



CANADIAN MUSEUM  
OF  
NATURE  
OTTAWA, ON

## Meeting Logo Design: Many thanks to Ashan Ayanarajan for creating our 2023 CSVP logo!

This year's CSVP meeting logo is courtesy of Carleton University MSc student Ashan Ayanarajan. The logo features the skull of a beluga whale (*Delphinapterus leucas*) over a backdrop of the ancient Champlain Sea (ca. 10,000 years ago). Beluga fossils from this time have been throughout eastern Ontario and southern Quebec, including in the Ottawa area.



Published 13 May, 2023

Editors: Alison M. Murray, Robert B. Holmes, and Mark J. Powers

© 2023 by the authors

DOI 10.18435/vamp29391

11<sup>th</sup> Annual Meeting  
Canadian Society of  
Vertebrate Palaeontology

May 24–26, 2023

Ottawa

Abstracts

# Acknowledgements

**Many thanks to CSVP 2023 local organizing committee members of the Canadian Museum of Nature:**

Danielle Fraser  
Marisa Gilbert  
Tetsuto Miyashita  
Jordan Mallon  
Shyong En Pan  
Scott Rufolo  
Xiao-chun Wu

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

Mark Powers  
Colton Coppock  
Emily Bamforth  
Ashan Ayanarajan  
Joshua Wasserlauf  
Trystan Warnock-Juteau  
Denny Maranga  
Michael Thompson  
Greg Funston  
Ryan Wilkinson  
Taia Wyenberg-Henzler  
Christiana Garros  
Misha Whittingham  
Howard Huynh  
Lea Veine-Tonizzo  
Khoi Nguyen  
Aaron Dyer  
Henry Sharpe  
Tom Dudgeon  
Talia Lowi-Merri  
Danielle Fraser

## TABLE OF CONTENTS

Horn size variation with latitude in <i>Bison bison</i> Ashan Ayanarajan, Danielle Fraser, and Jordan Mallon	.....8
Middle and Late Cretaceous forests of northern Alberta: new fossils and new insights into boreal dinosaur paleoecology Emily L. Bamforth	.....8
Discovery of a new Permian ichnofossil assemblage from Les Iles-de-la-Madeleine Louis-Philippe Bateman, Hans C.E. Larsson, Jérôme Dubé, Dirley Cortés, André Mueller, and Richard Cloutier	.....11
Revisiting caudal vertebral fusion in mosasaurs (Squamata: Mosasauridae) using paleohistology: functional implications Michael E. Burns, Jun Ebersole, and Sahara Gonzalez	.....12
First Pleistocene tetraodontid fish (Teleostei, Tetraodontiformes) from Tanegashima Island, Japan Mori Chida and Yoshitaka Yabumoto	.....12
Comparison of the efficacy of 2D and 3D tooth shape morphometrics for predicting the diets of carnivorous mammals Brigid E. Christison and Danielle Fraser	.....13
Immature <i>Daspletosaurus</i> (Tyrannosauridae, Tyrannosaurinae) material from the Dinosaur Park Formation of Alberta, Canada Colton C. Coppock, Mark J. Powers, Jared T. Voris, and Philip J. Currie	.....14
A new pliosaur from the Early Cretaceous Paja Formation of Colombia: insights into the diversification of Brachaucheniinae Dirley Cortés, Mary Luz Parra-Ruge, Alexandre Demers-Potvin, and Hans C.E. Larsson	.....14
Habitat heterogeneity and ape evolution in the Early Miocene of Eastern Africa Susanne M. Cote, Alan L. Deino, David L. Fox, John D. Kingston, Rahab N. Kinyanjui, William E. Lukens, Laura M. MacLatchy, Kieran P. McNulty, Daniel J. Peppe, James B. Rossie, and Caroline A.E. Strömberg	.....15
First definitive occurrence of <i>Centrosaurus apertus</i> in Saskatchewan reported from a multigeneric bonebed within the easternmost outcrop of the Dinosaur Park Formation Alexandre V. Demers-Potvin, Emily L. Bamforth and Hans C.E. Larsson	.....17
Disparate life histories contributed to the Palaeocene rise of Eutheria Gregory F. Funston, Sofia Holpin, Sarah L. Shelley, Thomas E. Williamson, and Stephen L. Brusatte	.....18
Mosasaur feeding ecology of the Bearpaw Formation, Alberta, Canada: the final chapter Femke M. Holwerda	.....18
Comparative dental microwear analyses of North American ursids to infer the dietary palaeoecology of extinct Pleistocene short-faced bears from the Yukon Howard M. Huynh, Prieyankaa Nirmalan, and Danielle Fraser	.....19
Size reduction in Beringian <i>Equus</i> throughout the Late Pleistocene leading up to their extinction Zoe Landry, Clément P. Bataille, and Danielle Fraser	.....20

Sense and sensibility: estimating the hearing capability of otophysan fish and implications for their fossil relatives Juan Liu	.....20
The timing and ecological evolution of modern ant lineages Elyssa Loewen, Caelan Libke, Christine Sosiak, Phillip Barden, Christopher Somers, and Ryan C. McKellar	.....21
A petrified struggle for survival from the Lower Cretaceous deposits of China Jordan C. Mallon, Gang Han, Aaron J. Lussier, Xiao-Chun Wu, Robert Mitchell, and Ling-Ji Li	.....22
Insights and limitations in reconstructing the musculature and skeletal arrangement of the foot in tyrannosaurids and other non-avian theropod dinosaurs Annie P. McIntosh, Corwin Sullivan, John Acorn, and Philip J. Currie	.....22
Bioerosion trace fossils on <i>Triceratops</i> bones from the latest Cretaceous Frenchman Formation, southwestern Saskatchewan, Canada Jack R. Milligan, Emily L. Bamforth, Luis A. Buatois, and M. Gabriela Mángano	.....24
The head, heart, and fins of a jawless stem gnathostome Tetsuto Miyashita, Michael I. Coates, Kristen Tietjen, Pierre Gueriau, and Philippe Janvier	.....25
A juvenile pachycephalosaur (Dinosauria: Ornithischia) skeleton from the upper Maastrichtian Frenchman Formation of Saskatchewan, Canada Bryan R.S. Moore, David C. Evans, Michael J. Ryan, R. Timothy Patterson, and Jordan C. Mallon	.....25
A multivariate comparison of the vertebrate faunas of the Horseshoe Canyon and Wapiti formations of Alberta, Canada with implications for vertebrate biogeography Nathaniel E.D. Morley, Lindsey R. Leighton, Eva B. Koppelhus, and Philip J. Currie	.....26
Identification of acanthomorph diversity in microvertebrate fossil sites Alison M. Murray and Donald B. Brinkman	.....27
Madtsoiidae: monophyletic clade or grouping of convenience? Mark J. Powers, Fernando F. Garberoglio, and Michael W. Caldwell	.....28
Vertebral pathology: A primer addressing its definitive features in the paleontological record Bruce Rothschild	.....28
A small early Permian parareptile with a lateral temporal fenestra from Richards Spur, Oklahoma Dylan Rowe, Erin Beaudesne, Joseph Bevitt, and Robert Reisz	.....29
A plesiosaur representing the first published vertebrate material from the foraminifera-dominated Peace River Formation, Alberta, Canada Maximilian Scott	.....30
Duck-faced and eagle-eyed: a well-developed visual system in a high-latitude hadrosaur Henry S. Sharpe, Philip J. Currie, and Corwin Sullivan	.....31
Quantitative reconstruction of feeding mechanics in <i>Leptoceratops gracilis</i> Brown, 1914 using novel digital methods: a proof-of-concept Emilia L. Silvestre, Louis-Philippe Bateman, and Hans C.E. Larsson	.....31
New and expanded preparation techniques from Pipestone Creek material leads to insights about this Late Cretaceous Wapiti Formation locality Jackson Sweder, Emily L. Bamforth, and Maximilian Scott	.....33

---

Changes in emplacement pattern and organization of the palatal dentition accompanied the evolution of herbivory in Edaphosauridae (Synapsida, Eupelycosauria)	
Andrew L. Traynor, Aaron R.H. LeBlanc, and Kenneth D. Angielczyk	.....34
Evaluation of enamel microstructures in small theropod dinosaurs	
Ashley Verstraete, Derek W. Larson, and Kirstin S. Brink	.....35
Redescription of a juvenile hadrosaurid from the Upper Cretaceous of Alberta using computed tomography	
Trystan M. Warnock-Juteau, Michael J. Ryan, R. Timothy Patterson, and Jordan C. Mallon	.....36
Isotope palaeoecology of duck-billed Dinosaurs (Ornithischia: Hadrosauridae) from the upper Campanian Dinosaur Park Formation	
Joshua Wasserlauf, Jordan Mallon, Thomas Cullen, François Therrien, Brian Cousens, and Clément Bataille	.....37
A new archosaurian skeleton from the Middle Triassic of China: shedding light on the phylogenetic position of <i>Wangisuchus</i> (Pseudosuchia, Gracilisuchidae)	
Xiao-Chun Wu, Zhi-Shuai Kang, Li-Yang Dong, Jian-Ru Shi, and Hai-Lu You	.....38
Hadrosaurid skull from the Wapiti Formation preserves evidence of new feeding behaviours in tyrannosaurids	
Taia C.A. Wyenberg-Henzler, Nicolas E. Campione, Phil R. Bell, and Corwin Sullivan	.....39
Investigating genetic mechanisms of early limb development in <i>Ambystoma mexicanum</i> and <i>Xenopus laevis</i>	
Jeffrey A. Yee, Tetsuto Miyashita, and Hillary C. Maddin	.....40

# Horn size variation with latitude in *Bison bison*

Ashan Ayanarajan<sup>1,2</sup>, Danielle Fraser<sup>1,2,3</sup>, and Jordan Mallon<sup>1,2</sup>

<sup>1</sup>Palaeobiology, Canadian Museum of Nature, PO Box 3443 Stn “D,” Ottawa, ON, K1P 6P4, Canada, DFraser@nature.ca, JMallon@nature.ca, AshanAyanarajan@cmail.carleton.ca

<sup>2</sup>Department of Earth Sciences, Carleton University, 1125 Colonel By Dr, Ottawa, ON K1S 5B6, Canada.

<sup>3</sup>Department of Biology, Carleton University, 1125 Colonel By Dr, Ottawa, ON K1S 5B6, Canada.

Ecometrics is a method used to evaluate the relationship between the observable traits of organisms and environmental parameters. By selecting traits whose structures are tightly related to their functions, and whose functions directly interact with the environment, it is possible to estimate climatic and other environmental parameters (e.g., mean annual temperature, and dominant local vegetation type) from morphology. Horns may be one such trait because they are composed of living tissue and have thermoregulatory functions that constrain their morphology; larger horns have a larger surface area through which body heat may be lost to the environment, which can be problematic in colder environments where lost body temperature can prove detrimental—even life-threatening—to the individual. Given that increased thermoregulatory demand may ultimately reduce overall fitness, we expect animals from colder environments to possess smaller horns with lower surface areas. This prediction is supported by a correlation between horn size and latitude for 15 species of bovid, with larger horn sizes observed in tropical and smaller horns in temperate regions. However, the phenomenon has never been studied within a species across a continuous latitude. We aim to test for a relationship between horncore size (horncore length, circumference, and surface area) and climate (i.e., mean annual temperature, and precipitation) for the North American bison (*Bison bison*) by analysing their horn morphology across the latitudes of 35°–65°N. Although not statistically significant ( $p = 0.427$ ), preliminary regression analyses suggest a negative correlation between horn size and latitude in *B. bison* from 50°–55°N and 60°–65°N ( $n = 37$ ), possibly indicating that *B. bison* horns may be used as climate proxies for the past. Ongoing work is aimed at testing for a relationship of horncore size with mean annual precipitation, temperature, and dominant local vegetation type.

---

# Middle and Late Cretaceous forests of northern Alberta: new fossils and new insights into boreal dinosaur paleoecology

Emily L. Bamforth

Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 3S0, Canada, and Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK, S7N 5E2, Canada; Ebamforth@dinomuseum.ca

Fossil plant assemblages are of critical importance for recreating paleoenvironments and understanding paleoecology. The diversity and nature of paleofloral assemblages can yield information on climate, photoperiod, latitudinal gradients, and seasonality, as well as providing information on the possible diets of animals living concurrently. Assemblages of woody angiosperm dicot leaves and ginkgoes can also be an invaluable proxy for paleoclimate reconstruction (Spicer 2006). Herein are described new paleofloral sites from the Late Cretaceous Wapiti Formation and the middle Cretaceous Dunvegan Formation, and their implications for understanding paleoecological and paleoenvironmental patterns.



The Late Cretaceous (80 – 68Ma) Wapiti Formation of northwestern Alberta and northeastern British Columbia spans an interval of geologic time from the lower Campanian to the upper Maastrichtian. The formation is well known for its vertebrate fossils, containing one of densest dinosaur deposits in North America known as the Pipestone Creek *Pachyrhinosaurus* Bonebed. Other finds include additional dinosaur bonebeds (e.g., Fanti et al. 2015), microvertebrate localities (Fanti and Miyashita 2009; Fanti et al. 2022), dinosaur trackway sites (Fanti et al. 2013; Enriquez et al. 2022), and soft-tissue preservation (Bell et al. 2014). While the dinosaur fossils and trackways have been well studied, the fossil plant deposits of the Wapiti Formation have received comparatively less attention.

The middle Cretaceous (96 – 93 Ma) Dunvegan Formation is a package of middle Cenomanian-aged rocks from northwest Alberta and northeast British Columbia. These rocks were deposited in nearshore and estuarine environments along the coast of the Western Interior Sea (Burns and Vavrek 2014). Vertebrate fossils from the Dunvegan Formation are rare, but include a trionychid turtle (Brinkman 2003), shark remains (Cook et al., 2008), ankylosaur bone fragments (Burns and Vavrek 2014; Arbour et al. 2020), a sturgeon fish (Vavrek et al. 2014) and dinosaur footprints (McCrea et al. 2001). The paleofloral record from the formation is little known, with published references limited to Arbour et al.'s (2020) note of leaf fossils in a paper describing ankylosaur fossils from the Dunvegan Formation of British Columbia.

Herein is described four new paleofloral assemblages from the Wapiti Formation, collected in 2022, and one from the Dunvegan Formation, collected in 2016. The first Wapiti assemblage, the Spring Creek Paleofloral Site, is dominated by the fronds and cones of the conifers *Metasequoia* and *Parataxodium*. Common leaves in this assemblage include *Platanus* and *Menispermities* morphotypes, three types of *Ginkgo* (including an unknown taxon), and a potential water plant (cf. *Ceratophyllum*). The Wapiti assemblage at the DC Bonebed Paleofloral Site contains comparatively few gymnosperms and is dominated by broad-leafed angiosperm fossils (*Colocasia*, *Menispermities*, *Vitis* morphotypes). The Wapiti assemblage at the Pipestone Creek Mouth Paleofloral Site has a lower diversity assemblage containing well-preserved fossils of an angiosperm tree (c.f. *Menispermities* morphotype) and at least one large *Ginkgo* taxon. At the Beaverlodge River Paleofloral Site, the Wapiti assemblage is dominated by the conifers *Metasequoia* and *Parataxodium* and contains well-presented fossils of both terrestrial and aquatic angiosperms (c.f. *Menispermities*, *Vitis* and *Cercidiphyllum* morphotypes).

The Dunvegan Paleofloral assemblage, known as the McCoy Leaf Site, was collected in 2016 by staff at the Philip J. Currie Dinosaur Museum. Despite a small sample of 20 specimens, the assemblage is surprisingly diverse, containing at least five morphotypes. The most common leaves were palmately lobed, similar to the *Sassafras* morphotype. Other leaves are similar to the morphotypes described as 122, 143 and 144 by Ash et al. (1999). Interestingly, the McCoy Leaf Site is entirely made up of angiosperms, lacking the conifer fossils so common in later Cretaceous forests.

While the sample size is still relatively small, these new paleofloral sites begin to create an interesting narrative about the development of forests in the Late Cretaceous of northern Alberta. The plant fossil record of the middle Cretaceous Albian period in Alberta has been well documented. Kalyniuk et al. (2023) described the paleoflora from the Albian Grande Cache Formation, and the stomach contents of the coeval nodosaur *Borealopelta markmitchelli* from the Fort McMurray area was described by Brown et al. (2020). These forests appear to have been dominated by seed ferns, horsetails, and cycads, with very few angiosperms. Some 40 million years later when the Wapiti Formation was deposited, the forests were fundamentally different, dominated by *Metasequoia* and abundant angiosperms. Although the sample size is small, the McCoy Leaf Site assemblage hints that the replacement of seed ferns and cycads may have occurred relatively rapidly as early as the Cenomanian, rather than as a gradual replacement across the intervening Turonian, Coniacian and Santonian periods. More Cenomanian palaeofloras will be needed to support this hypothesis.

Both vegetation type and forest structure greatly influence the type of animals these Late Cretaceous forests could support. Dinosaur body fossils from the Albian and Cenomanian deposits in northern Alberta are dominated by ankylosaurids (Burns and Vavrek 2014; Brown et al. 2020; Arbour et al. 2020), a taxon that are almost entirely absent from the Campanian Wapiti Formation. The same is largely true in the trace fossil (footprint) rec-

ord. Ankylosaurids such as *Borealopelta* may have been fern specialists (Brown et al., 2022), and the replacement of ferns by angiosperms may help to explain their demise. As we begin to understand the evolution of forests in northern Alberta, the evolutionary and diversity of patterns of megaherbivores may become more apparent.

## Literature Cited

- Arbour, V.M., D. Larson, M. Vavrek, L. Buckley, and D. Evans. 2020. An ankylosaurian dinosaur from the Cenomanian Dunvegan Formation of northeastern British Columbia, Canada. *Fossil Record* 23:179–189.
- Ash, A., B. Ellis, L.J. Hickey, K. Johnson, P. Wilf, and S. Wing. 1999. *Manual of leaf architecture*, Smithsonian Institution, Washington, D.C., Smithsonian Institution, 65 pp.
- Bell, P.R., F. Fanti, P.J. Currie, and V.M. Arbour. 2014. A mummified duck-billed dinosaur with a soft-tissue cock's comb. *Current Biology* 24:70–75.
- Brinkman, D.B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. *Canadian Journal of Earth Sciences*, 40: 557–571.
- Brown, C.M., D.R. Greenwood, J.E. Kalyniuk, D.R. Braman, D.M. Henderson, C.L. Greenwood, and J.F. Basinger. 2020. Dietary palaeoecology of an Early Cretaceous armoured dinosaur (Ornithischia; Nodosauridae) based on floral analysis of stomach contents. Article 200305. *Royal Society Open Science* 7(6).
- Burns, M.E., and M.J. Vavrek. 2014. Probable ankylosaur ossicles from the middle Cenomanian Dunvegan Formation of northwestern Alberta, Canada. *PloS One* 9(5):e96075.
- Cook, T.D., M.V.H. Wilson, and A.M. Murray. 2008. A middle Cenomanian euselachian assemblage from the Dunvegan Formation of northwestern Alberta. *Canadian Journal of Earth Sciences* 45:1185–1197.
- Enriquez, N.J., N.E. Campione, M.A. White, F. Fanti, R.L. Sissons, C. Sullivan, M.J. Vavrek, and P.R. Bell. 2022. The dinosaur tracks of Tyrants Aisle: an Upper Cretaceous ichnofauna from Unit 4 of the Wapiti Formation (upper Campanian), Alberta, Canada. *Plos One*, 17(2), p.e0262824.
- Fanti, F., and T. Miyashita. 2009. A high latitude vertebrate fossil assemblage from the Late Cretaceous of west-central Alberta, Canada: evidence for dinosaur nesting and vertebrate latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology* 275:37–53.
- Fanti, F., P.R. Bell, and R.L. Sissons. 2013. A diverse, high-latitude ichnofauna from the Late Cretaceous Wapiti Formation, Alberta, Canada. *Cretaceous Research* 41:256–269.
- Fanti, F., P.J. Currie, and M.E. Burns. 2015. Taphonomy, age, and paleoecological implication of a new *Pachyrhinosaurus* (Dinosauria: Ceratopsidae) bonebed from the Upper Cretaceous (Campanian) Wapiti Formation of Alberta, Canada. *Canadian Journal of Earth Sciences* 52:250–260.
- Fanti, F., P.R. Bell, M. Vavrek, D. Larson, E. Koppelhus, R.L. Sissons, A. Langone, N.E. Campione, and C. Sullivan. 2022. Filling the Bearpaw gap: evidence for palaeoenvironment-driven taxon distribution in a diverse, non-marine ecosystem from the late Campanian of west-Central Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 592:110923.
- Kalyniuk, J.E., C.K. West, D.R. Greenwood, J.F. Basinger, and C.M. Brown. 2023. The Albian vegetation of central Alberta as a food source for the nodosaurid *Borealopelta markmitchelli*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 611:111356.
- McCrea, R.T., M.G. Lockley, and C.A. Meyer. 2001. Global distribution of purported ankylosaur track occurrences; pp. 413–454 in: K. Carpenter (ed.), *The Armoured Dinosaurs*. Indiana University Press, Bloomington.
- Vavrek, M.J., A.M. Murray, and P.R. Bell. 2014. An early Late Cretaceous (Cenomanian) sturgeon (Acipenseriformes) from the Dunvegan Formation, northwestern Alberta, Canada. *Canadian Journal of Earth Sciences* 51:677–681.
- Spicer, R.A. 2006. CLAMP. [www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html](http://www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html)6/3/2006.
-

# Discovery of a new Permian ichnofossil assemblage from Les Iles-de-la-Madeleine

Louis-Philippe Bateman<sup>1</sup>, Hans C.E. Larsson<sup>1</sup>, Jérôme Dubé<sup>2</sup>, Dirley Cortés<sup>1,3,4</sup>, André Mueller<sup>1</sup>, and Richard Cloutier<sup>2</sup>

<sup>1</sup>Redpath Museum, Biology Department, McGill University, Montreal, QC, H3A 0C4, Canada; louis-philippe.bateman@mail.mcgill.ca; dirley.cortes@mail.mcgill.ca; andre.mueller@mail.mcgill.ca; hans.ce.larsson@mcgill.ca

<sup>2</sup>Université du Québec à Rimouski, Rimouski, QC, Canada; richard\_cloutier@uqar.ca; jerome\_dube@uqar.ca

<sup>3</sup>Smithsonian Tropical Research Institute, Balboa-Ancón 0843-03092, Panamá, Panamá

<sup>4</sup>Centro de Investigaciones Paleontológicas, Km. 5.2 vía Santa Sofía, Villa de Leyva, Colombia

Over the past two decades, locals, tourists, and geologists have found well-preserved early Permian ichnofossils in the Cap-aux-Meules Formation of les Iles-de-la-Madeleine, Québec. To follow up on these discoveries, fieldwork was conducted in October 2022. This led to the discovery of several in situ and ex situ tetrapod trackways preserved mainly on sandstone horizons representing at least eight distinct ichnofossil morphotypes and some other unidentifiable traces, possibly produced by invertebrates. All vertebrate trackways are from quadrupedal animals and footprint lengths range from 2 to 6 cm. The trackways are preserved at various depths and taphonomic levels, which may suggest multiple walking events of several individuals in one and/or several levels. A few samples preserve footprints displacing the sediment outwards in anterior portions of the footprints which may correspond to events of higher speeds or made over substrate of varied inclination. Others have characteristic downward tilted footbeds that we interpret as displacements during the end of the step cycle in wet but not saturated sands. The relatively similar footprint sizes suggest the tracks were produced by individuals of roughly similar body sizes. The tetrapod morphotypes preliminarily identified include potentially relatively well-known ichnotaxa such as *Dromopus*, *Chelichnus*, *Laoporus*, *Dicynodontipus*, and *Ichniotherium*. Preliminary comparisons with other ichnofossil assemblages from fossil collections in eastern Canada, the United States, and Europe suggest that les Iles-de-la-Madeleine had a typical Euramerican ichnofauna.

The age of the Cap-aux-Meules Formation remains to be determined, but based on previous research, and the potential presence of *Dromopus*, we suggest it to be equivalent to the *Dromopus* biochron, which is early Permian in age. The depositional environment of the site is still unresolved due to the complex Maritimes basin history. Specifically, the lack of bioturbation, the presence of the taphotaxon *Chelichnus*, and the presence of large scale cross-bedding suggests that the site was deposited in an aeolian, sand dune environment overall referable to the *Chelichnus* ichnofacies. However, some ichnofossils show evidence of animals sinking into a presumably humid substrate, which would suggest a wetter depositional environment. For this reason, we suggest that the depositional environment may have been variable through time. Future expeditions focused on the geology of the area will allow us to better understand the depositional paleoenvironments of the Cap-aux-Meules Formation and its concordant units. Altogether, this new ichnofossil site sheds new light on early Permian ecosystems in the Maritimes Basin. These ichnofossils are also the first tetrapod fossils from Quebec that date from before the Quaternary glaciations. They therefore showcase the potential of les Iles-de-la-Madeleine for becoming a fossil hotspot in the province. Ties were built with the municipal government during our visit, and we hope to set up a collaborative inter-institutional exhibit displaying these fossils on the islands in the near future to help support the education, culture, and science of the region.

# Revisiting caudal vertebral fusion in mosasaurs (Squamata: Mosasauridae) using paleohistology: functional implications

Michael E. Burns<sup>1</sup>, Jun Ebersole<sup>2</sup>, and Sahara Gonzalez<sup>3</sup>

<sup>1</sup>Department of Biology, Jacksonville State University, Jacksonville, AL, 36265, USA; mburns3@jsu.edu

<sup>2</sup>McWane Science Center, Birmingham, AL, 35203, USA; jebersole@mcwane.org

<sup>3</sup>Lincoln Memorial University College of Veterinary Medicine, Harrogate, TN, 37752, USA; xsahara7@hotmail.com

Mosasaurs were large-bodied predatory marine squamates, exhibiting a hypocercal caudal morphology rare among extinct and extant vertebrates. Secondary caudal functions, in addition to locomotion, have been ascribed to this anatomy as it pertains to mosasaurs. A high incidence of vertebral fusion has also been noted in their caudal regions since the 1870s. Little research has investigated the etiology of these abnormalities, although most diagnoses have been based on gross anatomy. Those that have examined bone microstructure have suggested etiologies such as avascular necrosis and healed injury, albeit on those specimens with clear gross signs of injury/pathology.

Alabama is rich in Cretaceous marine fossils, with at least 1,300 individual specimens collected to date. In this study, we test three hypotheses to explain the occurrence of caudal vertebral fusion: normal development, pathology (e.g., infectious spondylitis), or healed injury. Three specimens, collected from the Upper Cretaceous Mooreville Chalk Formation, were used for paleohistological analysis. To perform this analysis, they were molded and cast, stabilized by resin impregnation, and petrographically on frosted Plexiglass slides.

Externally, these specimens exhibit no indication of macroscopic abnormalities or healed injury. Our analysis indicates incomplete *in vivo* fusion in two of the specimens; however, an unfused specimen shows trabecular bone in the medullary regions of the vertebrae. Towards the cortex of the anterior and posterior margins, the bone tissue becomes denser, histology typical for normal vertebral development. A third specimen shows complete fusion. Trabecular bone density is constant, and no evidence of woven bone (indicative of injury or a pathology) can be observed. Histological evidence thus supports that this is indicative of normal bone development, and shares similarities with normal pygostyle development in birds; however, we cannot rule out remodeling as having erased some record of healed lesion or fracture. Future work should expand the histological sample size available for mosasaur vertebrae, regardless of their gross anatomy.

---

# First Pleistocene tetraodontid fish (Teleostei, Tetraodontiformes) from Tanegashima Island, Japan

Mori Chida<sup>1</sup>, and Yoshitaka Yabumoto<sup>2</sup>

<sup>1</sup>Department of Life and Environmental Engineering, University of Kitakyushu, Japan; gozdmori@gmail.com

<sup>2</sup>Kitakyushu Museum of Natural History and Human History; yabumoto@kmnh.jp

Tanegashima Island is located in southwest Japan and belongs to the Kagoshima Prefecture. Many fossil specimens were excavated in 1988 and 1989 from the marine deposits of the Pleistocene Masuda Formation of Katanoyama in the northern part of the island. These fossils were named the ‘Katanoyama fossil assemblage’ and contain various groups including plants, bivalves, crustaceans, amphibians, mammals, and a lot of fishes. The approximate age of



the deposits is 1.3 Ma. Currently, at least 7 orders, and 13 families with 18 species of fishes have been recognized, including clupeiforms, anguilliforms, osmeriforms, beloniforms, mugiliforms, perciforms, and pleuronectiforms. However, only two species have been formally named, the clupeiform *Clupanodon tanegashimaensis* (Saheki, 1929) and the perciform *Percichthys chibei* Saheki, 1929. Most of the fish specimens are now housed in the Kitakyushu Museum of Natural History and Human History (KMNH). In this study, we report on specimens that were rediscovered in the collections of the KMNH as the first well-preserved Pleistocene tetraodontids.

Tetraodontidae is a family of pufferfish that includes 28 extant genera with more than 180 species that live in marine, brackish, and freshwater environments of the temperate to tropical zones. Most tetraodontids have a unique neurotoxin called tetrodotoxin in their skin and organs, as well as in the muscles of some species. Diagnostic features of this group include having four beak-like fused teeth, lacking pelvic girdles, ribs, and intermuscular bones, and possessing 7-18 dorsal and anal fin rays with no fin spines. The fossil record of tetraodontids spans the Eocene of Italy, Oligocene of Russia, Miocene of Ukraine, and Pliocene of the United States, and some fragmentary specimens have also been found in Oligocene to Miocene deposits of the Middle East.

The specimens found in Tanegashima consist of five individuals. All of them are nearly complete except for one that lacks the anterior part of the skull. Two of the specimens lack small spines called prickles on the body, whereas the other three possess prickles on the anterior part of the body. Based on the overall osteology, presence/absence of prickles, and the number of fin rays and vertebrae, the specimens appear similar to the extant genus *Takifugu*. However, the specimens also possess some characters that differ from *Takifugu*, such as the morphology of the bones of the caudal skeleton. Thus, these specimens expand our knowledge of the pufferfish that lived in southwestern Japan and the Northwest Pacific Ocean a million years ago.

---

## Comparison of the efficacy of 2D and 3D tooth shape morphometrics for predicting the diets of carnivorous mammals

Brigid E. Christison<sup>1</sup> and Danielle Fraser<sup>2</sup>

<sup>1</sup>Canadian Museum for Human Rights, Winnipeg, MB, R3C 0L5, Canada; Brigid.Christison@Outlook.com

<sup>2</sup>Canadian Museum of Nature Natural Heritage Campus, Gatineau, QC, J9J 3N7, Canada; DFraser@nature.ca

Digital scanning and 3D models have revolutionized the study of morphological evolution. In some fields, 3D analyses have nearly supplanted more traditional studies based on 2D linear measurements. Digital scanning is more costly than 2D methods, yet few studies have compared the efficacy of 3D to 2D methods in the analysis of surface morphology. The objective of the present study is therefore to make direct comparisons of 3D and 2D methods for inferring diet based on tooth shape. Tooth shape reflects the average diets of extant mammals and has been applied to close relatives for the purpose of inferring the diets of extinct species. Here, we compare the efficacy of dietary inference among extant carnivores between 3D metrics of dental shape complexity (Orientation Patch Count and Relief Index), with several 2D metrics of quantifying surface shape. We compared rates of correct dietary classification using linear discriminant analyses and tests for statistically significant differences among dietary groups. The sample size and selection of included species also influences the separation of species by diet. Though higher sample sizes in this study correspond with lower percent correct classification, they are likely more accurate in terms of determining the true efficacy of the methods. We found that 2D and 3D metrics combined yielded the highest rates of correct classification, but that 2D metrics relating to the form of the carnassial tooth (lower first molar). We therefore suggest that 2D metrics are a valid means of inferring carnivorous mammal diet in the fossil record.

# Immature *Daspletosaurus* (Tyrannosauridae, Tyrannosaurinae) material from the Dinosaur Park Formation of Alberta, Canada

Colton C. Coppock<sup>1</sup>, Mark J. Powers<sup>1</sup>, Jared T. Voris<sup>2</sup>, and Philip J. Currie<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, B Edmonton, Alberta, T6G 2R3, Canada

<sup>2</sup>Department of Geoscience, University of Calgary, Calgary, Alberta, T2N 1N4, Canada

Understanding the extent to which ontogeny altered tyrannosaurid cranial morphology remains integral when referring tyrannosaurid specimens at varying life stages to a taxon. Yet, elements diagnostic to a tyrannosaurid species that belong to an immature tyrannosaurid specimen remain exceedingly elusive. Over the last century the University of Alberta has collected two isolated immature cranial elements referable to *Daspletosaurus* from the Dinosaur Park Formation of Dinosaur Provincial Park, Alberta: a pathologic jugal (UALVP 61561) and a lacrimal (UALVP 47955). To assess the diagnosability of these elements, they were compared to additional tyrannosaurid material from the Dinosaur Park Formation. This provided an opportunity to examine size-independent discrete characters in tyrannosaurid crania. The results of this study suggest that many jugal and lacrimal discrete characteristics observed in *Daspletosaurus* are constrained throughout ontogeny despite disparity in size. Ontogenetically invariant characters present on the *Daspletosaurus* jugal include, but are not limited to, the presence of a postorbital fossa and an anteroposteriorly broad medial flange along the postorbital contact shelf. The most axiomatic invariant lacrimal characters include a restricted pneumatic recess opening that does not approach the cornified region of the lacrimal horn and a lateral surface of the ventral ramus that is broadly confluent with the jugal ala. The presence of invariant characters on two cranial elements allows specimens of the tyrannosaurine *Daspletosaurus* and the albertosaurine *Gorgosaurus* to be confidently distinguished regardless of ontogenetic stage.

---

# A new pliosaur from the Early Cretaceous Paja Formation of Colombia: insights into the diversification of Brachaucheniinae

Dirley Cortés<sup>1,2,3</sup>, Mary Luz Parra-Ruge<sup>3</sup>, Alexandre Demers-Potvin<sup>1</sup>, and Hans C.E. Larsson<sup>1</sup>

<sup>1</sup>Redpath Museum, Biology Department, McGill University, Montreal, QC, H3A 0C4, Canada; dirley.cortes@mail.mcgill.ca; hans.ce.larsson@mcgill.ca; alexandre.demers-potvin@mail.mcgill.ca

<sup>2</sup>Smithsonian Tropical Research Institute, Balboa-Ancón 0843–03092, Panamá, Panamá.

<sup>3</sup>Centro de Investigaciones Paleontológicas, Villa de Leyva, Boyaca, Colombia; mlparra@centropaleo.com

Pliosaurid plesiosaurs are large-bodied, marine apex predators that lived throughout the Jurassic and Cretaceous. Only brachaucheniine plesiosaurs survived the end-Jurassic extinction with this clade radiating during the Early Cretaceous. Their radiation during this period is poorly documented with only a few known taxa.

This study presents a new Early Cretaceous pliosaur from the Paja Formation of Colombia. This new, exquisitely preserved pliosaur consists of a large complete skull about 1.2 m long with complete dentition. It features many autapomorphies, including a laterally constricted dentary and upper jaw near the orbits, similar to an odontocete whale, with a nearly tubular snout for almost half the skull length, and a hypertrophied frontal-parietal contact with rugose, striated ornamentation over the interorbital region, constructing a wide dorsal interorbital surface. These features are remarkable in comparison to morphological traits known in the other pliosaurs described from the formation. A phylogenetic analysis places the new pliosaur within Brachaucheniinae, contributing to the taxonomic diversity of this clade. This new taxon is coeval, or nearly at the same horizon in the Paja Formation, with *Stenorhynchosaurus*, *Kronosaurus* (= *Monquirasaurus*), and *Sachicasaurus*. The well-preserved nature of these taxa helps clarify phylogenetic hypotheses during the Early Cretaceous radiation of the clade. Most notably, this radiation is characterized not only by high morphological disparity, but also a high upper range of body sizes for all Plesiosauria. The high diversity of top predators in the Paja Formation is striking and differs from that of most other Mesozoic marine ecosystems. The different skull shapes and tooth morphologies suggest niche partitioning among these taxa. This implies an equally complex apex predator ecosystem for the Paja Biota, despite the paucity of smaller vertebrate fauna. We present morphometric comparisons across the teeth of these Paja brachaucheniines and hypothesize their feeding guilds within the known ecosystem. Our work on this new pliosaur taxon provides new data on the Paja's ecosystem complexity and food web interactions and sheds light on the ecological roles of the brachaucheniines, the last surviving pliosaur top predators, during the late Mesozoic before their imminent extinction.

**Funding:** The BESS-NEO program, NSERC CREATE 46283-2015, the Smithsonian Tropical Research Institute, the Anders Foundation, the 1923 Fund, and Gregory D. and Jennifer Walston Johnson, the Redpath Museum's Delise Alison Award-2019, the Sigma Xi Grant-in-aid-of-Research (GIAR), Canada-2019, and the Quebec Center for Biodiversity Science excellence award-2019, FRQNT, Canada.

---

## Habitat heterogeneity and ape evolution in the Early Miocene of Eastern Africa

Susanne M. Cote<sup>1</sup>, Alan L. Deino<sup>2</sup>, David L. Fox<sup>3</sup>, John D. Kingston<sup>4</sup>, Rahab N. Kinyanjui<sup>5</sup>, William E. Lukens<sup>6</sup>, Laura M. MacLatchy<sup>4</sup>, Kieran P. McNulty<sup>7</sup>, Daniel J. Peppe<sup>8</sup>, James B. Rossie<sup>9</sup>, and Caroline A.E. Strömberg<sup>10</sup>

<sup>1</sup>Department of Anthropology and Archaeology, University of Calgary, Calgary, AB, T2N 1N4, Canada; scote@ucalgary.ca

<sup>2</sup>Berkeley Geochronology Center, Berkeley, CA, 94709, USA; adeino@bgc.org

<sup>3</sup>Department of Earth & Environmental Sciences, University of Minnesota, Minneapolis, MN, 55455, USA; dlfox@umn.edu

<sup>4</sup>Department of Anthropology, University of Michigan, Ann Arbor, MI, 48109, USA; jkingst@umich.edu; maclatch@umich.edu

<sup>5</sup>Department of Earth Sciences, National Museums of Kenya, Nairobi, 0100, Kenya; rkinyanj@gmail.com

<sup>6</sup>Department of Geology & Environmental Science, James Madison University, Harrisonburg, VA, 22807, USA; lukenswe@jmu.edu

<sup>7</sup>Department of Anthropology, University of Minnesota, Minneapolis, MN, 55455, USA; kmcnulty@umn.edu

<sup>8</sup>Department of Geosciences, Baylor University, Waco, TX, 76706, USA; daniel\_peppe@baylor.edu

<sup>9</sup>Department of Anthropology, Stony Brook University, Stony Brook, NY, 11794, USA; james.rossie@stonybrook.edu

<sup>10</sup>Department of Biology, Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, 98195, USA; caestrom@uw.edu

Research on Eastern African Catarrhine and Hominoid Evolution (REACHE) is a consortium of paleontologists and geologists that work together to study the early Miocene (23–16 Ma) in eastern Africa. Early Miocene fossil localities in this region provide a critical window into early ape evolution, as this is the region in which the first clear hominoids occur. Fundamentally, we seek to understand what kinds of environments early apes were living in, and how those environments shaped their morphological adaptations and ecology. Apes today are largely confined to forested habitats, which is often assumed to represent the ancestral habitat for hominoids, but there is little data from the fossil record to support or refute this hypothesis.

In two recently published papers (MacLatchy et al. 2023; Peppe et al. 2023), we provide paleoenvironmental reconstructions for early Miocene fossil localities from across eastern Africa, with a particularly detailed reconstruction at Moroto, the oldest of the fossil sites (21 Ma). Our approach is multi-proxy, incorporating information from not only carbon isotopes in multiple paleosol-derived substrates (pedogenic carbonates, soil organic matter, and plant wax biomarkers) but also phytoliths, the silica remains of plant cells or cell walls, which can be diagnostic for different plant taxa. At Moroto, we combined these data with revised dating, stable carbon and oxygen isotopes from mammalian enamel, and detailed reconstructions of the locomotor and dietary adaptations of the early large-bodied hominoid, *Morotopithecus* (21 Ma).

Our results demonstrate that the early Miocene of eastern Africa was characterized by heterogeneous environmental conditions. Notably, we document that C<sub>4</sub> grasses appear in Africa more than 10 Myr earlier than previously thought. These grasses are widespread in the region and can be locally abundant. They contribute to diverse habitats that range from forests to wooded grasslands, including the oldest grass-dominated habitats (roughly 30% C<sub>4</sub> biomass or more) both in Africa and globally. Furthermore, multiple dietary and paleoecological proxies demonstrate that the oldest postcranially derived ape, *Morotopithecus*, which shows clear specializations for orthograde combined with vertical climbing abilities, lived in a seasonal woodland habitat with a fragmented canopy and significant C<sub>4</sub> grass cover and fed largely on leaves.

In conclusion, this research demonstrates that early Miocene apes were not confined to forested habitats, but lived in heterogeneous environments that included open habitats with sparse tree cover (wooded grasslands). Postcranial adaptations for suspensory locomotion and acrobatic climbing may not have evolved to help apes feed on fruit in a continuous canopy, but to forage for leaves in a habitat characterized by large gaps between trees.

## Literature Cited

- MacLatchy, L.M., S.M. Cote, A.L. Deino, R.M. Kityo, A.T. Mugume, J.B. Rossie, W.J. Sanders, M.N. Cosman, S.G. Driese, D.L. Fox, A.J. Freeman, R.J.W. Jansma, K.E.H. Jenkins, R.N. Kinyanjui, W.E. Lukens, K.P. McNulty, A. Novello, D.J. Peppe, C.A.E. Strömberg, K.T. Uno, A.J. Winkler, and J.D. Kingston. 2023. The evolution of hominoid locomotor versatility: evidence from Moroto, a 21 Ma site in Uganda. *Science* 380:eabq2935.
- Peppe, D.J., S.M. Cote, A.L. Deino, D.L. Fox, J.D. Kingston, R.N. Kinyanjui, W.E. Lukens, L.M. MacLatchy, A. Novello, C.A.E. Strömberg, S.G. Driese, N.D. Garrett, K.R. Hillis, B.F. Jacobs, K.E.H. Jenkins, R.M. Kityo, T. Lehmann, F.K. Manthi, E.N. Mbua, L.A. Michel, E.R. Miller, A.T. Mugume, S.N. Muteti, I.O. Nengo, K.O. Oginga, S.R. Phelps, P. Polissar, J.B. Rossie, N.J. Stevens, K.T. Uno, and K.P. McNulty. 2023. Oldest evidence of significant C<sub>4</sub> grasses and habitat heterogeneity in eastern Africa. *Science* 380:173–177.



# First definitive occurrence of *Centrosaurus apertus* in Saskatchewan reported from a multigeneric bonebed within the easternmost outcrop of the Dinosaur Park Formation

Alexandre V. Demers-Potvin<sup>1</sup>, Emily L. Bamforth<sup>2</sup> and Hans C.E. Larsson<sup>1</sup>

<sup>1</sup>Redpath Museum, McGill University, Montréal, QC, H3A 0C4, Canada; alexandre.demers-potvin@mail.mcgill.ca; hans.ce.larsson@mcgill.ca

<sup>2</sup>Philip J. Currie Museum, Wembley, AB, T0H 3S0, Canada; Curator@dinomuseum.ca

After more than a century of exploration, most of our knowledge on Canadian late Campanian communities comes from the fluvial-paralic deposits of the Dinosaur Park Formation (DPF) in Dinosaur Provincial Park (DPP), Alberta. However, a growing list of localities from isolated DPF outcrops offers a glimpse into palaeocommunities that evolved closer to the Western Interior Seaway, in approximate co-occurrence with the DPP biotas along an inland-coastal gradient. These include the Muddy Lake Bonebed near Unity, an associated ceratopsid skeleton near Herschel, and a multigeneric bonebed located along Lake Diefenbaker in Saskatchewan Landing Provincial Park. Over six field seasons from 2012 to 2018, field crews based in McGill University collected fossils from the latter locality as part of an annual palaeontology field course. The specimens were subsequently prepared and studied at the Redpath Museum, Montréal, on loan from the Royal Saskatchewan Museum. A palaeoecological analysis of this ancient coastal ecosystem based on the palynomorphs and vertebrate microfossils collected between 2012 and 2015 has now laid a foundation for the current study of its macrofossil assemblage.

Over a total of ~50 m<sup>2</sup> uncovered at the Lake Diefenbaker Bonebed, around 300 vertebrate macro- and microfossils found in the same bone layer were excavated (not including surface-collected microfossils). 73 of these macrofossils were identified as ceratopsid, one of which consists in an incomplete right lateral parietal bar that bears the hooked P1 and P2 parietal processes diagnostic of *Centrosaurus apertus*. Other ceratopsid elements are assigned to cf. *Centrosaurus* due to anatomical similarities with Albertan specimens combined with an absence of diagnostic characters. We refrain from classifying the Lake Diefenbaker Bonebed as a *Centrosaurus*-dominated catastrophic death assemblage because ceratopsid remains represent a minority of its identifiable fossils. Nonetheless, the description of the macrofauna from the most extensive dinosaur bonebed known from Saskatchewan to date increases the known diversity of the community that evolved in this coastal outpost of the DPF and represents a major contribution to the palaeontological heritage of this province.

The aforementioned parietal bar is shown to fall well within the range of variation in parietal process angulation observed in *Centrosaurus apertus* specimens from Alberta, which precludes its assignment to a new *Centrosaurus* species. Therefore, it constitutes the first diagnostic morphological evidence for the presence of *C. apertus* in Saskatchewan. The unequivocal presence of this ceratopsid on the eastern coast of Laramidia suggests that the Lake Diefenbaker Bonebed is closer in age to the lower DPF in DPP, which is at odds with a previous correlation to the upper DPF in DPP based on the palynoflora. Considering evidence of temporal turnover among centrosaurine species within DPP, as well as highly documented shifts in the geographic distributions of extant floral assemblages in response to environmental change, the presence of *Centrosaurus* in the Lake Diefenbaker Bonebed is proposed to be a more reliable indicator of relative age for this locality's Campanian deposits than its palynofloral composition. This contribution demonstrates how evidence from multiple localities in the DPF along a spatial gradient, beyond the temporal gradient available within DPP alone, completes the picture of this extensively studied metacommunity at a regional scale.

# Disparate life histories contributed to the Palaeocene rise of Eutheria

Gregory F. Funston<sup>1,2</sup>, Sofia Holpin<sup>2</sup>, Sarah L. Shelley<sup>2</sup>, Thomas E. Williamson<sup>3</sup>, and Stephen L. Brusatte<sup>2</sup>

<sup>1</sup>Royal Ontario Museum, Toronto, ON, Canada; greg.funston@rom.on.ca

<sup>2</sup>School of GeoSciences, University of Edinburgh, Edinburgh, UK; sofia.holpin@ed.ac.uk, sarah.shelley@ed.ac.uk, stephen.brusatte@ed.ac.uk

<sup>3</sup>New Mexico Museum of Natural History and Science, Albuquerque, NM, USA; thomas.williamson@state.nm.us

The early Palaeocene (66.0–61.6 mya) witnessed the establishment of mammal-dominated terrestrial ecosystems after the extinction of the non-avian dinosaurs. Understanding the mammals that formed these communities is crucial not only for disentangling the origin of living mammal clades, but also the dynamics that shaped these first antecedents of modern ecosystems. The potential role of life history as a driving factor in the composition of early mammalian ecosystems has long been appreciated but has historically been difficult to evaluate. A central focus thus far has been on differences in reproductive strategy between major mammal clades, particularly multituberculates, metatherians, and eutherians. However, virtually no work has considered whether variable reproductive strategies existed within these clades, and what effect it may have had on ecosystem dynamics. Recent advances combining palaeohistology with geochemistry have now opened a new window into the life histories of extinct mammals, revealing a highly precocial (rapidly-developing) lifestyle in the eutherian pantodont *Pantolambda*, but it is unclear whether this is representative of eutherians more broadly. Here we present preliminary results for another eutherian, the phenacodontid *Tetraclaenodon*, which is represented by several skeletons with deciduous dentition. Surprisingly, consilient evidence from both cementochronology and postcranial osteohistology indicate a much slower life history in *Tetraclaenodon*, at virtually the opposite end of the eutherian spectrum from *Pantolambda*, despite only minor differences in body mass. After a relatively short gestation period (~2 months), *Tetraclaenodon* retained the slow-growing deciduous teeth for as long as four years. The oldest individual in our sample grew exceptionally slowly towards the end of its life, which spanned at least 8–9 years. The intersection of gestation period and body size (10–15 kg) in *Tetraclaenodon* is similar to small-bodied carnivorans like the coyote (*Canis latrans*), caracal (*Caracal caracal*), and African civet (*Civettictis civetta*). However, these extant species vary significantly in the duration of suckling (1.5–4 months), so determination of the closest modern analogue for *Tetraclaenodon* awaits trace element geochemical work in progress. Nonetheless, these results indicate that eutherian life histories were already diverse in the early Palaeocene, and raise doubts that a more precocial ‘placental’-style life history is responsible for the greater proliferation of eutherians than other mammal clades during this interval.

---

## Mosasaur feeding ecology of the Bearpaw Formation, Alberta, Canada: the final chapter

Femke M. Holwerda

Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; Femke.Holwerda@gov.ab.ca

The Campanian Bearpaw Formation (~80–75 Ma) deposits of southern Alberta host a score of large marine reptiles: mosasaurs (typically *Mosasaurus missouriensis*, *Tylosaurus proriger*, *Prognathodon overtoni*, and

*Plioplatecarpus primaevus*), elasmosaurs, and turtles. Other vertebrate inhabitants were sharks, sawfish, other predatory fish like *Enchodus*, and invertebrates such as lobsters, ammonites, and bivalves.

Previously, microwear, Energy Dispersive X-ray (EDX) analysis, and isotope pilot studies were used to demonstrate niche partitioning amongst the large marine predators. However,  $\delta^{18}\text{O}$  range (indicative of salinity levels and water temperature), and  $^{87}\text{Sr}/^{86}\text{Sr}$  isotopes (indicative of migratory patterns) suggest that habitat partitioning is the main key to reducing competition for these large marine predators. *Prognathodon* shows the largest range in both oxygen and strontium isotopes, indicating migration, followed by *Plioplatecarpus*. Platecarpines have been suggested in prior studies to migrate between fresh and saltwater bodies. The  $\delta^{18}\text{O}$  range of marine turtles is equally wide. Interestingly, *Mosasaurus* shows a narrow range, and *Tylosaurus* shows an equally narrow, but decidedly offset range of values from all other mosasaurs. The latter overlaps with ammonites, showing a possible preference for foraging in the upper water column.

All lines of evidence together suggest that some mosasaurs had preferred foraging depths, and that others, like *Prognathodon*, foraged between offshore and nearshore habitats. It is interesting to note, however, that oxygen isotope studies across various localities of the Western Interior Seaway tend to find slightly offset values. This could reflect local water body differences, i.e., small differences in salinity, runoff, and temperatures.

---

## Comparative dental microwear analyses of North American ursids to infer the dietary palaeoecology of extinct Pleistocene short-faced bears from the Yukon

Howard M. Huynh<sup>1</sup>, Prieyankaa Nirmalan<sup>2</sup>, and Danielle Fraser<sup>1,3,4</sup>

<sup>1</sup>Beaty Centre for Species Discovery, Canadian Museum of Nature, PO Box 3443 Stn "D", Ottawa, ON K1P 6P4, Canada; hhuynh@nature.ca, dfraser@nature.ca

<sup>2</sup>Department of Biology, University of Ottawa, Ottawa, ON, K1N 9A7, Canada

<sup>3</sup>Department of Biology, Carleton University, Ottawa, ON, K1S 5B6, Canada

<sup>4</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, K1S 5B6, Canada

The extinction of the majority of North America's mammal megafauna occurred at the end of the Pleistocene approximately 11.7 Ka. Short-faced bears (*Arctodus simus*), the largest carnivoran members of the mammalian megafauna at the end of the Pleistocene, were amongst those that became extinct. However, the ecological characteristics (e.g., diet, behavior, life history) that may have increased extinction risk for *A. simus*, relative to the other extant North American bears, remain unresolved. Dietary specialization is particularly known to enhance extinction risk among mammals. Thus we aim to reconstruct the diet of *A. simus* from the Yukon, Canada using dental microwear analysis and compare it to extant sympatric North American ursids. Lower molars (m1 and m2) were molded, cast, and imaged using scanning electron microscopy from vouchers of *A. simus*, brown bear (*Ursus arctos*), black bear (*Ursus americanus*), and polar bear (*U. maritimus*). The number of pits and scratches were counted and statistically compared. Analyses of variance showed significant differences in mean numbers of pits ( $df = 3$ ,  $F = 7.343$ ,  $p < 0.05$ ) and scratches ( $df = 3$ ,  $F = 6.182$ ,  $p < 0.05$ ) among all species. Despite previous isotopic characterization of *A. simus* as a highly specialized carnivore, we show that this species may have had a more varied diet consisting of meat and hard foods such as leaves, seeds, and fruit similar to *U. arctos*. Hence, we surmise that *A. simus* may not have been a dietary specialist but rather a generalist omnivore, which means that diet may not have been an inherent extinction risk factor that contributed to their extinction.

---

# Size reduction in Beringian *Equus* throughout the Late Pleistocene leading up to their extinction

Zoe Landry<sup>1,2</sup>, Clément P. Bataille<sup>1,3</sup>, and Danielle Fraser<sup>2,4,5,6</sup>

<sup>1</sup>Department of Earth Sciences, University of Ottawa, Ottawa, ON, K1N 6N5, Canada; zland032@uottawa.ca

<sup>2</sup>Beaty Centre for Species Discovery, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; dfraser@nature.ca

<sup>3</sup>Department of Biology, University of Ottawa, Ottawa, ON, K1N 9A7, Canada; cbataill@uottawa.ca

<sup>4</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, K1S 5B6, Canada

<sup>5</sup>Department of Biology, Carleton University, Ottawa, ON, K1S 5B6, Canada

<sup>6</sup>Paleobiology Smithsonian National Museum of Natural History, Washington, DC, 20560, USA

Body mass changes in response to global climatic shifts are well-documented phenomena in mammals; large mammals tend to exhibit rapid decreases in body mass as temperatures rise, consistent with Bergmann's rule. Body mass estimates from limb bones suggest that Beringian horses (*Equus ferus*) from Alaska underwent a considerable decline in body mass (~15%) over approximately 25 ka leading up to their extinction near the end-Pleistocene. Here, we investigate whether the same trend can be observed in the teeth of Beringian horses from the Yukon, as, much like limb bones, mammalian teeth are considered good predictors of body mass. We took measurements from 3rd and 4th premolars of Beringian *Equus lambei* and *Equus* sp. specimens from the collections of the Canadian Museum of Nature to generate body mass estimates, and we subsequently radiocarbon dated the specimens at the A.E. Lalonde AMS Laboratory. Preliminary analyses show that Yukon Beringian horses underwent a drastic reduction in body mass (~60%) from >44–4 ka. We suggest that, consistent with previous work, the decrease in body mass was likely driven primarily by either: 1) changes in climatic and/or vegetation regimes, or 2) by species-specific differences in body mass and species turnover, although we acknowledge that further research is required in order to determine which of these two possible explanations is better supported. These early results lend support for Bergmann's rule in perissodactyls and could help to inform future research regarding extinction drivers of northern North American Pleistocene megafauna.

---

## Sense and sensibility: estimating the hearing capability of otophysan fish and implications for their fossil relatives

Juan Liu

Department of Integrative Biology, University of California, Berkeley, Berkeley, CA 94720, USA; and University of California Museum of Paleontology, Berkeley, CA 94720, USA)

Sensory biology is an area of vertebrate evolution and paleontology that has remained relatively inaccessible because of the rarity of preservation. Recent advances in imaging and computational modelling have permitted a renewed research program focusing on sensory system structure and function. Here I introduce a new framework for studying auditory system variation and adaptation in fishes using dynamic finite element analysis (dFEA). The model organism utilized in this study was zebrafish (*Danio rerio*) which allowed for creation of a baseline and 3D geometric models of Weberian ossicles of a sample of otophysans were constructed from high-resolution x-ray computed tomographic data. The 3D models were subjected to modal and harmonic dynamic finite element analyses to evaluate how ossicle chains respond to a range of auditory frequencies. Results indicate that the simu-



lated resonance frequency in the dFEA models matches hearing frequencies obtained from behavioral and electrophysiological audiogram data. Furthermore, resonance frequency exhibits a negative covariation with ossicle size but appears to be isometric after size correction. These findings suggest that dFEA demonstrates potential to permit improved estimation and reconstruction of the hearing capability of extinct otophysan fish taxa. This approach forms a basis for future applications to analyzing hearing ossicles in other vertebrates in non-aquatic habitats such as terrestrial, subterranean, and aerial environments.

## The timing and ecological evolution of modern ant lineages

Elyssa Loewen<sup>1,4</sup>, Caelan Libke<sup>1</sup>, Christine Sosiak<sup>2</sup>, Phillip Barden<sup>2</sup>, Christopher Somers<sup>1</sup>, and Ryan C. McKellar<sup>1,3,4</sup>

<sup>1</sup>Biology Department, University of Regina, Regina, SK, S4S 0A2, Canada; elyssa.loewen18@gmail.com; caelan.libke@gmail.com; chris.somers@uregina.ca

<sup>2</sup>Federated Department of Biological Sciences, New Jersey Institute of Technology, Rutgers-Newark University, Newark, New Jersey, 07102, USA; ces43@njit.edu, barden@njit.edu

<sup>3</sup>Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas, 66045, USA

<sup>4</sup>Royal Saskatchewan Museum, Regina, SK, S4P 2V7, Canada; ryan.mckellar@gov.sk.ca

Ants are an integral and ubiquitous component of modern ecosystems where they play an outsized role as ecosystem engineers due their significant phylogenetic and ecological diversity, and sheer abundance. Our understanding of ant evolution and how they came to dominate modern ecosystems is severely limited by a 17-million-year gap in the ant fossil record spanning the Maastrichtian to the early Eocene. During this gap, which buffers the end-Cretaceous (K-Pg) mass extinction (66 Ma), all stem ant lineages appear to go extinct; when the fossil record resumes in the Eocene, only crown lineages (i.e., lineages that diverged from the common ancestor of modern ants) remain. Here, we report two crown ants (Formicidae) from a diverse Late Cretaceous ( $67.04 \pm 0.16$  Ma) amber assemblage in the Big Muddy Badlands of Saskatchewan that fills this critical faunal gap. The unexpectedly high abundance of crown ants in Big Muddy amber suggests that the stem-to-crown ant faunal turnover occurred, or at least was underway, before the K-Pg extinction. These two ant fossils represent only the second record of Aneuretinae from Cretaceous amber, and the oldest record for the genus *Tetraponera* (Pseudomyrmecinae), pushing their estimated age and split from other Pseudomyrmecinae genera back into the Cretaceous. Both ants also have relictual modern relatives: Aneuretinae is restricted to a single species in Sri Lanka, *Aneuretus simoni*, and the genus *Tetraponera* is restricted to the Palaeotropics and Australia. We reconstructed the palaeoecology of the Big Muddy ants and compared them to the ecological occupations of their modern relatives using a predicted Random Forest model. We determined that the ecology of these now relictual lineages has shifted since the Maastrichtian when these ants lived in the northern hemisphere. We recovered the Big Muddy Aneuretinae as a carton-nesting arboreal omnivore (Out-of-bag (OOB) error 21.4%), in contrast to modern *Aneuretus simoni*, which is a leaf-litter omnivore. The fossil *Tetraponera* species appears to be a leaf-litter nesting epigeaic omnivore (OOB error 16.25%) in contrast to modern *Tetraponera* species, which are lignicolous arboreal phytophages. These results indicate that, in addition to occupying a larger geographic distribution in the Cretaceous, both ant lineages occupied a wider range of ecological niches. It is likely that palaeoenvironmental and biotic changes in the Late Cretaceous and throughout the Cenozoic impacted the evolution and ecological occupations of these ant lineages, resulting in their extirpation from large portions of their ancestral range. The faunal turnover of ecologically dominant ant groups may indicate significant changes within terrestrial environments and biotic communities one million years before the K-Pg mass extinction.

# A petrified struggle for survival from the Lower Cretaceous deposits of China

Jordan C. Mallon<sup>1,2</sup>, Gang Han<sup>3,4</sup>, Aaron J. Lussier<sup>5</sup>, Xiao-Chun Wu<sup>1</sup>, Robert Mitchell<sup>6</sup>, and Ling-Ji Li<sup>7</sup>

<sup>1</sup>Beaty Centre for Species Discovery and Palaeobiology section, Canadian Museum of Nature, Ottawa, ON, Canada; jmallon@nature.ca; xcwu@nature.ca.

<sup>2</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, Canada

<sup>3</sup>Hainan Vocational University of Science and Technology, Haikou City, Hainan Province, China; hg0805@126.com

<sup>4</sup>Hainan Tropical Ocean University, Sanya City, Hainan Province, China

<sup>5</sup>Beaty Centre for Species Discovery and Mineralogy section, Canadian Museum of Nature, Ottawa, ON, Canada; alussier@nature.ca

<sup>6</sup>Department of Geography, University of Calgary, Calgary, AB, Canada; robert.mitchell1@ucalgary.ca

<sup>7</sup>Weihai Ziguang Shi Yan School, Weihai City, Shandong Province, China; lilingji@unisedu.com

Dinosaurs and mammals arose during the Late Triassic, and have coexisted for the last 230 million years (the former as birds, following the end-Cretaceous mass extinction). Mesozoic dinosaurs are commonly depicted as having overshadowed the contemporaneous mammal fauna, and several examples of fossil gut contents reveal that small mammals were regularly incorporated into the diets of the larger dinosaurs. It was not until the Cenozoic that mammals eventually outgrew and regularly preyed upon the available avifauna.

However, the interaction of dinosaurs and mammals during the Mesozoic was not always so unilateral. In 2005, a fossil was described from the Lower Cretaceous Lujiatun beds of China showing the opossum-sized mammal *Repenomamus robustus* with gut contents consisting of the juvenile remains of the parrot-beaked dinosaur *Psittacosaurus* cf. *P. lujiatunensis*. Here, we report on a yet more impressive find from the same beds, showing these two species locked in mortal combat. The dinosaur is approximately three times larger than the mammal by body mass, estimated from standard limb scaling relationships. Their skeletons are intimately intertwined, with the mammal gripping both the lower jaw and hindleg of the dinosaur as it bites into the dinosaur's ribcage. We consider various hypotheses for this unique association, but conclude that the evidence on balance supports the interpretation that this fossil represents a predation attempt on the part of the mammal, suddenly entombed by a lahar-type volcanic debris flow, approximately 125 million years ago.

---

## Insights and limitations in reconstructing the musculature and skeletal arrangement of the foot in tyrannosaurids and other non-avian theropod dinosaurs

Annie P. McIntosh<sup>1</sup>, Corwin Sullivan<sup>1</sup>, John Acorn<sup>2</sup>, and Philip J. Currie<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; apmcinto@ualberta.ca; corwin1@ualberta.ca; pjcurrie@ualberta.ca

<sup>2</sup>Department of Renewable Resources, University of Alberta, Edmonton, AB, T6G 2E9, Canada; jacorn@ualberta.ca

The reconstruction of the skeleton and its associated musculature in fossil taxa depend on the ability to identify the locations of the tendinous muscle insertions and ligamentous bone-to-bone contacts on the fossilized skeletal elements. However, researchers have not agreed on the identifications of various rugose marks on the bones of the foot in tyrannosaurids and other non-avian theropods, resulting in inconsistent reconstructions of the foot, and specifically of the contact between the first and second metatarsals (Tarsitano 1984; Norell and Makovicky 1997; Carrano and Hutchinson 2002; Hattori 2016). At some point during the evolution of birds, the first digit (hallux) migrated distally along the second metatarsal from the ankle and became reversed to oppose the other digits (Botelho et al. 2015). Additionally, whereas the gastrocnemius muscle (m. gastrocnemius) inserts onto the tarsometatarsus in modern birds, it inserts onto the calcaneum in crocodylians and other tetrapods (Reilly and Blob 2003; Klinkhamer et al. 2017). This indicates that a distal migration of the insertion of m. gastrocnemius occurred at some point on the evolutionary line to birds. Ligaments and tendons, which attach bone to bone and to muscle, respectively, are structurally similar and both composed of collagen (Zschäbitz 2005), and studies have found it difficult to accurately identify osteological correlates of these types of soft tissue insertions on bone and to distinguish between them (Petermann and Sander 2013; Rothschild et al. 2016). Therefore, any rugose marks present on the bones of the foot in fossil taxa could in principle represent either muscle attachments or contacts with other bones, and osteological evidence of these attachments may not be present at all in some taxa. In extant birds, m. gastrocnemius leaves proximally-positioned rugose patches on the medial and lateral edges of the posterior surface of the tarsometatarsus and the contact of the first metatarsal is easily identifiable by a distinct fossa located posterodistally on the tarsometatarsus (Botelho et al. 2017). However, such clear osteological correlates are not always evident in fossil taxa, and undistorted, articulated specimens are relatively scarce. Although reconstructions remain somewhat speculative and should be made cautiously, assumptions can be made based on the skeletal morphology and musculature of modern birds while recognizing the limitations of those assumptions. The morphology of the metatarsals is fairly consistent across Late Cretaceous North American tyrannosaurids, which have two posterior-facing rugose patches on the second metatarsal and one on the fourth metatarsal that is consistent with the proximal patch on the second metatarsal. Based on the relative positions of the insertion of m. gastrocnemius and the contact of the hallux to the tarsometatarsus in modern birds, it is likely that the rugose patch on the fourth metatarsal and the proximal patch on the second metatarsal represent the insertions of m. gastrocnemius, whereas the distal patch on the second metatarsal represents the contact with the first metatarsal. This indicates that the hallux was distally positioned on the second metatarsal in tyrannosaurids and was to some degree reversed to oppose the other digits, similar to the conditions seen in modern birds. The metatarsals of dromaeosaurids and troodontids, however, are relatively smooth and lack distinct rugose patches like those found in tyrannosaurids, and more research is needed to more accurately reconstruct their morphology.

## Literature Cited

- Botelho, J.F., D. Smith-Parades, S. Soto-Acuña, J. Mpodozis, V. Palma, and A.O. Vargas. 2015. Skeletal plasticity in response to embryonic muscular activity underlies the development and evolution of the perching digit of birds. *Scientific Reports* 5:1–11.
- Botelho, J.F., D. Smith-Parades, S. Soto-Acuña, D. Núñez-León, V. Palma, and A.O. Vargas. 2017. Greater growth of proximal metatarsals in bird embryos and the evolution of hallux position in the grasping foot. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 338:106–118.
- Carrano, M.T., and J.R. Hutchinson. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology* 253:207–228.
- Hattori, S. 2016. Evolution of the hallux in non-avian theropod dinosaurs. *Journal of Vertebrate Paleontology* 36:e1116995.
- Klinkhamer, A.D., D.R. Wilhite, M.A. White, and S. Wroe. 2017. Digital dissection and three-dimensional interactive models of limb musculature in the Australian estuarine crocodile (*Crocodylus porosus*). *PLoS ONE* 12:e0175079.
- Norell, M.A., and P.J. Makovicky. 1997. Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates* 3215:1–28.

- Petermann, H., and M. Sander. 2013. Histological evidence for muscle insertion in extant amniote femora: implications for muscle reconstruction in fossils. *Journal of Anatomy* 222:419–436.
- Reilly, S.M., and R.W. Blob. 2003. Motor control of locomotor hindlimb posture in the American alligator (*Alligator mississippiensis*). *Journal of Experimental Biology* 206:4327–4340.
- Rothschild, B.M., D.R. Wilhite, D.S. McLeod, and H. Ting. 2016. *Historical Biology* 28:842–848.
- Tarsitano, S. 1983. Stance and gait in theropod dinosaurs. *Acta Palaeontologica Polonica* 28:251–264.
- Zschäbitz, A. 2005. Anatomie und Verhalten von Sehnen und Bändern. *Der Orthopäde* 34:516–525.
- 

## Bioerosion trace fossils on *Triceratops* bones from the latest Cretaceous Frenchman Formation, southwestern Saskatchewan, Canada

Jack R. Milligan<sup>1</sup>, Emily L. Bamforth<sup>1,2</sup>, Luis A. Buatois<sup>1</sup>, and M. Gabriela Mángano<sup>1</sup>

<sup>1</sup>Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK, S7N 5E2, Canada; jrm451@mail.usask.ca; luis.buatois@usask.ca; gabriela.mangano@usask.ca

<sup>2</sup>Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 3S0, Canada; curator@dinomuseum.ca

Bioerosion trace fossils are biogenic structures that record evidence of behaviour in hard substrates, including rocks, wood, shells, and bones. Vertebrate fossils with associated osteic bioerosion structures have been well documented globally throughout the Mesozoic and Cenozoic (251.90–66.0 ma, 66.0–0.0 ma). Invertebrate and vertebrate trace makers have been identified in many instances, offering unique insights into taphonomy and paleoecology. While non-avian dinosaurs are commonly the focus of these studies elsewhere in the world, documented cases of bioeroded dinosaur material are less common in Canada. Herein, we present several *Triceratops* specimens that feature a suite of bioerosion trace fossils from the Maastrichtian Frenchman Formation in southwestern Saskatchewan. Several cranial fragments from one associated individual, RSKM P3336, display large, unbranching tunnel-like structures that penetrate through the bone. These structures appear to be ornamented with bioglyphs as scratches and/or engravings inscribed in negative relief on the inner wall of the borings. A rib from another individual, RSKM P3127.1, displays several trace fossils, including a deep, rounded chamber with constructed walls, and several smaller borings that are present on the cortical bone surface. These skeletal fragments occur in massive mudstones with abundant organic material interpreted as paleosols. Trace fossils on vertebrate bones in continental settings have been commonly attributed to insects, dermestid beetles, and termites being the most cited. This assumption is partly due to the size of the trace fossils, and observations of modern dermestids as capable of necrophagous and osteophagous behaviour. These bioerosion structures were likely created post-mortem since there is no evidence of bone regrowth around the borings. Analyzing the mechanisms behind the creation of these structures on *Triceratops* bones is important for understanding the depositional setting and corresponding taphonomic pathway of these specimens, and the hidden diversity of invertebrate decomposers in the Late Cretaceous. This study hopes to serve as a template for future studies on the taphonomy of bioeroded vertebrate fossils using ichnology and sedimentology, especially when body fossil evidence of the trace maker is absent.

---



# The head, heart, and fins of a jawless stem gnathostome

Tetsuto Miyashita<sup>1</sup>, Michael I. Coates<sup>2</sup>, Kristen Tietjen<sup>3</sup>, Pierre Gueriau<sup>4</sup>, and Philippe Janvier<sup>5</sup>

<sup>1</sup>Palaeobiology Section, Canadian Museum of Nature, Ottawa, ON, Canada; TMiyashita@nature.ca

<sup>2</sup>Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL, USA

<sup>3</sup>Biodiversity Institute and the Museum of Natural History, University of Kansas, Lawrence, KS, USA

<sup>4</sup>Institut photonique d'analyse non-destructive européen des matériaux anciens, Université Paris-Saclay, Gif-sur-Yvette, France

<sup>5</sup>Centre de recherche en paléontologie – Paris, Museum national d'Histoire naturelle, Paris, France

A conventional sister group to jawed vertebrates, osteostracans anchor synapomorphies and symplesiomorphies of the clade. This canonical view sets osteostracans in a mosaic of derived gnathostome traits (such as cellular bone) against the background of lamprey-like overall morphology (such as a blind nasohypophyseal canal). Extensive studies of their perichondrally ossified endoskeletons have provided support for this interpretation. However, few CT scans have been undertaken for osteostracan internal anatomy.

Here we present preliminary results from a synchrotron X-ray tomography scan of a new specimen of *Norselaspis*, and reveal surprisingly derived gnathostome traits in this osteostracan exemplar. Contrary to the earlier interpretations, the vestibular sinus superioris is as tall in *Norselaspis* as those in jawed vertebrates. The pericardial chamber is closed dorsally, which precludes the lamprey-like single midline Cuvierian duct. There is no articular facet in the pectoral cavity, which suggests an entirely fleshy base of the pectoral fin. Our three-dimensional model also enhances key findings from the previous reconstruction, including: configurations of the extraocular muscles and associated motor nerves, exogeneous infillings in the labyrinth, and brachial nerve arising as the most anterior spinal projections.

These findings both refine and revise the stem-to-crown continuum of gnathostome characters. *Norselaspis* has derived gnathostome conditions in the inner ear and circulatory system. However, we present evidence that endoskeletal joints emerge with the evolutionary origin of jaws; in this respect, *Norselaspis* remains resolutely plesiomorphic. Interestingly, an apparent lack of the crown-like hypobranchial system in *Norselaspis* implies its independent and divergent evolution in cyclostomes and gnathostomes.

---

## A juvenile pachycephalosaur (Dinosauria: Ornithischia) skeleton from the upper Maastrichtian Frenchman Formation of Saskatchewan, Canada

Bryan R.S. Moore<sup>1,2</sup>, David C. Evans<sup>3,4</sup>, Michael J. Ryan<sup>1,5</sup>, R. Timothy Patterson<sup>1</sup>, and Jordan C. Mallon<sup>1,5</sup>

<sup>1</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, K1S 5B6, Canada; bryan.moore@ucalgary.ca

<sup>2</sup>Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4, Canada

<sup>3</sup>Department of Natural History, Royal Ontario Museum, Toronto, ON, M5S 2C6, Canada

<sup>4</sup>Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, M5S 3B2, Canada

<sup>5</sup>Beaty Centre for Species Discovery and Paleobiology Section, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada

Pachycephalosaurs are small (~2–6 m in length), bipedal, ornithischian dinosaurs that lived during the Late Cretaceous in Asia and North America. They are best known for the characteristic fusion of their frontal and parietal bones into a thickened skull dome. These domes are their most commonly preserved element, in part because the less robust elements of their postcrania are more easily lost to post-mortem taphonomic processes. As a result, most inferences about pachycephalosaur growth, anatomy, and phylogenetics are based primarily on skull morphology.

In this study we describe a small, partial pachycephalosaur postcranium (CMN 22039) from the uppermost Maastrichtian Frenchman Formation of Saskatchewan. The specimen was discovered by Dale Russell in 1973 at the base of a 6.7 m thick claystone unit, approximately 14 m below the Ferris No. 1 Coal Seam (which approximates the K-Pg boundary in this area). Preserved elements include portions of the dorsal, sacral, and caudal vertebrae, assorted ribs, the complete pelvic girdle, and portions of the hind limb. The specimen was originally assigned to *Thescelosaurus*, but was subsequently recognized as a pachycephalosaur based on several diagnostic characters, including the presence of a prominent flange projecting medially from the dorsal margin of the ilium, a double ridge-and-groove articulation of the pre- and post-zygapophyses of the dorsal vertebral arches, and an extremely reduced pubis that is nearly excluded from the acetabulum. Osteohistological analysis of the tibia and fibula reveals an immature woven bone texture which lacks any lines of arrested growth or secondary remodeling. This, together, with the unfused neurocentral sutures of the vertebrae and the small size of the specimen (femur length = 84.5 mm), attest to the juvenile status of the individual. A cladistic parsimony analysis including CMN 22039 recovered it in a basal position in Pachycephalosauridae, likely due to its lack of skull characters and its inferred juvenile status. Based on its stratigraphic age, geographic location, size, and postcranial character states, we hypothesize that CMN 22039 represents a specimen of *Sphaerolithus buchholtzae* and may be the first postcranial skeleton known for this genus. Other possible taxonomic identities for CMN 22039 (*Alaskacephale gongloffi*, *Pachycephalosaurius wyomingensis*, and *Stygomoloch spinifer*) either do not share diagnostic overlapping material with the specimen, or possess conflicting postcranial character states, and cannot be compared on this basis.

CMN 22039 demonstrates that diagnostic pachycephalosaur characters are present in the postcranial skeleton even at the earliest stages of ontogeny, probably before the development of the characteristic skull dome. Our study highlights the importance of evaluating the postcranial skeleton during taxonomic identification and shows that pachycephalosaur remains can be recognized at a young age even without cranial material.

---

## A multivariate comparison of the vertebrate faunas of the Horseshoe Canyon and Wapiti formations of Alberta, Canada with implications for vertebrate biogeography

Nathaniel E.D. Morley<sup>1</sup>, Lindsey R. Leighton<sup>1</sup>, Eva B. Koppelhus<sup>2</sup>, and Philip J. Currie<sup>1</sup>

<sup>1</sup>Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB, T6G 2E3, Canada; nmorley@ualberta.ca; lindseyrleighton@gmail.com

<sup>2</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; eva.koppelhus@ualberta.ca; pjcurrie@ualberta.ca

The terrestrial biota of the latest Campanian and early Maastrichtian of Alberta, Canada is largely represented by two geological units: the Horseshoe Canyon Formation and the Wapiti Formation. The strata of these formations were deposited in one geographically contiguous basin, with the former representing a coastal setting and

the latter representing a somewhat more inland setting. The numerous well-sampled bonebeds from these formations provide an excellent opportunity to test whether a coastal-to-inland environmental gradient led to vertebrate endemism in the Western Interior Basin, as has been previously hypothesised by qualitative studies. This study used ordination and multivariate statistical techniques on both occurrence- and abundance-based data to test for compositional heterogeneity among eight well-sampled (>100 identifiable specimens) bonebeds from the Horseshoe Canyon-Wapiti system during a 2.7 Ma time interval in the latest Campanian. The results indicated that there is no significant compositional difference between the two formations, failing to support prior claims of vertebrate endemism resulting from a coastal-to-inland environmental gradient in the Western Interior Basin. This study demonstrates the importance of assessing community-level data before drawing inferences on the community palaeoecology of a given system.

---

## Identification of acanthomorph diversity in microvertebrate fossil sites

Alison M. Murray<sup>1</sup> and Donald B. Brinkman<sup>1,2</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; ammurray@ualberta.ca

<sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; don.brinkman@gov.ab.ca

Innumerable fossil fish specimens have been recovered from fossil microvertebrate sites – areas in which small, isolated elements of the skeleton from multiple individuals have been amassed. The accumulation of these skeletal elements is often the result of transportation by moving waters (e.g., rivers) for some distance prior to deposition, and thus they may be time averaged (i.e., accumulated over an unknown period of time). These accumulations provide an important window on the fauna that was present in a wider area during a broader period of time than that represented by individual articulated specimens. Although microvertebrate sites provide important records of taxa, the disarticulated condition of the fossil elements can cause difficulties for taxonomical identification. This is particularly true for many fish. The most common fish element preserved in microfossil sites are vertebral centra; however, fish centra are notoriously difficult to identify at lower taxonomic levels, partly because of the vast numbers of living fish and lack of comparative collections. Among one higher group, Acanthomorpha, some progress is being made. Arguably the most distinctive vertebral centrum among all fish is the first abdominal centrum of Acanthomorpha. In acanthomorphs, the first centrum differs from that of all other groups of fishes in that it bears two distinct (separate left and right) facets for articulation with the exoccipitals, which are more or less dorsolateral to the articular facet for the basioccipital. This creates a unique tri-partite morphology of the first centrum in acanthomorphs. Because there is only a single first vertebra in each fish, recognizing these first centra allows an accurate count of the minimum number of individual acanthomorph fishes that were present in the locality. These centra are also useful to identify the minimum number of different acanthomorph lineages present in the site, based on different morphologies of the first centrum. While different morphologies indicate the presence of different acanthomorph taxa, we are interested in gleaning more information from these elements by identifying the centra to lower taxonomic levels. This will allow us to gain an understanding of which acanthomorph lineages are present, rather than just numbers of lineages. To enable a better understanding of the acanthomorph taxonomic diversity in fossil sites, we are documenting the diversity of morphologies in extant taxa. Ultimately, this research will lead to identifying specific features that are of phylogenetic value, and that will allow us to more narrowly identify which acanthomorphs are present in microvertebrate sites.

# Madtsoiidae: monophyletic clade or grouping of convenience?

Mark J. Powers<sup>1</sup>, Fernando F. Garberoglio<sup>2</sup>, and Michael W. Caldwell<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; powers1@ualberta.ca

<sup>2</sup>CONICET-Fundación de Historia Natural Félix de Azara, Centro de Ciencias Naturales Ambientales y Antropológicas, Universidad Maimónides, Hidalgo 775, 1405 Buenos Aires, Argentina

Madtsoiidae is currently defined as an extinct family of snakes that share several vertebral characteristics. They appeared in the Late Cretaceous of Gondwana and reached a nearly global distribution by the Eocene, frequently acquiring large body sizes and utilizing narrow intercontinental seaways for dispersal. Early discovered specimens were referred to Boidae or Pythonidae due to general similarities of vertebral proportions. However, frequent observations of several key vertebral features such as the absence of accessory prezygapophyseal processes, the presence of laterally expanded para-diapophyses and the presence of parazygantral foramina led to the hypothesis that Madtsoiidae represents a valid clade of snakes. Due to cranial material being quite rare, most named taxa within Madtsoiidae are described from isolated or segments of articulated vertebrae, including the type species *Madtsoia bai* from Eocene deposits of the Chubut province, Argentina. Because of the paucity of well-preserved specimens for madtsoiids, species diagnoses and phylogenetic relationships are resolved almost entirely on vertebral characters, which can show considerable variation along the vertebral column of an individual. The variability of madtsoiid synapomorphies across the vertebral column has not been critically assessed due to the lack of cervical (anterior trunk) and caudal (post-cloacal) vertebrae. An articulated series of madtsoiid cervicals from upper Eocene deposits of the Divisadero Largo Formation in the Cuyo Basin of the Mendoza province, Argentina, are referred to *Madtsoia* sp. based on identified madtsoiid synapomorphies (parazygantral foramina), age (mid-late Eocene) and proximity to the holotype locality. Comparison of this specimen to others from extinct and extant snake clades reveals a wide range of putative madtsoiid synapomorphies are variably expressed in non-madtsoiid clades. The variability of these “synapomorphies” across a single vertebral series demonstrates problematic degrees of intraspecific variation when diagnosing isolated vertebrae. These observations reinforce the poor utility of vertebral characters in snake phylogenetics, and stress the importance of relatively complete specimens in constructing species diagnoses.

---

## Vertebral pathology: A primer addressing its definitive features in the paleontological record

Bruce Rothschild

Indiana University Health, Muncie, IN, 47304, USA; spondylair@gmail.com

With the increasing complexity of a skeletal system, more numerous are the opportunities for its structural integrity to be compromised. This is especially true for the vertebral column which consists of bones stabilized anteriorly/ventrally by their intervertebral anatomy and dorsally/posteriorly by zygapophyseal/facet joints. These two components are interdependent; alterations of one places stresses on the other, with the anticipated biomechanical response. Vertebrae are predominantly, but not invariably, separated by discs in mammals, by diarthrodial (synovial lined) joints in lower vertebrates and are subject to both mechanical forces and hazards related to surrounding structures. Vertebral pathology could potentially and not mutually exclusively be divided into bone loss and bone accretion.

Bone loss in the form of lysis or erosion is relatable to trauma, inflammatory arthritis infection, neoplasia, pressure phenomena and potentially osteoporosis (allowing vertebral collapse). The pressure phenomenon responsible for aneurysm formation can also leave a sharply defined imprint as can spondyloarthropathy and gout. Infectious lesions tend to be less sharply defined, but it is the reactive filigree reaction and draining sinuses that allow confident diagnosis, at least of the “pyogenic” variety. Space-occupying infections (often referred to as non-pyogenic or granulomatous) produce quasi-spheroid lesions, often with quite minimal bone response. Specific among those is the endplate groove apparently related to brucellosis. Neoplasia generally produces irregular-shaped damage, with residual normal trabeculae at edges. A major differential clue to distinguishing between infection and neoplasia is endplate involvement. Neoplasia may affect multiple vertebrae but does not cross joint/disc spaces. Last among the bone loss phenomena are the vertebral endplate depressions referred to as pressure derived Schmorl’s nodes in mammals with intervertebral discs. Most reptiles, however, seem to have synovia-lined cavities rather than discs separating/joining their vertebrae and thus their articular surface alterations represent erosions rather than pressure phenomena. Differential considerations then are limited to inflammatory arthritis (e.g., spondyloarthropathy) and infectious arthritis.

Bone accretion is relatable to spondylosis deformans or osteoarthritis, inflammatory arthritis, infection, neoplasia and healing responses and paraspinal ligamentous [e.g., diffuse idiopathic skeletal hyperostosis (DISH)] phenomena. Endplate-derived overgrowths of bone that are perpendicular to the long axis of the vertebral column are referred to as osteophytes. If the vertebral endplates involved are separated by synovia-lined joints (diarthrodial), osteoarthritis is defined. Since osteoarthritis is a disease of joints, it is not the appropriate term if the bones involved are not-so separated and the correct designation would be spondylosis deformans.

With respect to fusion/ankylosis of vertebrae, any alteration that reduces joint stability may be associated with new bone formation that bridges the joint components, restoring stability. Arthritis-related bridging, referred to as syndesmophytes, may appear as gracile or bulky bridging, always involving the edge of the vertebral endplate as well as ligamentous structures, in contrast to DISH in which ossification is solely ligamentous. Apposition of calcific material on endplate surfaces identifies calcium pyrophosphate depositional disease (CPPD), an inflammatory arthritis. Differential consideration includes what has been referred to as central osteophytes, a phenomenon in search of an explanation. As vertebrae are the “measure” of Vertebrata, it seems appropriate to systematically examine related organismal “vulnerabilities” and to establish an epidemiological data base.

---

## A small early Permian parareptile with a lateral temporal fenestra from Richards Spur, Oklahoma

Dylan Rowe, Erin Beaudesne, Joseph Bevitt, and Robert Reisz

Department of Biology, University of Toronto Mississauga, Toronto, ON, Canada

A small, pristinely preserved specimen from the Dolese Brothers limestone quarry near Richards Spur, Oklahoma provides evidence for the presence of a new early Permian parareptile. The specimen includes an articulated, nearly complete skull roof with the right premaxilla, right quadratojugal and most of the right palate, as well as the right epipterygoid and the sphenethmoid. Although similar in many respects to the other contemporary parareptiles *Acleistorhinus*, *Delorhynchus* and *Colobomycter* from Oklahoma, it can be distinguished from other acleistorhinids by the presence of autapomorphic dental characters. Phylogenetic analysis places the specimen closer to *Delorhynchus* and *Colobomycter* within Acleistorhinidae than to *Acleistorhinus pteroticus*. Unique aspects of the present specimen include the pronounced anterior extension of the lacrimal bone, largely homodont dentition composed of simple conical crowns with slight recurvature in the premaxillary and anterior maxillary teeth,



and simple conical crowns in posterior maxillary dentition. The discovery of this new parareptile along with the large number of other parareptiles at Richards Spur highlights the importance of this site which has preserved a number of articulated specimens. This early Permian site is unique in that it has such a wide diversity of parareptilian taxa and provides important insights into the complex community of these ancient terrestrial vertebrates. The present specimen highlights the morphological diversity among Parareptilia occupying relatively similar niches within the locality of Richards Spur.

---

## A plesiosaur representing the first published vertebrate material from the foraminifera-dominated Peace River Formation, Alberta, Canada

Maximilian Scott

Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 3S0, Canada; mscott@dinomuseum.ca

A plesiosaur (Reptilia, Sauropterygia) catalogued in the collections of the Philip J Currie Dinosaur Museum, specimen PJCDM 2017.13.1, from the middle Albian Cadotte member represents the first published vertebrate material from the Peace River Formation of Northwestern Alberta. The Peace River Formation (Lower Cretaceous, Albian stage) consists of sediments consistent with a shallow, coastal marine environment transitioning from an intertidal bay to a lower marine environment on the west coast of the Western Interior Seaway.

The specimen is represented by the impression of a section of three and a half articulated dorsal vertebrae (each measuring 7 cm in length and 5 cm in width at the center), 14 exposed partial gastralia, several impressions of missing gastralia, a partially broken left coracoid (measuring 40 cm in length), a faint impression of the lower center-facing portion of the right coracoid, and a concentration of gastroliths in the belly. The morphology of the coracoid, bearing an intercoracoid vacuity, is diagnostic to Elasmosauridae, of an age comparable with only one named Albertan elasmosaurid from the Albian stage, *Wapuskaneptes betsynichollsae*. Based on coracoid length, this individual is smaller than *W. betsynichollsae*, and the coracoid of this specimen is morphologically distinct from that of *W. betsynichollsae* given that the posterior end of the coracoids on the Peace River specimen are unfused. The presence of a posterolateral cornua indicates the individual was ontogenetically mature at the time of death, unlike a morphologically similar specimen in the collections of the Royal Tyrrell Museum of Palaeontology from the Lower Albian Clearwater formation of north-eastern Alberta, TMP 1999.068.0001, which is less robust than PJCDM 2017.13.1 and lacks a posterolateral cornua.

It is possible that PJCDM 2017.13.1 represents a new species of North American elasmosaurid given its morphological distinctness from similar-aged taxa, though may be taxonomically similar to the Albian elasmosaur TMP 1999.068.0001. This specimen may also indicate the potential for future fossil discoveries from the Peace River Formation, which has historically been under-sampled for vertebrate material.

---

# Duck-faced and eagle-eyed: a well-developed visual system in a high-latitude hadrosaur

Henry S. Sharpe<sup>1</sup>, Philip J. Currie<sup>1</sup>, and Corwin Sullivan<sup>1,2</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada; hssharp@ualberta.ca corwin1@ualberta.ca; pjcurrie@ualberta.ca

<sup>2</sup>Philip J. Currie Dinosaur Museum, Wembley, AB, Canada

*Edmontosaurus* is a large hadrosaurid dinosaur known from the Campanian and Maastrichtian of North America, with a biogeographic range spanning from the southern United States to the north slopes of Alaska. *Edmontosaurus* is distinguished from other hadrosaurids by the presence of a “pocket” in the postorbital bone, a large fossa expanding posteriorly and laterally from the orbit. Three-dimensional cranial reconstruction of an *E. regalis* skull showed that development of the postorbital pocket displaced the posterior margin of the orbit laterally relative to the plesiomorphic condition. This likely gave *Edmontosaurus* a degree of binocular overlap in its field of vision comparable to advanced tyrannosaurids. Continuous resorption of the inner walls of the postorbital pocket even in the largest specimens of *Edmontosaurus* renders identification of soft-tissue correlates problematic, and indicates continuous enlargement of this feature throughout adulthood. Although the exact nature of the contents filling the postorbital pocket is unknown, the inner shape of the pocket resembles the external morphology of an expanded ophthalmic rete, a large thermoregulatory blood vessel plexus behind the eye in modern birds. The optic nerve foramina in *E. annectens* and *E. regalis* are significantly larger in cross-sectional area compared to braincase length than the typical hadrosaurid (e.g., *Hypacrosaurus*, *Maiasaura*) condition. *Edmontosaurus* was likely able to see with better acuity and depth perception than other known hadrosaurids, adaptations that aid modern crepuscular and nocturnal birds and mammals in finding food in low-light conditions. *Edmontosaurus* was capable of inhabiting high latitudes, where enhanced vision may have aided feeding during seasonal darkness.

---

# Quantitative reconstruction of feeding mechanics in *Leptoceratops gracilis* Brown, 1914 using novel digital methods: a proof-of-concept

Emilia L. Silvestre, Louis-Philippe Bateman, and Hans C.E. Larsson

McGill University, Montreal, QC, H3A 0C4, Canada; emilia.silvestre@mail.mcgill.ca; louis-philippe.bateman@mail.mcgill.ca; hans.ce.larsson@mcgill.ca

The study of functional morphology in dinosaurs and other extinct animals has traditionally been inhibited by a lack of reproducible methods. Indeed, simulating the biomechanics of ancient creatures *in silico* is difficult and requires simultaneously considering the biomechanical effects of muscles and responses of a myriad of hard and soft tissues, positions of bones and muscles, and the presence of cartilage. Digital methods are a promising alternative to practical methods. This study aims to serve as a proof-of-concept for high-precision surface scanning and biomechanical reconstructions. Blender, a free open-source software that is becoming the scientific standard for organic 3D modelling, was used to reconstruct and assess the feeding system of the basal ceratopsian *Leptoceratops gracilis* Brown, 1914.

The skull of *Leptoceratops gracilis* (Canadian Museum of Nature specimen CMN 8889) was surface scanned using a handheld 3D scanner. Models generated from the scan were subsequently retrodeformed in Blender. We reconstructed its bite cycle based on anatomical limits of the jaw joint, tooth and beak occlusion, and previously published research on the tooth microwear of this taxon (Varriale 2016). In parallel, we digitally reconstructed all major jaw-closing musculature based on osteological correlates and previous reconstructions of ornithischian cranial musculature. Two muscle arrangements were modelled according to competing hypotheses in the literature after Holliday (2009) and Nabavizadeh (2018). In addition, m. adductor mandibulae externus ventralis (mAMEV) and m. pseudomasseter (mPSM) were added to these models based on previous reconstructions that have been proposed in *Heterodontosaurus* (mAMEV) and *Psittacosaurus* (mAMEV and mPSM) (Serenio 2012; Serenio et al. 2010). Following muscle reconstruction, we estimated the bite force of *Leptoceratops gracilis* at various tooth positions for each model to quantitatively assess the efficiency of the feeding system.

We discovered that the range of motion of the lower jaw did not restrict the jaw to simple orthal movements. Instead, we found that the bite cycle was characterised by a two-part power stroke beginning with an orthal component that smoothly grades into a palinal component. Our results are consistent with those of previous workers, which suggest that *Leptoceratops gracilis* had a circumpalinal power stroke during its bite cycle (Varriale 2016). We also discovered that known muscle physiology in conjunction with maximum gape could aid in constraining origin and insertion limits of some muscles. We found that, for our model following Holliday (2009), the bite force of *Leptoceratops gracilis* would have ranged from 550 N at the tip of the beak to 2520 N at the posterior-most tooth. For our model following Nabavizadeh (2018), the bite force would have ranged from 590 N to 2650 N at the same positions. Each muscle's force contribution to bite force throughout the jaw closing cycle reveals a complex interplay between them.

Overall, this study is a powerful proof-of-concept for novel digital methods which have become increasingly used in paleontological research within the past decade. We have developed a complete methodology for surface-scanning complex fossil objects, editing them to anatomical correction, applying muscle vectors, and reconstructing their biomechanics in Blender. This approach is fully modular, meaning that it could be applied to any living or extinct animal. We hope to extend this methodology to other neoceratopsians to examine the evolution of cranial musculature and chewing mechanics across this clade.

## Literature Cited

- Holliday, C.M. 2009. New insights into dinosaur jaw muscle anatomy. *The Anatomical Record* 292:1246–1265.
- Nabavizadeh, A. 2018. New reconstruction of cranial musculature in ornithischian dinosaurs: implications for feeding mechanisms and buccal anatomy. *The Anatomical Record* 303:247–362.
- Serenio, P.C. 2012. Taxonomy, morphology, masticatory function and phylogeny of heterodontosaurid dinosaurs. *ZooKeys* 226:1–225.
- Serenio, P.C., Z. Xijin, and T. Lin. 2010. A new psittacosaur from Inner Mongolia and the parrot-like structure and function of the psittacosaur skull. *Proceedings of the Royal Society B* 277:199–209.
- Varriale, F.J. 2016. Dental microwear reveals mammal-like chewing in the neoceratopsian dinosaur *Leptoceratops gracilis*. *PeerJ* 4:e2132.



# New and expanded preparation techniques from Pipestone Creek material leads to insights about this Late Cretaceous Wapiti Formation locality

Jackson Sweder<sup>1</sup>, Emily L. Bamforth<sup>1,2</sup>, and Maximilian Scott<sup>1</sup>

<sup>1</sup>Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 3S0, Canada; jsweder@dinomuseum.ca; curator@dinomuseum.ca; mscott@dinomuseum.ca

<sup>2</sup>Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK, S7N 5E2, Canada

The Pipestone Creek Bonebed was discovered in the 1970's and has contributed to the understanding of the Late Cretaceous (80 – 68 Ma) Wapiti Formation of northwestern Alberta and northeastern British Columbia for 50 years (Tanke 2006). This bonebed is one of the densest in North America, with up to 300 bones per square meter, and extends an estimated 5000 m<sup>2</sup>. The Pipestone Creek Bonebed is dominantly monotaxic and represents a herd of the ceratopsian *Pachyrhinosaurus lakustai* at several ontological stages (Currie et al. 2008). Alongside these large vertebrates, several other taxa are represented, including fossil turtles, reptiles, tyrannosaurid and dromaeosaurid teeth, and bones of the dromaeosaur *Boreonykus certekorum* (Bell and Currie 2015).

Since late 2021, preparation of material from the Pipestone Creek Bonebed has evolved to be more mindful of the non-macrovertebrate fauna and also flora. Many fossil preparation labs incorporate screen washing of overburden matrix removed during the preparation process to locate micro-vertebrate fossils. This technique has proven difficult with the Pipestone Creek Bonebed matrix, as it does not respond well to manual screen washing after the material is soaked in water. Expanding the techniques to include constant agitation of the material during soaking has also resulted in limited success. However, the addition of hydrogen peroxide into the soaking solution and screen washing small samples with only hydrogen peroxide has yielded exciting results. Examples of this new technique on the Pipestone Creek Bonebed material has resulted in the discovery of fish and reptile material not previously found with traditional manual preparation and water soaking techniques. These new discoveries add to the understanding of the fossil locality and provide insights about the palaeoenvironment of this Pipestone Creek deposit.

## Literature Cited

- Tanke, D.H. 2006. Sixty years of *Pachyrhinosaurus* (Dinosauria: Ceritopsidae) discoveries in North America; pp. 38–56 in: H. Allen (ed.) Alberta Palaeontological Society Tenth Annual Symposium, Abstracts. Alberta Palaeontological Society, Calgary, AB.
- Currie, P.J., W. Langston, Jr., and D.H. Tanke. 2008. A New Horned Dinosaur from an Upper Cretaceous Bone Bed in Alberta. NRC Research Press, Ottawa, Ontario, Canada. 144 pp.
- Bell, P. R., and P. J. Currie. 2015. A high-latitude dromaeosaurid, *Boreonykus certekorum*, gen. et sp. nov. (Theropoda), from the upper Campanian Wapiti Formation, west-central Alberta. *Journal of Vertebrate Paleontology* 36. DOI 10.1080/02724634.2015.1034359

# Changes in emplacement pattern and organization of the palatal dentition accompanied the evolution of herbivory in Edaphosauridae (Synapsida, Eupelycosauria)

Andrew L. Traynor<sup>1</sup>, Aaron R.H. LeBlanc<sup>2</sup>, and Kenneth D. Angielczyk<sup>3</sup>

<sup>1</sup>Carleton University, Ottawa, ON, K1S 5B6, Canada; andrewtraynor@cmail.carleton.ca

<sup>2</sup>King's College London, London, UK; arl@ualberta.ca

<sup>3</sup>Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL, 60605, USA; kangielczyk@fieldmuseum.org

Although palatal dentition is a ubiquitous trait among early tetrapods, many major amniote lineages display a tendency towards its reduction. However, among the earliest synapsids (i.e., 'pelycosaurs'), edaphosaurids uniquely elaborated the palatal dentition, interpreted as one of an array of cranial specializations (e.g., palinal jaw movement, high mechanical advantage of the jaw, and accommodations for large adductor jaw muscles) resulting from the evolution of high-fiber herbivory. Although previous studies have detailed the gross morphological trends of the palatal dentition among pelycosaurs, there has been little consideration of the extent to which feeding strategy correlates with changes in the developmental processes that governed the organization of the palatal dentition. We assessed  $\mu$ CT scans of the palatal dentition of *Edaphosaurus novomexicanus* and the ophiacodontid *Varanosaurus acutirostris* using indicators of emplacement patterns first outlined for *Captorhinus aguti*, a contemporaneous eureptilian taxon with a similarly arranged and implanted marginal dentition. Emplacement indicators include the cross-cutting relationships of teeth (i.e., when a newly-formed tooth causes partial resorption of an existing tooth), relative tooth size, and the location of emplacement pits on tooth-bearing element. Together, these indicators facilitate the recognition of vectors of tooth addition that inform broader organization of the palatal dentition. There is little pattern to emplacement in *V. acutirostris* and instances of cross-cutting relationships are rare, suggesting its denticle fields lacked strict organization. We consider the state in *V. acutirostris* to be representative of the ancestral pelycosaur condition. Conversely, the presence of a clear pattern of palatal tooth addition and numerous instances of cross-cutting relationships in *E. novomexicanus* indicate a greater level of organization of its denticle fields and a potentially higher rate of tooth emplacement. A higher level of organization was likely an important component of the elaboration of the denticle fields in *Edaphosaurus* for use in oral processing of food as part of its herbivorous diet. There is a trend toward increased numbers of denticles in derived *Edaphosaurus* species, and future research should investigate whether they were accompanied by further refinements to emplacement patterns. The increased organization of the palatal dentition in *E. novomexicanus* demonstrates that the evolution of high-fiber herbivory not only effected changes to the morphology of the palatal dentition, but also to the developmental processes governing its formation.

**Funding:** University of Chicago Department of Ecology and Evolution Undergraduate Fellowship

---

---

# Evaluation of enamel microstructures in small theropod dinosaurs

Ashley Verstraete<sup>1</sup>, Derek W. Larson<sup>2</sup>, and Kirstin S. Brink<sup>1</sup>

<sup>1</sup>Department of Earth Sciences, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada; verstraa@myumanitoba.ca; kirstin.brink@umanitoba.ca

<sup>2</sup>Research and Collections Management Department, Royal British Columbia Museum, Victoria, BC, V8W 9W2, Canada; dlarson@royalbcmuseum.bc.ca

The theropod dinosaurs known from the Cretaceous Dinosaur Park Formation (DPF), Alberta, include several taxa erected based solely on isolated teeth. With the recent discovery of articulated specimens of *Saurornitholestes langstoni* preserving the tooth taxon *Zapsalis abradens*, it is possible that other “tooth taxa” are also part of the heterodont dentitions of small dinosaurs and not individual species, or may even belong to other archosaur groups. Therefore, our understanding of archosaur diversity in the DPF might be skewed towards theropods. Previous studies of enamel microstructures in dinosaurs have shown species-specific traits that may be useful for taxonomic identifications. In this study, we examined the enamel microstructure of eight small theropod tooth morphotypes that have previously been regarded as being separate species from the DPF to determine the distribution of enamel microstructure characters, including both morphotypes of *S. langstoni*. We also examined the enamel microstructure of two pterosaur species from the Cenomanian Kem Kem beds of Morocco for a comparison to small theropod enamel microstructure. These data allowed us to determine which enamel microstructure characters are useful for determining shared ancestry, or if enamel microstructure depends more on tooth shape and thus is determined by tooth function. We sectioned the teeth in transverse and longitudinal planes and examined the microstructures with a scanning electron microscope. Results show that no major taxonomically informative patterns in enamel microstructure among the theropods and pterosaurs examined here. The archosaurs in this study all had parallel enamel with basal unit layers, and many with incremental lines. The heterodont teeth of *Saurornitholestes* show differences in the positioning of incremental lines, crystallite sizes, and the presence of tubules, suggesting enamel microstructure is reflective of tooth shape and function based on its position in the mouth. This study concludes that enamel microstructure is less useful for taxonomic identification than previously thought, especially for lower-level taxonomic comparisons and archosaurs that share relatively thin, simple enamel. Enamel microstructure is likely linked to tooth function and placement in the mouth of an organism and less-so to evolutionary history.

---

# Redescription of a juvenile hadrosaurid from the Upper Cretaceous of Alberta using computed tomography

Trystan M. Warnock-Juteau<sup>1</sup>, Michael J. Ryan<sup>1,2</sup>, R. Timothy Patterson<sup>1</sup>, and Jordan C. Mallon<sup>1,2</sup>

<sup>1</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, K1S 5B6, Canada; trystanwarnockjuteau@cmail.carleton.ca; michaelj.ryan@carleton.ca; tim.patterson@carleton.ca

<sup>2</sup>Palaeobiology, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; jmallon@nature.ca

Canadian Museum of Nature specimen CMN 8917 is a partial skull originally described by Charles M. Sternberg (1956) that is one of only several nestling-sized, juvenile hadrosaurines known to date. Sternberg's original description of the specimen was limited to what was visible externally. We report here on new data obtained using computed tomography (CT) to create 3D models of individual skull elements, allowing for a more thorough description and precise identification of the specimen.

Support for its placement within Hadrosaurinae includes the presence of an anterodorsal maxillary process, a maxillary dorsal process that is anteroposteriorly wider than dorsoventrally tall, and a narial vestibule not enclosed within the premaxillary dorsal and lateral processes.

The skull also possesses two tooth traits traditionally associated with lambeosaurines (Horner et al. 2004) — secondary ridges on the maxillary and dentary crowns, and denticulation on some of the maxillary crowns. The occurrence of these features in a juvenile hadrosaurine suggests that they are modified during ontogeny, thus calling into question their utility for the taxonomic identification of juvenile specimens.

The morphology of the occlusal surface on the dentary teeth of CMN 8917 is similar to those of late nestlings of the hadrosaurine *Maiasaura peeblesorum* (Horner et al. 2000; Prieto-Márquez and Guenther 2018) and those of many adult hadrosaurids (Erickson et al. 2012), possessing a concave occlusal surface with steeper lingual and shallower buccal wear zones. This differs from the morphology of hatchling lambeosaurine *Hypacrosaurus stebingeri*, which possess shallow-angle cup-shaped occlusal surfaces (Erickson and Zelenitsky 2014). Differences in occlusal surface morphology between CMN 8917 and *H. stebingeri* (Erickson and Zelenitsky 2014) at early ontogenetic stages suggests interspecific differences in dental battery development, possibly reflective of dietary differences early in ontogeny.

## Literature Cited

- Erickson, G.M., B.A. Krick, M. Hamilton, G.R. Bourne, M.A. Norell, E. Lilleodden, and W.G. Sawyer. 2012. Complex dental structure and wear biomechanics in hadrosaurid dinosaurs. *Science (American Association for the Advancement of Science)* 228:98–101.
- Erickson, G.M. and D. Zelenitsky. 2014. Osteohistology and occlusal morphology of *Hypacrosaurus stebingeri* teeth throughout ontogeny with comments on wear-induced form and function; pp. 422–432 in: D.A. Eberth and D.C. Evans (eds.), *Hadrosaurs*. Indiana University Press, Bloomington, IN, USA.
- Horner, J.R., A. De Ricqlès, and K. Padian. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology* 20:115–129.
- Horner, J. R., D.B. Weishampel, and C.A. Forster. 2004. Hadrosauridae; pp 438–463 in D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria* 2nd edition. University of California Press Ltd, London, UK.
- Prieto-Márquez, A., and M.F. Guenther. 2018. Perinatal specimens of *Maiasaura* from the Upper Cretaceous of Montana (USA): insights into the early ontogeny of saurolophine hadrosaurid dinosaurs. *Peer J* 6.
- Sternberg, C.M. 1956. A juvenile hadrosaur from the Oldman Formation of Alberta. *Bulletin No. 136. Annual Report of the National Museum for the fiscal year 1953–54* 136:120–122.

# Isotope palaeoecology of duck-billed Dinosaurs (Ornithischia: Hadrosauridae) from the upper Campanian Dinosaur Park Formation

Joshua Wasserlauf<sup>1</sup>, Jordan Mallon<sup>1,2</sup>, Thomas Cullen<sup>3</sup>, François Therrien<sup>4</sup>, Brian Cousens<sup>1</sup>, and Clément Bataille<sup>5</sup>

<sup>1</sup>Carleton University Department of Earth Sciences, Ottawa, ON, K1S 5B6, Canada; joshuawasserlauf@cmail.carleton.ca; brian Cousens@cunet.carleton.ca

<sup>2</sup>Beaty Centre for Species Discovery and Palaeobiology section, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; JMallon@nature.ca

<sup>3</sup>Auburn University Department of Geosciences, Auburn, AL, 36849, USA; thomas.cullen11@gmail.com

<sup>4</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; francois.therrien@gov.ab.ca

<sup>5</sup>Department of Earth Sciences, University of Ottawa, Ottawa, ON, K1N 6N5, Canada; cbataill@uottawa.ca

Size-frequency distributions of North American hadrosaurid bone-beds reveal possible behavioural differences between juvenile to sub-adult/adult stages. Bonebed data suggest that juvenile hadrosaurids may have lived in separate groups isolated from adults and subadults. Moreover, the co-occurrence and similar morphology between hadrosaurid sub-families (Hadrosaurinae and Lambeosaurinae) has led to questions regarding their ecology, diets, and potential competition. Detecting ecological behaviors and habitat use patterns can be difficult using morphological data alone, and although the morphology of vertebrate bones remains a useful palaeoecological indicator, recently there has been increased emphasis on augmenting these indicators with the inclusion of morphology-free approaches to palaeoecological analyses, including isotope geochemistry.

Isotopic proxies such as  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , and  $^{87}\text{Sr}/^{86}\text{Sr}$ , provide valuable insights into a fossil organism's ancient living conditions, potential feeding habits, and geographical pathways of migration. Aspects of migration and range size, dietary specializations, and growth in hadrosaurid dinosaurs can therefore be revealed using isotope geochemistry to convey how these animals coexisted and to test how their ecological niche shifted in an ontogenetic context.

In this study, we measured isotope composition in hadrosaurid tooth enamel from several individuals from the Dinosaur Park Formation, of various ages and sub-familial affinities, to test for differences in the palaeoecology of hadrosaurines and lambeosaurines, as well as for changes in the ecology of these animals through ontogeny. Because hadrosaurid dental batteries contain multiple generations of teeth, formed across multiple years, sampling the growth record of these teeth allows seasonal, annual, and multi-year patterns to be recorded.

Preliminary analyses of the enamel isotopic signatures reveal a detectable shift in average  $^{87}\text{Sr}/^{86}\text{Sr}$ ,  $\delta^{18}\text{O}$ , and  $\delta^{13}\text{C}$  from juveniles to adults, both in absolute values and in the amount of dispersion around each value. Ranges for  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , and  $^{87}\text{Sr}/^{86}\text{Sr}$  signals are considerably more constrained in the juvenile samples than in values obtained for adults. Greater dispersion in  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{18}\text{O}$  ranges in both lambeosaurine and hadrosaurine adults may indicate a shift to more widespread/wide-ranging feeding behaviours. The analysed juvenile specimen exhibits a more positive mean  $\delta^{13}\text{C}$  (-0.10‰ VPDB vs -3.40‰ VPDB in adults) than the adults, contrary to a predicted depletion in the signal consistent with feeding on plants under dense canopy, but potentially related to or offset by other habitat factors such as feeding on more osmotically stressed plants in coastal forest/mangrove forest settings. Finally, we observe distinct seasonal profiles of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  between hadrosaurines and lambeosaurines, with some specimens demonstrating positive correlations between these two signals and others exhibiting an inverse correlation. These findings may reflect divergent use of landscape and habitat resources between the two sub-families.



# A new archosaurian skeleton from the Middle Triassic of China: shedding light on the phylogenetic position of *Wangisuchus* (Pseudosuchia, Gracilisuchidae)

Xiao-Chun Wu<sup>1</sup>, Zhi-Shuai Kang<sup>2</sup>, Li-Yang Dong<sup>2</sup>, Jian-Ru Shi<sup>2</sup>, and Hai-Lu You<sup>3</sup>

<sup>1</sup>Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; xcwu@nature.ca

<sup>2</sup>Shanxi Museum of Geology, Binhexilu Zhongduan, Taiyuan, Shanxi 030024, China; sxdzbgkzs@163.com; ryyuunang\_919@yeah.net; shijianru@126.com

<sup>3</sup>Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, China; youhailu@ivpp.ac.cn

*Wangisuchus* Young, 1964 is a monospecific genus. Its type species, *Wangisuchus tzeyii* Young 1964, was established mainly based on four incomplete maxillae from the upper Ermaying Formation (Middle Triassic) near Louzeyu Village of Wuxiang County, Shanxi Province, China. Of the four maxillae, one was appointed as the holotype (in the collections of the Institute for Vertebrate Paleontology and Paleoanthropology, IVPP V 2701) and the other three as the paratypes (IVPP V 2702 to 2704) of the species. At the same time, Young (1964) also assigned many incomplete postcranial elements to the species. Most of the assigned specimens came from the same quarry where the type and paratypes were excavated.

Young (1964) placed *W. tzeyii* in Euparkeridae (v. Huene 1920). Sennikov (1989) referred *W. tzeyii* (with *Halazhaisuchus qiaoensis* Wu, 1982, and *Turfanosuchus shageduensis* Wu, 1982) to the putative euparkeriid subgroup Dorosuchinae along with *Dorosuchus neoetus* from Russia. Lucas (2001) also considered the Chinese taxa as euparkeriids. Some other studies (Kuhn 1976; Parrish 1993; Gower and Sennikov 2000; Nesbitt 2011) argued that only the holotype could represent *W. tzeyii*. Sookias et al. (2014) restudied the material of *W. tzeyii* and considered *W. tzeyii* as a nomen dubium due to the absence of any feature that can diagnose the holotype and the lack of any convincing evidence that the previously referred additional specimens represent the same taxon as the holotype. Since *W. tzeyii* was established, it has not been included in any phylogenetic study on archosaurians due to its fragmentary nature. After examining the material of Young (1964), we consider one (IVPP V 2704) of the three paratypes as also belonging to *W. tzeyii* based on the antorbital fossa that extends along the dorsolateral margin of the maxilla as in the type specimen.

In 2013, a field team of Shanxi Museum of Geology (SXMG) collected an archosaurian skeleton (SXMG V2014) from the upper Ermaying Formation at a site which is about 11 km northwest to the locality where the type and paratypes of *W. tzeyii* were collected. In 2019, we conducted fieldwork around the fossil locality in Wuxiang County. According to our stratigraphical correlation, the new and type localities of *W. tzeyii* are roughly situated in the same horizon of the upper Ermaying Formation. Most parts of the new archosaurian skeleton are well-preserved but the posterior section of the tail is missing. We refer the new archosaurian skeleton to *W. tzeyii* based on characters from the maxilla (characters 1 and 2 below). With the new specimen, *W. tzeyii* can be diagnosed by a set of characters, the most important of which include 1) the antorbital fossa extending onto the dorsolateral side of the maxilla, 2) the orbit anteroposteriorly shorter than the antorbital fenestra, 3) the maxilla possessing a posterodorsal process around the posteroventral corner of the antorbital fenestra, 4) the jugal terminating before the posteroventral margin of the lower temporal fenestra, 5) the height of the scapular nearly equal to the humeral length, 6) the humerus and ulna nearly same in length, and 7) the postacetabular process of the ilium trunked posteriorly.

In our phylogeny analysis, we coded *W. tzei* based on the new skeleton into the data set used by Lecuona et al. (2017). Our preliminary results suggest that *W. tzei* is a gracilisuchid and supports the monophyly of Gracilisuchidae. Our new analysis suggests that *Turfanosuchus dabanensis* and *W. tzei* form a set of successive sister-groups towards the *Gracilisuchus stipanicorum*–*Yonghesuchus sangbiensis* clade within the family. The discovery of the new archosaurian skeleton not only established the phylogenetic relationships of *W. tzei* for the first time but also indicates that the clade Gracilisuchidae originated in what is now China during the Middle Triassic.

### Literature Cited

- Gower, D.J. and A.G. Sennikov. 2000. Early archosaurs from Russia; pp. 140–159 in M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin, (eds.), *The age of dinosaurs in Russia and Mongolia*. Cambridge University Press, New York.
- Huene, F. v. 1920. Osteologie von *Aetosaurus ferratus* O. Fraas. *Acta Zoologica* 1:465–491.
- Kuhn, O. 1976. *Handbuch der Paläherpetologie*. Gustav Fischer Verlag, Stuttgart/New York, 137 pp.
- Lecuona, A., J.B. Desojo, and D. Pol. 2017. New information on the postcranial skeleton of *Gracilisuchus stipanicorum* (Archosauria: Suchia) and reappraisal of its phylogenetic position. *Zoological Journal of the Linnean Society* 181:638–677. DOI 10.1093/zoolinnean/zlx011.
- Lucas, S.G. 2001. *Chinese Fossil Vertebrates*. Columbia University Press, New York, 376 pp.
- Nesbitt, S.J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* 352:1–292. DOI 10.1206/352.1.
- Parrish, M.J. 1993. Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology* 13:287–308. DOI 10.1080/02724634.1993.10011511.
- Sennikov, A.G. 1989. Novyy euparkeriid (Thecodontia) iz srednego triasa Yuzhnogo Priuralya. *Paleontologicheskii Zhurnal*. 1989:71–78.
- Sookias, R.B., C. Sullivan, J. Liu, and R.J. Butler. 2014. Systematics of putative euparkeriids (Diapsida: Archosauriformes) from the Triassic of China. *PeerJ* 2: e658. DOI 10.7717/peerj.658.
- Wu, X.-C. 1982. The pseudosuchian reptiles from Shan-Gan-Ning basin. *Vertebrata Palasiatica* 20:289–301 (in Chinese with English summary).
- Young, C.C. 1964. The pseudosuchians in China. *Palaeontologia Sinica* 151:1–205 (in Chinese and English).

---

## Hadrosaurid skull from the Wapiti Formation preserves evidence of new feeding behaviours in tyrannosaurids

Taia C.A. Wyenberg-Henzler<sup>1</sup>, Nicolas E. Campione<sup>2</sup>, Phil R. Bell<sup>2</sup>, and Corwin Sullivan<sup>1,3</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada; wyenberg@ualberta.ca; corwin1@ualberta.ca

<sup>2</sup>School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia; pbell@une.edu.au; ncampion@une.edu.au

<sup>3</sup>Philip J. Currie Dinosaur Museum, Wembley, AB, Canada

Marks left on bone due to tooth-to-bone contact (i.e., tooth marks) represent direct evidence of behaviour in extinct vertebrates, particularly carnivores. In theropod dinosaurs, tooth marks have been used to infer behav-

ious such as intraspecific combat and carcass defleshing. Here, we report an almost complete, articulated adult hadrosaurid skull (University of Alberta Laboratory for Vertebrate Palaeontology collections, specimen UALVP 60000) from the Upper Cretaceous (Campanian–Maastrichtian) Wapiti Formation of northern Alberta, which bears tooth marks and other signs of damage. Damaged surfaces that could potentially represent tooth marks were sampled using Smooth-On Dragon Skin 10 Very Fast silicone. Tooth marks were then identified using these silicone peels, based on similarities in shape and texture to tooth marks previously described in the literature. A total of 38 tooth marks were identified on UALVP 60000, ~87% of which are on the left, less intact side of the skull. By contrast, the right side of the skull is almost pristine below the crest, suggesting that this side of the head was likely resting on or even embedded in the substrate following the animal's death. Most of the tooth marks are oriented in an anteroposterior to posteroventral-anterodorsal direction on the portions of the premaxillae anterior to the orbits, and the anterior portions of the maxillae. The deepest tooth marks are on the anterior end of the left maxilla. One posterodorsally-anteroventrally oriented tooth mark is on the posterior end of the left maxilla, and two tooth marks are on the anterior end of the palatal surface of the right premaxilla. Based on their location, spacing, and orientation, the tooth marks in the snout region were likely produced by a tyrannosaurid attempting to manipulate the skull from multiple angles. In particular, the deepest tooth marks are posterodorsally convex and anteroposteriorly oriented, and are interpreted as resulting from forceful attempts to either tear away the upper jaw for better access to the mouth cavity or roll/reposition the head. The single mark observed on the lateral surface of the posterior end of the left maxilla was likely produced when the tyrannosaurid was removing the nearby adductor musculature, such as the *m. pseudotemporalis superficialis*. Consumption of adductor musculature likely also resulted in the incidental removal or deliberate destruction of the left jugal, quadratojugal, and quadrate. To our knowledge, UALVP 60000 is the first formally reported example of a hadrosaurid skull showing evidence of powerful and repeated attempts at manipulation by a tyrannosaurid.

---

## Investigating genetic mechanisms of early limb development in *Ambystoma mexicanum* and *Xenopus laevis*

Jeffrey A. Yee<sup>1,2</sup>, Tetsuto Miyashita<sup>1,2</sup>, and Hillary C. Maddin<sup>1</sup>

<sup>1</sup>Earth Sciences Department, Carleton University, Ottawa, ON, K1S 5B6, Canada; JeffreyYee@Cmail.Carleton.ca; HillaryMaddin@Cunet.Carleton.ca

<sup>2</sup>Palaeobiology, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; TMiyashita@nature.ca

Varying in body-axis placement and developmental timing, tetrapod limbs are highly specialized, but conserved homologous structures. In the case of most amniotes, limbs are completely patterned during gestation. In contrast, amphibians provide a useful model for studying early limb development, as they develop limbs as free-living larvae. The genes and regulatory mechanisms of early limb development are ostensibly conserved across vertebrate species. Previous work has found that a genetic element controlling early hindlimb development, hindlimb enhancer B (HLEB), maintains functionality and drives the same mechanism across vertebrate groups. However, experiments demonstrating this have only been performed in mouse, and used HLEB orthologues from *Python bivittatus*, *Danio rerio*, and *Anolis sagrei*. Under the hypothesis of HLEB being a universal marker of vertebrate hindlimb development, we investigate the function of HLEB in the extant amphibian species *Ambystoma mexicanum*, and *Xenopus laevis* via reciprocal reporter assay. This is a method wherein we introduce a transgene containing HLEB and a fluorescent protein. Using GFP as our reporter, we infer locations where HLEB is active



by observing patterns of fluorescence. Early fluorescence of a *X. laevis* transgene in *A. mexicanum* suggests that HLEB may maintain spatial function across amphibian species in a similar manner as previous work. While we have observed some fluorescence in transgenic *A. mexicanum*, we also consider that we will need a greater sample size to justify our conclusion, and that naturally fluorescent cell populations in *A. mexicanum* may obscure fluorescence truly generated by our transgene. Notwithstanding our current limitations, our work will allow us to refine hypotheses of limb development mechanisms in ancestral tetrapods, and perhaps vertebrates.

---