridae)

Marissa C.H. Livius[1], Hillary C. Maddin[1], Michael J. Ryan[1, 2], and Jordan C. Mallon[1, 3]

[1]Department of Earth Sciences, Carleton University, 1125 Colonel By Drive, Herzberg Laboratories, Ottawa, ON, K1S 5B6, Canada; marissalivius@cmail.carleton.ca; hillary.maddin@carleton.ca; michaelj.ryan@carleton.ca
[2]Palaeobiology Section, Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, ON, K1P 6P4, Canada
[3]Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, ON, K1P 6P4, Canada; jmallon@nature.ca

The heavily armoured and hyperossified skulls of ankylosaurs have presented challenges for the description of their internal anatomy which is, therefore, poorly known. The quality of data that can be obtained using computed tomography (CT) imaging has increased in recent years, providing a valuable tool for examining endocranial features that are otherwise inaccessible. Even so, highly detailed endocranial descriptions are available for only a very few ankylosaurid ankylosaurs; data for the sister clade, Nodosauridae, are also scarce. Here we present a digital reconstruction and description of the holotype skull for *Panoplosaurus mirus* (CMN 2759) and compare it to published data for other ankylosaur taxa. Preliminary results reveal that the endocast of CMN 2759 exhibits a less pronounced flexure between the main structures of the brain (forebrain, midbrain, and hindbrain) than has been reported in other nodosaurids and more closely resembles those of ankylosaurids. We also found convoluted nasal passages with distinct rostral and caudal loops that correspond to those described for the nodosaurid specimen ROM 1215 (variably attributed to *Panoplosaurus* or *Edmontonia*). Similarly convoluted nasal passages have also been described for the basal nodosaurid *Pawpawsaurus campbelli*. Although the nasal morphology of CMN 2759 is not as complex as that of the ankylosaurid *Euoplocephalus tutus*, this specimen demonstrates that highly sophisticated nasal passages were also present and more complex in nodosaurids than previously reported. These findings provide the first insights into the endocranial anatomy of *Panoplosaurus mirus*, and will facilitate comparisons with other ankylosaurs to assess both systematic and paleobiological trends within Ankylosauria.

First record of a parasaurolophin hadrosaur from the Oldman Formation of southern Alberta

Bradley D. McFeeters[1], David C. Evans[2,3], Michael J. Ryan[1], and Hillary C. Maddin[1]

[1]Department of Earth Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada; bradleymcfeeters@cmail.carleton.ca; michaelj.ryan@carleton.ca; hillary.maddin@carleton.ca
[2]Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, ON, M5S 2C6, Canada
[3]Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON, M5S 3B2, Canada; d.evans@utoronto.ca

Hollow-crested hadrosaurs (Hadrosauridae: Lambeosaurinae) are well represented in the Dinosaur Park Formation of Alberta, but are poorly known from older units, including the underlying Oldman Formation (Upper Cretaceous: Campanian). A new braincase from the Comrey sandstone (middle unit) zone at the Milk River Ridge Reservoir locality in southern Alberta represents the first diagnostic cranial material of an adult

lambeosaurine from the Oldman Formation. It shares with other lambeosaurines an anteroposteriorly short parietal and short supraoccipital-exoccipital shelf. Derived characters shared with *Parasaurolophus* include a thickened and steeply angled frontonasal contact, and the wide angle of the anterior frontals without a median cleft, allowing for the identification of the first definitive record of Parasaurolophini in the Oldman Formation. However, in contrast to a previously described adult *Parasaurolophus* braincase from the Dinosaur Park Formation, the nasal contact of the frontal lacks the pronounced posterodorsal extension that underlies the posteriorly projecting crest. The posterior margin of the contact has only a small vertical projection, resembling the condition described in juvenile *Parasaurolophus*, despite the large size and fused interfrontal contact of the Milk River Ridge Reservoir braincase, indicating its adult ontogenetic status. This difference may be attributable to heterochrony, with the ancestral adult development of the nasofrontal contact being attained in the juvenile stage of the stratigraphically higher form. As one of the stratigraphically lowest records of the clade Parasaurolophini, the Milk River Ridge Reservoir specimen is a significant source of new information concerning the timing and process of this clade's phylogenetic and morphological divergence from other derived lambeosaurines.

Palaeobiodiversity statistics and paleoenvironmental implications of microvertebrate localities from the Frenchman Formation (latest Cretaceous, Maastrichtian) of Saskatchewan, Canada

Jack R. Milligan[1], and Emily L. Bamforth[1,2]

[1]Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK, S7N 5E2; jrm451@mail.usask.ca
[2]Royal Saskatchewan Museum, *T. rex* Discovery Centre, Eastend, SK, S0N 0T0; emily.bamforth@gov.sk.ca

The latest Mesozoic rocks of Chambery Coulee in southwest Saskatchewan have offered insight into the paleobiodiversity and paleoenvironment leading up to the end-Cretaceous (K-Pg) mass extinction event. The late Maastrichtian (Lancian) Frenchman Formation, coeval with the Hell Creek and Lance formations in the USA contain a mixture of fluvial-floodplain and terrestrial paleoenvironments less than 20 m below the K-Pg boundary. These strata are well-known for producing notable specimens of large trionychid turtles, as well as large non-avian dinosaurs including a large specimen of *Tyrannosaurus rex* (RSM P2523.8) from Chambery Coulee. Within the vicinity of the *T. rex* site, there are microvertebrate fossil localities that contain an assemblage of taxa useful in paleoecological studies. Here we present the alpha and beta diversity statistics from several microvertebrate sites found within Chambery Coulee including the 'Kangaroo Down,' 'Bingo,' 'Hairpin,' and 'West-point' sites. Analysis of the sedimentary stratigraphy and biodiversity statistics were integrated together to determine the paleobiodiversity patterns of these microvertebrate sites and how the paleoenvironment reflects patterns of diversity at the regional level of Chambery Coulee immediately prior to the K-Pg mass extinction event. A ~9.5 m stratigraphic section at the Kangaroo Down site was correlated with previously studied sections at Hairpin, Bingo, and West-point. The Kangaroo Down and Bingo sites are higher in section than the Hairpin and West-point sites with the former being interpreted as low energy inland fluvial environments and the latter being interpreted as higher energy coastal environments. Raw abundance data were used to calculate alpha diversity indices including Chao-1 and Jackknife-2, and occurrence data were used to calculate beta diversity indices including the Bray-Curtis similarity and Whittaker's global beta diversity. When we compare the statistics of each of the Chambery Coulee microvertebrate sites, we find a high diversity of microvertebrates represented across all the

sites we studied after accounting for preservation bias and collection methods. The Kangaroo Down and Bingo sites appear to include a high abundance and greater occurrence of terrestrial taxa including salamander and trionychids (soft-shelled turtles), and semiaquatic taxa including *Champsosaurus*, whereas the Hairpin and Westpoint sites seem to include a high abundance and higher occurrence of aquatic taxa including *Myledaphus* and *Lepisosteus*. This suggests that paleobiodiversity statistics including alpha and beta diversity based on abundance and occurrence data can be used as a probable measure for discerning microhabitats at stratigraphically similar microvertebrate sites within a larger paleoenvironment. This will help elucidate biodiversity patterns across a wide range of taxa in Chambery Coulee during the time just before to the K-Pg mass extinction event.

A bird coracoid from the Horseshoe Canyon Formation (earliest Maastrichtian) of Alberta, Canada

Sydney R. Mohr[1], Gregory F. Funston[2], and Thomas A. Stidham[3]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada; smohr@ualberta.ca
[2]School of GeoSciences, University of Edinburgh, Edinburgh, UK; Gregory.Funston@ed.ac.uk
[3]Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; presbyornis@gmail.com

A new fragmented left avian coracoid represents the first confirmed avian skeletal element from the early Maastrichtian (71.8–71.5 Ma) of the Horseshoe Canyon Formation of Alberta, Canada. This specimen also represents one of the largest fossil bird coracoids found in the province. A number of features, including a prominent acrocoracoid process and a well-defined procoracoid process, places this specimen within the Ornithurae. In addition to several neornithine-like features, it retains numerous ornithurine plesiomorphies, and this mosaic of traits indicates it is unlikely to represent a neornithine bird. As its fragmentary nature prevents a specific diagnosis, we therefore refer to it here as Ornithurine H (UALVP 59403). This specimen bears particular resemblance to four unassigned ornithurine coracoids from other Campanian and Maastrichtian localities in North America, all of which share numerous distinctive traits not found in other contemporaneous ornithurine coracoids. These include a shallow and weakly-defined triangular scapular cotyle, a humeral articular facet positioned lateral to the scapular cotyle, and a prominent, hooked procoracoid process. However, several features including its larger body size (~3.0 kg), a large supracoracoideus nerve foramen situated midway on the coracoid shaft, and a dorsally-projecting caudal rim of the scapular cotyle distinguish this specimen from other coracoids and indicate that Ornithurine H likely represents a new taxon. The projecting rim of the cotyle and laterally-oriented humeral articular facet are also present in the coracoid of the Turonian ornithurine *Ichthyornis dispar*, underscoring the distinct combination of features that characterizes Ornithurine H. Whereas this new specimen adds to the growing list of North American fossil birds represented primarily by isolated and incomplete material, it nevertheless expands on our understanding of early Maastrichtian paleobiodiversity in Alberta, and provides further evidence of a widespread and diverse assemblage of ornithurine birds throughout the Late Cretaceous of North America.

A quantitative analysis of morphological variation in dentition among Thescelosauridae with implications for thescelosaurid palaeoecology, macroevolution, and microsite identification

Nathaniel E.D. Morley[1], Michael Naylor Hudgins[1], Caleb M. Brown[2], Philip J. Currie[1], Han Feng-Lu[3,4], and Corwin Sullivan[1,5]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; nmorley@ualberta.ca, hudgins@ualberta.ca, pjcurrie@ualberta.ca, corwin1@ualberta.ca
[2]Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; caleb.brown@gov.ab.ca
[3]School of Earth Sciences, China University of Geosciences, Wuhan, 430074, China; hanfl@cug.edu.cn
[4]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, China; hanfl@cug.edu.cn
[5]Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 3S0, Canada; corwin1@ualberta.ca

Thescelosauridae is a poorly studied clade of small, herbivorous ornithischians that existed from the Aptian until the end of the Cretaceous in Asia and western North America. Although fossils of these gracile taxa are generally rare, isolated thescelosaurid teeth are common at microfossil sites. However, due to their generalized morphology, their teeth are easily confused with those of other contemporaneous small-bodied ornithischians. We use twelve linear measurements to document morphometric variation among the unworn, heterodont teeth of various thescelosaurid taxa based on teeth preserved in identifiable skeletons of *Haya griva, Jeholosaurus shangyuanensis, Parksosaurus warreni, Thescelosaurus neglectus, Thescelosaurus* sp. (SDSM 7210; formerly *Bugenosaura*), and *Zephyrosaurus schaffi*. In a principal components analysis (PCA) of the measurements, PC1 and PC2 accounted for 77% and 12% of the total variation, respectively. In a canonical variates analysis (CVA), CV1 and CV2 explained 73% and 12% of the separation among the groups, respectively, and an associated confusion matrix correctly classified 92% of the teeth. This accurate confusion matrix classification holds promise for the identification of isolated thescelosaurid teeth using morphometrics. A PERMANOVA showed statistically significant separation among thescelosaurid taxa ($F = 3.72$, $p(a) > 0.01$). In both the PCA and the CVA, *P. warreni, T. neglectus, T*. sp. and *Z. schaffi* clustered closely together with significant overlap among the premaxillary, maxillary, and dentary teeth. However, the premaxillary teeth of *H. griva* and maxillary teeth of *J. shangyuanensis* formed discrete clusters on the same plots. The morphometric overlap among the North American taxa (*P. warreni, T. neglectus, T.* sp. and *Z. schaffi*) suggests that they may have shared similar feeding strategies and dietary preferences. In contrast, the disparate morphologies of the Asian taxa (*H. griva* and *J. shangyuanensis*), relative both to the North American taxa and to each other, suggest that they had divergent feeding strategies and dietary preferences. This morphometric analysis should facilitate the identification of thescelosaurid teeth from microsites and the testing of hypotheses on the biogeography, macroevolution, palaeoecology, and temporal distribution of Thescelosauridae using microsite data.

New data on the distal tarsals of Ornithomimidae provided by a partially articulated specimen from the Kaiparowits Formation (late Campanian) of southern Utah, USA

Rachel E. Nottrodt[1] and Andrew A. Farke[2]

[1]Department of Geoscience, University of Calgary, 2500 University Dr. NW, Calgary, AB, T2N 1N4, Canada; rachel.nottrodt@ucalgary.ca
[2]Raymond M. Alf Museum of Paleontology at The Webb Schools, 1175 West Baseline Road, Claremont, CA, 91711, USA; afarke@webb.org

The ankle in non-avian theropod dinosaurs consists of the astragalus and calcaneum proximally and a distal series of tarsal bones capping the metatarsals. Nearly all theropod taxa have only two distal tarsals, identified as distal tarsals 3 and 4. Historically, the morphology and anatomical relationships of these distal tarsals is uncertain in ornithomimosaurs due to lack of preservation and/or disarticulation, but even in articulated specimens, the bones can be difficult to access. A previously undescribed, partially articulated ornithomimid hind limb fossil from the Kaiparowits Formation (late Campanian) of southern Utah, USA, uniquely preserves both distal tarsals completely and in articulation with their surrounding elements. This is the first ornithomimid specimen from North America for which the distal tarsals can be described in comprehensive detail from multiple views. Distal tarsal 3 contacts both metatarsals II and III, whereas distal tarsal 4 contacts only metatarsal IV. Distal tarsal 4 also shows a tab-like process that projects laterally. Comparison of the new fossil specimen with other ornithomimosaurs shows that distal tarsals in Ornithomimosauria can be generalized as: i) paired, representing distal tarsals 3 and 4; ii) not fused to one another or to the proximal metatarsals; and iii) proximo-distally compressed. Furthermore, tarsal morphology and position across Ornithomimosauria vary in: i) shape of the posterior surface of distal tarsal 3; ii) antero-posterior position of the distal tarsals relative to the proximal ends of the metatarsals; iii) extent of distal tarsal coverage of the proximal metatarsal surfaces; and iv) presence of a lateral flange on distal tarsal 4. As the first ornithomimid specimen from North America to reveal both the proximal and distal surfaces of both distal tarsals, and one of the very few ornithomimids for which tarsal morphology can be seen in articulation from multiple views, this fossil shows the importance of articulated specimens for tracking tarsal evolution and variation.

New shallow snouted species of *Velociraptor* sheds light on intraspecific variation in *Velociraptor mongoliensis* and possible niche partitioning between species

Mark J. Powers[1], Mark A. Norell[2], and Philip J. Currie[1]

[1]Department of Biological Sciences, University of Alberta, CW-405 Biological Sciences Building, Edmonton AB, T6G 2E9, Canada; powers1@ualberta.ca; pjcurrie@ualberta.ca

[2]Macaulay Curator, Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA; norell@amnh.org

Despite being some of the largest representatives of Dromaeosauridae, eudromaeosaurians were small to medium sized predators in their respective ecosystems. Predatory adaptations such as serrated teeth, recurved claws, and a specialized sickle claw on the end of their second pedal digit would have allowed them to flourish in small- to medium-sized predator niches, as well as providing variability among close relatives. This makes understanding their phylogenetic relationships and morphological disparity of utmost importance to addressing broad scoping questions about dinosaur ecology. Unfortunately, in North America the fossil skeletons of dromaeosaurids are generally rare and are largely incomplete when found. This has been largely attributed to preservation biases for large-bodied animals in many depositional environments (particularly fluvial systems). Strata with dinosaur fossils in the Djadokhta Formation of Mongolia are represented by aeolian deposits associated with sand accumulation or large dune collapses. Within this depositional environment, small-bodied vertebrates are preserved more readily. Half a dozen skeletons, varying between 60 to 95% completeness, and numerous more isolated specimens have been collected and assigned to *Velociraptor mongoliensis*. Referral of these specimens to *V. mongoliensis* has been based on general morphological similarity and paleogeographical provenance and variation has been assumed to be intraspecific without any formal analysis. The holotype of *V. mongoliensis* was discovered at the Flaming Cliffs locality in Mongolia. However, most referred specimens come from further west, at or near the Tögrögiin Shiree locality.

One nearly complete specimen collected from the Flaming Cliffs locality in 1995 (MPC-D 100/982), has morphological features distinct from all other specimens referred to *V. mongoliensis* in possessing an antorbital region of the skull (snout) that is distinctly shallow dorsoventrally. Examination of the temporal region of the skull and postcranium, reveals at least four features distinct from other specimens referred to *V. mongoliensis*. These include an anteriorly abbreviated cerebellar fossa with an elongate olfactory canal, a lacrimal notch of the frontal that is more vertically oriented as opposed to transverse in *V. mongoliensis*, a subvertical ridge on the ilium anterodorsal to the acetabulum. This specimen has been referred to *V. mongoliensis* in several previous publications and its morphological differences from *V. mongoliensis* specimens were suggested to be individual variation; however, despite the striking profile of the skull of MPC-D 100/982 no tests of variation were performed.

Up to 15 linear measurements were taken from velociraptorine and non-velociraptorine eudromaeosaurian maxillae — a highly complex and diagnostic element within eudromaeosaurians — to perform Principal Component Analysis (PCA) and examine phenetic clustering within morphospace. The results show that MPC-D 100/982 falls well outside the range of variation observed in other specimens referred to *V. mongoliensis*. The degree to which MPC-D 100/982 varies from *V. mongoliensis* specimens is even greater than that observed for the holotype of *Velociraptor osmolskae* (IMM99NM-BYM-3/3A), supporting the separation of MPC-D 100/982 on a species level. A notable linear spread of *V. mongoliensis* specimens in the PCA shows a positively allometric trend, with smaller specimens plotting more negatively along PC 1 and PC 2 and may represent an ontogenetic shift. To examine possible ontogenetic trends in *V. mongoliensis* further, linear regressions of individual maxillary variables with a high degree of taxonomic variance (maxillary height, anterior ramus length, antor-

bital fossa length, and lateral lamina height below the antorbital fossa anteriorly) were performed. These features show positive allometry in relation to maxillary length across *Velociraptor mongoliensis* specimens. MPC-D 100/982 does not fit with these trends and falls well outside the 95% confidence regression intervals. MPC-D 100/982 possesses a long antorbital fossa, a distinct maxillary fenestra morphology, and the most elongate (high length/height ratio) snout of any eudromaeosaurian known. Discrete morphological characters and morphometric analyses support separating MPC-D 100/982 from *V. mongoliensis* as representing its own distinct species. Variation in the snouts of *V. mongoliensis* and the new species may have allowed them to have some overlap in home ranges with reduced competition.

In modern terrestrial ecosystems, snout shapes are shown to often correlate to preferred prey size. This is most notably demonstrated in canids, a clade with carnivorous members of similar size to most eudromaeosaurians. The advantage of snout shapes in prey capture, for canids and many other vertebrates, is supported by functional morphology studies. Such studies have demonstrated that longer jaws are more effective for rapid biting and limited power, whereas stout jaws perform more efficiently in biting and handling. The former being more effective at catching small-bodied, fast-moving prey, while the latter is better for taking prey of larger body size that may put up more of a fight. Although we cannot observe the preferred prey of eudromaeosaurians directly, we can use the principles of functional morphology relating to jaw biomechanics, examine the faunal composition of ecosystems containing eudromaeosaurians, and make preliminary hypotheses about drivers for variation in snout shape within the clade through time and space. Small-bodied vertebrates are common in the Djadokhta Formation and the shallow condition in the rostrum of the new species of *Velociraptor* may have been an adaptation for specializing on these prey items. Conversely, *V. mongoliensis* possessed a deeper snout that became deeper as they grew and may have allowed members of this species to have a more diverse diet as suggested by the 'Fighting Dinsaurs' specimen (a *Protoceratops* and *V. mongoliensis* locked in combat)

Reconstructing life history of the sabre-toothed cat *Smilodon fatalis* using bone histology

Ashley R. Reynolds

Royal Ontario Museum, Department of Natural History, 100 Queen's Park, Toronto, ON, M5S 2C6, Canada, and University of Toronto, Department of Ecology and Evolutionary Biology, 25 Willcocks St, Room 3055, Toronto, ON, M5S 3B2, Canada; ashraereynolds@gmail.com

The life history strategy (e.g., growth rate, time to maturity) of an organism is a fundamental aspect of its biology that may be correlated with other ecological traits such as the degree of sociality exhibited by a species. However, assessing the life history strategy of extinct vertebrates is difficult because their growth and behaviour must be estimated using limited material, usually hard tissues. Osteohistology, the histological study of bone, is increasingly being used by palaeobiologists to study life history strategies in extinct vertebrates (specifically, assessing time to maturity using growth curves), though there has historically been a heavy focus on reptiles. Studies of mammalian osteohistology have become more common, but the rigorous mathematical methods for growth curve reconstruction used for reptiles have not been adequately tested in any major mammalian group. The purpose of this study was to test the viability of these methods on extant felids and reconstruct the growth of the sabre-toothed cat *Smilodon fatalis* using osteohistological data. Specifically, two hypotheses were tested relating to the palaeobiology of *S. fatalis*: that it was not as sexually dimorphic as extant felids and that it was social.

Age and weight data were collected from wild and captive individuals from 71 extant species in the carnivoran suborder Feliformia, from which growth curves were calculated. Additionally, osteohistology of the extant lion (*Panthera leo*) and tiger (*Panthera tigris*), the two extant felids closest in body mass to *S. fatalis*, were documented. To conduct growth curve reconstruction for *S. fatalis*, 20 femora from Pit 3 of the Rancho La Brea tar pits were thin sectioned at the minimum circumference of the diaphysis and lines of arrested growth (LAGs) were counted and their circumferences measured. Growth curves for extant feliforms and *S. fatalis* were created using the best-fit model from the Richards family of growth models, as determined using the Akaike Information Criterion. Curves generated for extant felids perform well in capturing the overall pattern of growth typical of a species but tend to overestimate body mass at birth. Sexual dimorphism in adult body mass is common among extant feliforms, with the predominant mode of sexual dimorphism being male-biased. The age at which adult body mass is reached is positively associated with large adult body mass, while maximum daily growth rate (kg/day) is negatively associated with social behaviour, such that social species like *P. leo* have a lower maximum daily growth rate than solitary species like *P. tigris*. Collectively, these results suggest that sex differences in body mass and the varying correlates with growth rate should be considered in the analysis of *S. fatalis* growth. Osteohistology of *P. leo* and *P. tigris* femora indicate that lines of arrested growth (LAGs) are deposited during femoral growth and may be reliably used to determine approximate age at death and growth curves. *S. fatalis* femora classified as juvenile never had more than two LAGs preserved, and adults had a variable number of LAGs greater than two. Specimens with three or more preserved LAGs were included in a growth curve reconstruction using a mixed-effects process-error Richards growth model. There is a large amount of variation in the adult body mass of the sabre-toothed cat, ranging from 160 to 255 kg, suggesting that these cats may have showed a similar degree of sexual dimorphism in body mass as extant felids. Growth periods were prolonged relative to extant big cats, with individuals taking around five years to reach adult body mass. Comparatively, asymptotic body mass is reached in *P. leo* and *P. tigris* at 2.4 and 1.8 years, respectively. Maximum daily growth rates in *S. fatalis* are lower than in *P. leo* and *P. tigris*. This may indicate gregarious social behaviour in the sabre-toothed cat. Additionally, such low growth rates and long time to maturity are known to increase risk of extinction in extant animals. This should therefore be explored as a contributing factor to the end-Pleistocene extinction of *S. fatalis*. Overall, this study has produced the first growth curve for any fossil carnivoran, and the methods used provide a framework within which the evolution of life history strategies in felids can be examined.

Identifying competitive exclusion in the vertebrate fossil record: lessons from early vertebrate morphometrics

Bradley Scott and Philip Anderson

101 Shelford Vivarium, 608 East Healey Street Champaign, IL 61820, USA; brscott2@illinois.edu; andersps@illinois.edu

Competition with gnathostomes is the most common hypothesis for the extinction of the ostracoderms (Janvier 1996; Long 2011); however, it is not clear whether competition between clades is even testable in the fossil record (Purnell 2001). We review different qualitative and quantitative methods for differentiating competition from alternative hypotheses of extinction and whether competition between gnathostomes and agnathans, specifically, can be rejected using the fossil record. Competition in the fossil record is often recognized by the appearance of one taxon followed by the disappearance of another morphologically similar taxon in the same geographic region. As one taxon increases in abundance the other taxon should decrease (Tilman 1987; Purnell 2001; Anderson et al. 2011). Explicitly this is competitive exclusion (e.g., Krause 1986). Competitive exclusion can only include co-existence for an ecologically brief time, because lengthy coexistence of two taxa followed by the disappearance of

one taxon requires cause beyond presence of the remaining taxon. The problem with hypothesizing competitive exclusion as a cause of extinction is that patterns in the fossil record attributed to competitive exclusion are nearly identical to extinction of an incumbent followed by invasion by a new species (replacement), unless there is fine spatial and temporal resolution of first and last appearance of each taxon. Character displacement (changes in each taxon so they are less similar over time) is another method for identifying hypothetical competition between taxa (Tyler and Leighton 2011); however, character displacement is not suitable as a test of competition as a cause of extinction because it cannot reject predation, environmental changes or other alternative causes of extinction. Early vertebrate fossil bearing sequences rarely possess the temporal and spatial resolution necessary to reject replacement or coexistence between taxa, and even partially complete specimens are too rare to test for character displacement. Even if alternatives to competition cannot be rejected, rejecting competition may still be feasible. Methods for rejecting competition in the fossil record will rely on clear definitions of competition. One challenge is that ecological definitions of competition are rarely explicit and are often broadly inclusive of any negative interactions between two taxa (Tilman 1987). In order to create falsifiable criteria for competition with broad utility in this study, we constrain our definition of competition to the following: the use of the same resources (food or habitat) by more than one taxon in the same place at the same time, distinct from predation, bioengineering, or other indirect negative interactions. Under this definition, competition between two or more taxa can be rejected if any of the following are true: 1. Taxa are not present at the same time, 2. Taxa are not present in the same place, 3. Taxa do not use the same habitat, or 4. Taxa do not consume the same food. Identifying criteria 1 and 2 depends on the temporal and spatial resolution of the fossil record. While criteria 3 and 4 can never be known for certain in fossil taxa, they can be estimated using functional morphology and biomechanics. Neontological studies have shown competition is often stronger between morphologically similar taxa and weaker between morphologically different taxa (e.g. Montoya and Burns 2007; Adams 2004). If two taxa are sufficiently different from each other, then competition can be rejected. We present preliminary morphometric analysis of ostracoderms and early gnathostomes with discussion of how we intend to establish a standard for morphological difference sufficient to reject competition among early vertebrates. Our standard will be based on comparison with ecomorphology in extant sharks (Neoselache). By rejecting competition, we can focus on alternative hypotheses, as well as narrow the range of taxa for which extinction due to competition is a plausible hypothesis.

Literature cited

Adams, D.C. 2004. Character displacement via aggressive interference in Appalachian salamanders. Ecology 85:3664–3670.

Anderson, P. S. L., M. Friedman, M.D. Brazeau, and E.J. Rayfield. 2011. Initial radiation of jaws demonstrated stability despite faunal environmental change. Nature 476:206–209.

Janvier, P. 1996. Early vertebrates. Clarendon Press, Oxford, 408 pp.

Krause, D.W. 1986. Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America; pp. 95–117 in K.M. Flanagan, and J.A. Lillegraven (eds.). Contributions to Geology Special Paper 3, Vertebrates, Phylogeny, Philosophy. University of Wyoming, Laramie, WY.

Long, J. 2011. The Rise of Fishes—500 Million years of Evolution. 2nd ed. John Hopkins University Press, Baltimore, MD, 224 pp.

Montoya, I., and K.C. Burns. 2007. Community-wide character displacement in New Zealand skinks. Journal of Biogeography 34:2139–2147.

Purnell, M. A. 2001. Scenarios, selection, and the ecology of early vertebrates; pp. 188–208 in P.E. Ahlberg (ed.). Major events in early vertebrate evolution. Taylor & Francis, London, UK.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. The American Naturalist 129:769–774.

Tyler, C.L., and L.R. Leighton. 2011. Detecting competition in the fossil record: support for character displacement among Ordovician brachiopods. Paleogeography, Paleoclimatology, Paleoecology 307:205–217.

A hesperornithiform (Avialae: Ornithuromorpha) from the Upper Cretaceous Nemegt Formation (lower Maastrichtian) in Mongolia

Tomonori Tanaka[1, 2], Yoshitsugu Kobayashi[3], Yuong-Nam Lee[4], Robin Sissons[5], Michael Ryan[6], Tsogtbaatar Chinzorig[7], and Khishigjav Tsogtbaatar[8]

[1]Tamba Dinosaur Fossil Lab, 1110, Tanigawa, Sannan, Tamba, Hyogo, Japan; tomotanaka2020@gmail.com
[2]University of Hyogo, Yayoigaoka 6, Sanda, Hyogo, Japan
[3]Hokkaido University Museum, Kita10, Nishi 8, Sapporo, Hokkaido, Japan; ykobayashi@museum.hokudai.ac.jp
[4]Seoul National University, Bldg #25-1, Rm #510, 1 Gwanak-ro, Gwanak-gu, Seoul, Korea; ynlee@snu.ac.kr
[5]University of Alberta, Edmonton, Alberta, T6G 2E9, Canada; robin.sissons@gmail.com
[6]Carleton University, 2115 Herzberg Laboratories, Ottawa, Ontario, K1S 5B6, Canada; michaelj.ryan@carleton.ca
[7]North Carolina State University, 121 West Jones Street, Raleigh, North Carolina, 27601, USA; ctsogtb@ncsu.edu
[8]Institute of Paleontology of Mongolian Academy of Sciences, Chingeltei district-4, Sambuu Street, Ulaanbaatar-14201, Mongolia; tsogtmondin@gmail.com.

Hesperornithiforms have been predominantly reported from the marine Cretaceous deposits of the Western Interior Seaway of North America, although sparse records of this group have also been reported from fluvial deposits in Asia and North America especially from the Maastrichtian. Because Asian hesperornithiform fossils are extremely rare compared to North American specimens, the diversity of Asian taxa remains unclear. Here, we report a complete right tibiotarsus (KID 310) of a hesperornithiform from the inner continental fluvial deposits of the Nemegt Formation (lower Maastrichtian) in the Gobi Desert of southwestern Mongolia, which was collected in 2008 during the Korea-Mongolia International Dinosaur Expedition. The proximal tarsals (the astragalus and the calcaneum) are completely fused to the distal epiphysis, indicating that it is an adult individual. It has a fibular crest extending to the mid-shaft and a laterally angled proximolateral articular surface. These characters are only seen in Hesperornithiformes. A shallow tibial incision further suggests the specimen can be assigned as a non-hesperornithid hesperornithiform. Although the phylogenetic position of KID 310 within the clade of Hesperornithiformes is ambiguous due to its preservation as an isolated bone, it presents unique morphological characters such as the lateral margin of the cnemial crest being pointed and expanded laterally, and the fibular crest being remarkably expanded laterally. However, it is not clear if it is a new taxon because two other hespeornithiforms (*Judinornis nogontsavensis* and *Brodavis mongoliensis*) from the same formation do not preserve the tibiotarsus. The body size of KID 310 is estimated to have been similar to that of *Brodavis mongoliensis*, which is one of the smallest hesperornithiforms known. Inland hesperornithiforms in the Maastrichtian such as *Judinornis nogontsavensis, Brodavis mongoliensis, Brodavis americanus,* and *Brodavis baileyi* have smaller body sizes in comparison to the contemporary taxa from marine deposits (e.g., *Asiahesperornis* sp. and *Canadaga* sp.), indicating that hesperornithiform body sizes maybe related to their habitat environment (freshwater or marine).

A kinetic model of the palaeognath ribcage with implications for understanding avian ventilation

Yan-yin Wang[1] and Corwin Sullivan[1,2]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; yanyin@ualberta.ca; corwin1@ualberta.ca

[2]Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 3S0, Canada,

In respiratory biology, ventilation is typically regarded as the process of transporting gas between the respiratory organ and the external environment. Scholars have acquired extensive knowledge of many aspects of ventilation in archosaurs, including the anatomy of respiratory organs, the activity patterns of relevant muscles, and the kinematics of the ribcage during ventilation. However, the kinetic forces and moments involved in ventilation have been addressed in few studies, and most of these have been two-dimensional in scope and have focused on only a portion of the thorax. A three-dimensional kinetic model can examine the thorax comprehensively and has the potential to incorporate knowledge from other studies of respirations.

Here we present a kinetic model of the paleognathic ribcage to represent the condition of the flightless birds. The skeletal elements were created by scanning the disarticulated thoracic bones of an ostrich using a FlexScan 3D surface scanner. The model was set up for analysis in Autodesk Maya and SIMM (Software for Interactive Musculoskeletal Modelling). The kinematics of skeletal elements were described in terms of three kinematic rotations ('caliper', 'bucket handle', and 'pump handle') around the relevant joint centres, whose positions and orientations could only be estimated but were consistently positioned using anatomical landmarks in both Maya and SIMM. The muscles of the left thorax were modelled as a total of 122 muscle vectors, based on dissection of an emu and avian anatomical literature . Most hypaxial muscles have broad insertions on the ribs and cannot be accurately represented as single vectors. Instead, individual muscles were modelled as multiple vectors spaced throughout the area of insertion, with each vector representing a bundle of similarly oriented fibres. Muscle properties used in the model were based on data from human studies, as comparable information was not available for avians.

When a single skeletal element moves relative to the rest of the ribcage, the kinetic model indicates that some muscles undergo substantial changes in moment arms which influences the efficiency of the muscles at rotating the rib segments. Overall, muscle moment arms change according to non-linear curves (e.g., hyperbola, hyperbolic tangent) as joint rotation occurs. For a given vertebral rib, the moment arms of some muscles (e.g., Mm intercostales externi) follow similar curves for all three kinematic rotations, but for other muscles (e.g., M levator costarum) the three types of rotation cause moment arms to change in distinct ways. For a given M intercostalis connecting two adjacent vertebral ribs, the moment arms change sign (and therefore the direction of the angular acceleration) at different stages of rib rotation. The moment arm curves for some muscles suggest they may not function exclusively in inspiration or in expiration, as previously indicated by experimental studies of *Caiman crocodilus* and *Gallus domesticus*. However, the moment arm curves for Mm appendicocostales suggest these muscle slips are solely inspiratory, which agrees with previous studies. Moment arm curves for Mm appendicocostales resemble those for Mm intercostales externi, suggesting that Mm appendicocostales may have originated as distinct slips of Mm intercostales externi like those present in crocodylians. Examinations of the muscle moment arms suggest that M. appendicocostalis in paleognathes inherited from their archosaur ancestors may have originated to improve the efficiency in avian ventilation in response to high metabolic demands.

Refining the current kinetic model should provide further insights into the drivers of ventilatory motions. Furthermore, applying this modelling approach to other archosaurs may shed light on the evolution of ventilation in this major amniote group.

Taxonomy of a new goniopholidid specimen from the Upper Jurassic Morrison Formation and their diversity in North America

Junki Yoshida[1], Atsushi Hori[1], Yoshitsugu Kobayashi[1], Michael J. Ryan[2], Yuji Takakuwa[3], and Yoshikazu Hasegawa[3]

[1]Hokkaido University, Sapporo, Hokkaido, Japan; junkiyoshida9@gmail.com; ykobayashi@museum.hokudai.ac.jp
[2]Carleton University, Ottawa, Ontario, Canada; michaelj.ryan@carleton.ca
[3]Gunma Museum of Natural History, Tomioka, Gunma Prefecture, Japan; takakuwa@gmnh.pref.gunma.jp; hasegawa@gmnh.pref.gunma.jp

Goniopholididae is a group of basal neosuchians found in the northern hemisphere during the Jurassic and Early Cretaceous, and is closely related to the clade of Paralligatoridae and Eusuchia. Goniopholididae is the earliest crocodyliform group to acquire the modern crocodylian body plan and an inferred semi-aquatic lifestyle. Understanding the anatomy, phylogeny, and functional morphology of this group is important for revealing the origin of the modern crocodylian body plan (e.g., platyrostrum and secondary palate) and lifestyle. Here we describe a well-preserved, nearly complete skeleton of a goniopholidid (GMNH-PV229), discovered from the sandstone of the Brushy Basin Member of the Upper Jurassic Morrison Formation at the East *Camarasaurus* Quarry, Wyoming, USA, in 1993, and examine its phylogenetic relationships within the family.

Although most of the cranial and neurocentral sutures of the caudal vertebrae are fused, the cervical, dorsal, and sacral vertebrae remain unfused, indicating the immaturity of the individual at death. The rostral skull length (preorbital length) is 42 cm, one of the largest in goniopholidids, and 60% of the skull length, indicating a medium long rostrum. The ratio of rostral width at the midpoint of the maxilla to the skull width is 0.64, while other goniopholidids (e.g., *A. stovalli*) show a ratio of less than 0.5. The number of subfossae in the maxillary depression is five as in *Goniopholis simus*, while it is four in *Amphicotylus lucasii* and three in *Goniopholis kiplingi* and *Anteophthalmosuchus hooleyi*. Posterior to the nasopharyngeal passage, the pterygoid has a small, shallow, rectangular-shaped postchoanal fossa that is not perforated or connected to the passage and sinus.

Our data matrix for the phylogenetic analyses was composed of 486 characters and 102 ingroup and one outgroup (*Gracilisuchus*) taxa, including GMNH-PV229. A heuristic search was performed to obtain the most parsimonious trees using PAUP v. 4.0a. Our initial analysis produced 2592 most parsimonious trees with tree lengths of 2400. Strict consensus trees in both analyses place GMNH-PV229 within Goniopholididae. A sister-taxa relationship of GMNH-PV229 and *Amphicotylus stovalli* is supported by four synapomorphies: the anterior end of the frontal is posterior to the prefrontal, the palatal shelves of the palatines do not fully contact at the mid-line, the anterior border of the internal naris is positioned anterior to the suborbital fenestra, and the internal choana is lanceolated. However, GMNH-PV229 differs from *Amphicotylus stovalli* in having a broad rostrum, a straight lateral border of the nasals, a rounded anterior margin of the palatine, and lacking 'Crest C' on the ventral surface of the quadrate. GMNH-PV229 has a unique combination of the following features: broad rostrum, five subfossae in the maxillary depression, anterior projection at the posterior margin of the naris, triangular palpebral, lack of 'Crest C' on the quadrate, presence of postchoanal fossa, perichoanal fossa being wider than the nasopharyngeal passage, and the posterior border of the internal choana located at the midpoint of the pterygoid. These characters suggest that GMNH-PV229 is a new species of *Amphicotylus*.

Our results show a greater diversity of goniopholidids than previously known in the Upper Jurassic Morrison Formation, which currently comprises *Eutretauranosuchus, Amphicotylus stovalli,* and *A. lucasii*, by adding the taxon represented by GMNH-PV229. GMNH-PV229 is characterized by its broad rostrum, suited for feeding on

large and agile prey, as in some derived Cretaceous goniopholidids such as *Goniopholis simus, Goniopholis kiplingi,* and *Anteophthalmosuchus hooleyi*. We infer that a broad rostrum may have evolved much earlier than previously suggested within goniopholidids for feeding on large, highly mobile animals in the freshwater environment.

How to make monsters: cladistic analysis of ontogeny recovered evidence of anagenesis in North American Tylosaurines

Amelia R. Zietlow

Richard Gilder Graduate School – American Museum of Natural History, 200 Central Park West, New York, NY 10024, USA; azietlow@amnh.org

Mosasaurs were large, globally distributed aquatic lizards that lived during the Late Cretaceous. Despite numerous specimens of varying maturity, a detailed growth series has not been proposed for any mosasaur taxon. *Tylosaurus* is a genus of particularly large mosasaurs with long, edentulous anterior extensions of the premaxilla and dentary that lived in Europe and North America during the Late Cretaceous (90 to 66 million years ago). Three taxa—*Tylosaurus proriger, T. kansasensis,* and *T. nepaeolicus*—have robust fossil records with specimens spanning a wide range of sizes. Furthermore, because they lived in the same place and at the same time, and *T. kansasensis* are generally smaller than *T. nepaeolicus*, previous work has hypothesized that they are a single taxon, and *T. kansasensis* are juveniles. Therefore, these species are ideal for testing hypotheses of ontogeny, synonymy (*T. kansasensis* with *T. nepaeolicus*), sexual dimorphism, anagenesis, and heterochrony.

Fifty-nine hypothetical growth characters were identified, including size-dependent, size-independent, and phylogenetic characters. Quantitative cladistic analysis was used to recover a growth series for each taxon: *T. proriger*, 23 specimens and 17 growth stages (consistency index = 0.6, homoplasy index = 0.4); and *T. nepaeolicus*/*kansasensis*, 19 specimens and 12 growth stages (consistency index = 0.6, homoplasy index = 0.4. The results supported the synonymy of *T. kansasensis* with *T. nepaeolicus* and that *T. kansasensis* are juveniles of *T. nepaeolicus*. A Spearman rank-order test resulted in a significant ($p < 0.05$) correlation between size (skull length and quadrate height) and maturity for both taxa, and evidence for skeletal sexual dimorphism was not found. Eleven growth characters, including the development of a knob-like rostrum and increase in quadrate height relative to skull length, were shared by both taxa.

Finally, a novel hypothesis of anagenesis (i.e., evolution within a single lineage) in Western Interior Seaway *Tylosaurus* species, driven by peramorphy (extension of growth), was tested and supported by a third cladistic analysis including specimens of both *T. proriger* (15 specimens) and *T. nepaeolicus*/*kansasensis* (13 specimens), which recovered evidence of intermediate morphologies in both taxa and peramorphy of skull size and development in *T. proriger*.

Many thanks to CSVP 2021 virtual local organizing committee members:

Bassel Arnaout

Emily Bamforth

Julien Divay

Annie McIntosh

Hallie Street

Yan-yin Wang

Thanks also to the following people who served as abstract reviewers:

Hoai-Nam Bui

James Campbell

Nicola Howard

Sydney Mohr