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Abstracts

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## TABLE OF CONTENTS

## Acknowledgements

The potential for postcranial material in hadrosaurid identification below the family level; a review of hadrosaurid scapular variation in Dinosaur Provincial Park Janet Alexander, Corwin Sullivan, and Philip J. Currie	.....13
The nature of cranial developmental divergence at the base of Galloanserae: combining comparative ontogeny with the avian fossil record Bassel Arnaout, Guillermo Navalon, Olivia Plateau, Stephan Lautenschlager, Benjamin Steventon <sup>3</sup> , and Daniel Field	.....13
You should look at a gift horse in the mouth: using the Patterning and Inhibitory Cascade Models to study the evolution of molarization in hoofed mammals Austin J. Ashbaugh, Heather A. Jamniczky, and Jessica M. Theodor	.....14
A frill a minute: new material informs cranial morphology and intraspecies cranial variation in <i>Pachyrhinosaurus lakustai</i> from the Campanian (73 Ma) Pipestone Creek Bonebed, Wapiti Formation, northwest Alberta Emily L. Bamforth, Jackson Sweder, Aidan Kerr, and Alexander Baxter	.....15
Interspecies variation of the nasal airways in Ankylosauria from Upper Cretaceous deposits of southern Alberta Ollie Barnett, Darla K. Zelenitsky, Jared T. Voris, Jordan Mallon, and François Therrien	.....16
Unlocking the Lockhart Pit: further investigations into a new Plio-Pleistocene(?) vertebrate locality in southeastern Alberta Christina I. Barrón-Ortiz, Katherine K. Bramble, René W. Barendregt, Dale A. Leckie, Christopher N. Jass, Serhiy Burak, Britta Jensen, Fatima Iftikhar, and Kelsey Martin	.....17
Predicting Species Interactions and their Eco-evolutionary Consequences in the Fossil Record Louis-Philippe Bateman and Hans Larsson	.....18
A possible pachycephalosaur supraorbital from the Frenchman Formation, southwest Saskatchewan Mollie K. Black, Jack R. Milligan, and Jordan C. Mallon	.....19
Etiology of colour banding in Cretaceous marine reptile teeth Kirstin S. Brink and Virginia K. Gold	.....20
Characterizing dromaeosaurid (Theropoda; Paraves) feeding traces, and repeated occurrence on azhdarchid (Pterosauria) bones Caleb Brown	.....20
Theropod tracks at the Nîsôtêw Nimisêw Waciy Tracksite, Gething Formation (Early Cretaceous), northeastern British Columbia Dakota Camarena and Victoria Arbour	.....21
A rare juvenile mosasaur provides potential insights into ontogenetic change within the subfamily Plioplatecarpinae (Squamata, Mosasauridae) Amy A. Cameron, Takuya Konishi, and Michael W. Caldwell	.....22
Historical confusion and the evolution of the dinosaur pelvis Leon P.A.M. Claessens	.....23

Reexamination of hypothesized sexual dimorphism in the Early Permian non-mammalian synapsid <i>Dimetrodon limbatus</i> Nathan Cochran and Jason S. Anderson	.....23
A specimen of <i>Gorgosaurus libratus</i> from the Wapiti Formation of northeastern British Columbia, Canada Colton C. Coppock, Hans C.E. Larsson, and Philip J. Currie	.....24
Filter-feeding evolutionary trends in Late Cretaceous lamniform sharks Bruno P. Costa, Ricardo L. Silva, and Kirstin S. Brink	.....25
New research at the early Miocene site of Tonde Bridge (formerly “Meswa Bridge”), Kenya Susanne Cote, Kieran P. McNulty, Daniel Peppe, Alan Deino, Michelle Wanjiru Kioko, Cliff Ochieng, Kirsten Jenkins, Abigail Hall, Jason Head, and Joshua Siembo	.....25
2.5 million years of variation in trophic community structure during a marine transgression across the Late Cretaceous (Campanian) Belly River Group of Dinosaur Provincial Park Alexandre V. Demers-Potvin, Louis-Philippe Bateman, André S. Mueller, and Hans C.E. Larsson	.....27
Evolution of early primate vision: insights from petrosal lobule size in <i>Dryomomys szalayi</i> (late Paleocene, Wyoming) Eri C. Dixon, Jonathan I. Bloch, and Mary T. Silcox	.....28
Discovering fish and fish lizards: fieldwork along the mid-Cretaceous riverbanks of the Hay River, Northwest Territories, Canada Joshua A. Doyon, Luke E. Nelson, Meghan E. Dueck, Mondo Miyazato, and Alison M. Murray	.....29
Using ichnology to improve the understanding of Cenomanian palaeoecology of northeastern British Columbia: insights from ichnofossil sites near Tumbler Ridge, B.C. Eamon T. Drysdale, Roy Rule, Charles W. Helm, and Victoria A. Arbour	.....30
Paleoenvironmental reconstructions of the Dinosaur Park Formation: insights from sedimentology and stratigraphy Paul R. Durkin	.....31
Multiple forms of dental pathology in a <i>Brachychampsa montana</i> (Eusuchia; Alligatoroidea) from the Upper Cretaceous (Maastrichtian) Hell Creek Formation Aaron D. Dyer and David C. Evans	.....32
Stable isotope geochemistry of Cretaceous vertebrate enamel in comparison to amber Ben Egan, Maria Velez, Ryan McKellar, and Leslie Robbins	.....32
The first record of Rhizodontida (Tetrapodomorpha, Sarcopterygii) from the Upper Mississippian (Serpukhovian) Tar Springs Formation of Indiana, U.S.A., and a review of global <i>Strepsodus</i> occurrences Adam I. Eliezer, Ryan Shell, Caleb P. Bohus, and Charles N. Ciampaglio	.....33
Environmental influences on dinosaur assemblages in the Horseshoe Canyon and Upper Wapiti Formations Sebastian Feng and Philip J. Currie	.....34
The validity of <i>Nodosaurus textilis</i> , Nodosauridae, and Nodosauria Tracy L. Ford	.....35
Life history filters in mammalian extinction at the end of the Cretaceous Gregory F. Funston, Elis Newham, David C. Evans, and Gregory P. Wilson–Mantilla	.....37

Histology and $\mu$ CT scanning allow detailed diagnoses of multiple pathologies in a large <i>Gorgosaurus</i> (Theropoda: Tyrannosauridae)	
Christiana W. Garros, Henry S. Sharpe, Jared Voris, Kyla Beguesse, François Therrien, and Philip J. Currie	.....37
We're all ears: a comparison of five merycoidodontid petrosals	
Jay M. Gegner, S.V. Robson, and Jessica M. Theodor	.....38
Stable oxygen isotopes of mosasaur teeth from the Pierre Shale, Manitoba: separating diagenetic and physiologic signals	
Virginia K. Gold, Gina Bilic, Ryan Sharpe, Mostafa Fayek, and Kirstin S. Brink	.....39
Preparation, analysis and description of sub-adult <i>Mosasaurus missouriensis</i> (Squamata, Mosasauridae) from the Bearpaw Formation, Late Cretaceous, western Canada	
Corbin G. Gomez	.....40
Fossil dermal denticles as a tool for understanding the ecology of subrecent and ancient (pre- and post-human impact) shark communities across the Isthmus of Panama	
María M. Gómez, Erin Dillon, Irene García, Brígida De Gracia, and Aaron O'Dea	.....40
Morphology of trionychid shell material of the Scollard Formation	
Madeline E. Groat and Corwin Sullivan	.....41
Mammalian communities preserved at Mfangano Island and Rusinga Island, Kenya, provide a crucial framework for understanding early Miocene ape evolution in Eastern Africa	
Abigail S. Hall	.....42
Reconstruction of a plesiosaur skull using low-resolution scan data and comparative anatomy	
Gillian C. Halliday and Hallie P. Street-Sampson	.....43
Latest Middle Triassic tetrapod footprints from the Brown Hill section, Williston Lake, British Columbia, Canada	
Kendra Harrington, Mahdiyeh Gholizadeh, Ryusuke Kimitsuki, Ciara Stewart, and John-Paul Zonneveld	.....44
Secondarily aquatic tetrapod twins: <i>Crassigyrinus</i> and <i>Vancleavea</i> — an example of convergent evolution	
Donald M. Henderson	.....45
Using teiid lizards to understand tooth attachment and resorption in extinct mosasaurs	
Fatima Iftikhar, Michael W. Caldwell, and Aaron R. H. LeBlanc	.....45
Variability of soft tissue preservation in a juvenile hadrosaurid dinosaur from the Dinosaur Park Formation of Alberta, Canada	
Tristan Joubarne, Caleb M. Brown, Paul Durkin, and Kirstin S. Brink	.....46
Possible osteosarcoma on the neural spine of <i>Edmontosaurus regalis</i> from the Danek Bonebed, Edmonton, Alberta, Canada	
Kaiki Kobayashi and Philip J. Currie	.....47
The epaxial ossified tendon lattice and musculature of <i>Centrosaurus apertus</i> (Ornithischia: Ceratopsidae)	
Kaiki Kobayashi and Corwin Sullivan	.....48
The strongest fossil evidence of intraspecific face-biting demonstrated by an adult <i>Mosasaurus missouriensis</i> (Squamata: Mosasauridae) specimen from Alberta, Canada	
Takuya Konishi, Maximillian Scott, Caleb Brown, Kirstin Brink, and Donald Brinkman	.....49

First Saskatchewan Paleocene amber — geochemistry and bioinclusions Katie D. Kreutzer, Kaitlin T. Lindblad, Ben M.J. Egan, Lauren Lindsay, Seyed Samaei, Jinkai Xue, Maria I. Velez, Ryan C. McKellar, and Leslie J. Robbins	.....50
Finally! The most complete hind paddle of <i>Plioplatecarpus</i> (Squamata, Mosasauridae) from the Bearpaw Formation, Late Cretaceous, Alberta Marilyn C. Laframboise	.....51
Collapse of the mammoth steppe and the late Pleistocene decline of eastern Beringian horse populations: insights from stable isotopes and body mass modeling Zoe Landry, Joshua Miller, Clément Bataille, and Danielle Fraser	.....52
The ace of spades? A new anuran from the late Campanian (Late Cretaceous) of North America illuminates early diversification of spadefoot toads (Pelobatoidea) Alfred J. A. Lemierre, Amy C. Henrici, David J. Varricchio, Jianye Chen, and James D. Gardner	.....53
The devil is in the details: a new stem iguanian from the Late Cretaceous of Alberta, Canada Alfred J. A. Lemierre, Ilaria Paparella, François Therrien, and Darla K. Zelenitsky	.....53
Bergmannian body size trend in <i>Triceratops</i> (Dinosauria, Ceratopsia) Caelan Libke, Landon Burgener, Hillary C. Maddin, and Jordan C. Mallon	.....54
Spot the difference: comparisons of dentition and postcrania of <i>Leidyosuchus</i> (Campanian) and <i>Borealosuchus</i> (Maastrichtian, Paleocene) Kaitlin T. Lindblad and Jack R. Milligan	.....55
<i>Pachyrhinosaurus</i> pathologies from Pipestone Creek Kai O. MacFarlane, Angela R. Lieveise, and Emily L. Bamforth	.....56
Filling in the gaps in the insect fossil record before the end-Cretaceous extinction event Ryan C. McKellar, Kano Sasaguchi, and Ben Egan	.....56
Comparative body size distributions of Pleistocene and Recent Canadian wolves ( <i>Canis lupus</i> ) Logan Micucci, Zoe Landry, Kamal Khidas, and Danielle Fraser	.....57
Taphonomy and palaeoecology of the Deadfall Hills Bonebed of the Wapiti Formation, northern Alberta Jack R. Milligan, Taia Wyenberg-Henzler, Jordan Stock, Henry S. Sharpe, Emily L. Bamforth, Nicolás Campione, and Corwin Sullivan	.....58
Historical contingency of early vertebrate phylogeny: what if and what now Tetsuto Miyashita	.....59
The histology and biomechanics of ossified tendons Bryan R.S. Moore and Jason S. Anderson	.....60
Craniodental analysis of the oldest fossil lorid, <i>Mioeuticus bishopi</i> (Strepsirrhini, Primates) Hiruni N. Mudannayake, Holly E. Anderson, Sergi López-Torres, Laura MacLatchy, and Susanne Cote	.....61
A biodiverse multitaxic bonebed provides insights into megaherbivore assemblage transitions in the Dinosaur Park Formation, Alberta, Canada André S. Mueller, Alexandre V. Demers-Potvin, Don Brinkman, Caleb M. Brown, Mark Powers, Gabrielle Bonin, Louis-Philippe Bateman, Dirley Cortés, Olivia Osterreicher, and Hans C.E. Larsson	.....62

First large, articulated teleostomorph fish from the lower Shaftesbury Formation (Albian) of British Columbia, Canada Alison M. Murray, Luke E. Nelson, and Joshua A. Doyon	.....63
Structural and functional heterogeneity in epaxial ossified tendons of <i>Triceratops</i> Marco Muscioni, Simone A.M. Lemmers, Kaiki Kobayashi, Ilaria Carlomagno, Maurizio Polentarutti, Giorgio Bais, Henning Markotter, Marko Prasek, Paula Sanchez, Lucia Mancini, Diego Dreossi, Giorgia Bacchia, and Federico Fanti	.....63
Taxonomic revision of <i>Enchodus dirus</i> leads to the recognition of a new species of <i>Enchodus</i> from North America Luke E. Nelson, Alison M. Murray, and Megan E. Sims	.....64
Expanded caudalmost sternal ribs in extant pelicans suggest stabilizing function for the morphologically similar ribs of the Cretaceous toothed bird <i>Jeholornis prima</i> Ping Nixon-Hermansen and Corwin Sullivan	.....65
Perinate hadrosaur remains and associated eggshells from the Upper Cretaceous Oldman Formation of southeastern Alberta, Canada Ayari Otomo, Darla K. Zelenitsky, Kohei Tanaka, François Therrien, Corwin Sullivan, and David C. Evans	.....66
Estimating the body mass of hadrosaurids in Alberta using the anteroposterior lengths of the alveolar grooves in maxillae and dentaries Ayari Otomo, Colton Coppock, and Philip J. Currie	.....67
Reassessment of a purported deinocheirid from the Judith River Formation (Campanian) of Montana Shyong En Pan, Caelan Libke, Gianni Zambonin, and Jordan C. Mallon	.....67
Evolution and reconstruction of the mosasaurian pelvic girdle and pelvic-axial articulation Ilaria Paparella	.....68
No metamorphosis in tetrapods across the fin-to-limb transition Jason D. Pardo, Franklin Duffy, and Arjan Mann	.....69
Taxonomic reassessment of juvenile tyrannosaurine specimens reveal large biogeographic ranges in tyrannosaurids Gorm S. Raun, Colton C. Coppock, Demchig Badamgarav, Khishigjav Tsogtbaatar, and Philip J. Currie	.....70
Testing the limits of petrosal data and their utility in resolving camelid evolutionary relationships Selina-Viktor Robson	.....70
A reassessment of referred material supports the validity of <i>Dromiceiomimus brevitertius</i> Declan Rourke, Bradley McFeeters, and Philip J. Currie	.....71
Applications of reflectance transformation imaging (RTI) to insect compression fossils with implications for vertebrate specimens Kano Sasaguchi, John Acorn, and Felix Sperling	.....72
Marine reptiles from Japanese Upper Cretaceous: progress in the last decade Tamaki Sato	.....73
Testing hypotheses of competition between gnathostomes and agnathans based on hydrodynamic performance Bradley Scott	.....74

The Calgary 2E mammalian local fauna: 100 years later Craig S. Scott	.....75
Assessing grasping ability in early bird antecedents, and implications for the origins of avian flight Parker A. Senger and Corwin Sullivan	.....75
Getting our ducks in a row: scientific philosophy in hadrosaurid dinosaur character, taxon, and tree construction Henry S. Sharpe	.....76
A specimen of <i>Edmontonia</i> with an unusual cranial pathology Connor Sievwright and Philip J. Currie	.....77
Ecological drivers of biodiversity dynamic shifts of terrestrial amniotes during the Permian-Triassic climatic crises Tiago R. Simões, Arielli F. Machado, Shelley Wang, Voltaire D. Paes-Neto, Alexander Farnsworth, Felipe L. Pinheiro, and Stephanie E. Pierce	.....78
A reassessment of early Eocene equid species distribution from South Pass, Wyoming Mikenna A. Smith and John-Paul Zonneveld	.....79
Taxonomic diversity and development of Late Carboniferous amphibamiforms from the Mazon Creek Lagerstätte Cal So, Miranda E. Montgomery, Naiomi I. Cookson, Jason D. Pardo, Hillary C. Maddin, Hans-Dieter Sues, and Arjan Mann	.....79
Fossil resource management and palaeontological research permits in Canada Daniel N. Spivak, Scott Rufolo, Patrick Brunette, Kim Cloutier, Pascale Daoust, Tim J. Fedak, Todd Keith, Glen MacKay, Leanne J. Pyle, and Grant Zazula	.....80
Relocating historic dinosaur quarries in the Horseshoe Canyon Formation (Late Cretaceous, Alberta) to refine and preserve biostratigraphic data Jordan C. Stock, Jordan C. Mallon, Caleb M. Brown, François Therrien, Mark J. Powers, Colton C. Coppock, and Philip J. Currie	.....81
The developmental origin of the ornithischian predentary and its derived morphology Giles D. Suddert and Philip J. Currie	.....82
Theropod feeding traces provide insight into the taphonomy of the Danek Bonebed Victor T. Sumka, Colton C. Coppock, Mikenna A. Smith, and Philip J. Currie	.....83
<i>Cryptoryctes</i> is a micropternodontid, but not a synonym of <i>Micropternodus</i> : new lipotyphlans from John Day Fossil Beds, Oregon Jessica M. Theodor, Jonathan J-M. Caledo, Craig Scott, and Joshua X. Samuels	.....83
Dinosaur running abilities and predator-prey relationships in iconic Late Cretaceous tyrannosaur-dominated ecosystems of North America and Asia François Therrien, Jared Voris, Kohei Tanaka, and Darla K. Zelenitsky	.....84
Femoral morphology and muscle moment arm estimates suggest an unusual hindlimb posture in ceratopsid dinosaurs Brandon Theurer	.....85

Re-evaluation of megaherbivore faunal turnover in the Dinosaur Park Formation, Alberta using a newly resolved biostratigraphic framework Mira Thompson, Kirstin Brink, Caleb Brown, and Paul Durkin	.....86
New perspectives on the origins and evolution of Eutyranosauria (Theropoda: Tyrannosauroidae) Jared T. Voris	.....87
The Morrin Bridge fossil flora: vegetation and palaeoclimate of the Upper Cretaceous Horseshoe Canyon Formation, Alberta Christopher K. West, Katharina Halbwidl, Leyla J. Seyfullah, Tammo Reichgelt, and David R. Greenwood	.....88
New insights into the early evolution of parvipelvian ichthyosaurs based on undescribed material from the Pardonet Formation (Upper Triassic) of British Columbia Andrzej S. Wolniewicz and Ilaria Paparella	.....88
Cretaceous leftovers: behavioural implications of theropod tooth marks on hadrosaurid cranial elements from the Late Cretaceous of western North America Taia C.A. Wyenberg-Henzler, Jack Milligan, Michael Willis, Caleb Brown, Darren H. Tanke, Phil R. Bell, Nicolás E. Campione, Emily Bamforth, Jackson Sweder, and Corwin Sullivan	.....89
Tale of the tail: tooth marked caudal vertebrae suggest tyrannosaurs systematically processed hadrosaur tails Taia Wyenberg-Henzler and Darren H. Tanke	.....90
Stable isotopes from tooth enamel provide novel implications for Late Cretaceous tyrannosaurid ecology Gianni Zambonin, Thomas Cullen, Jordan Mallon, and Hillary Maddin	.....91
Tooth-like dermal structures in osteostracans and implications for the origin of vertebrate teeth Jad Zouein and Bradley Scott	.....93

# The potential for postcranial material in hadrosaurid identification below the family level; a review of hadrosaurid scapular variation in Dinosaur Provincial Park

Janet Alexander, Corwin Sullivan, and Philip J. Currie

Department of Biological Sciences University of Alberta, Edmonton, AB, T6G 2E9, Canada: jalexand@ualberta.ca; corwin1@ualberta.ca; pjcurrie@ualberta.ca

Isolated hadrosaurid scapulae are rarely, if ever, identified to a rank below the level of Hadrosauridae. Small sample sizes of articulated skeletons identified to species level in combination with the substantial intraspecific variation present in many hadrosaur species make it difficult to find taxonomically meaningful differences. Despite these issues, scapulae clearly do vary morphologically across hadrosaurid taxa, which suggests that it should be possible to narrow down the identification of isolated scapulae below Hadrosauridae. For example, a strong expansion on the medial side of the anterior end of the scapula appears to be consistently present in lambeosaurines, but not in hadrosaurines. Other variations occur within, rather than between, the two major hadrosaurid clades. Several hadrosaurid taxa possess a distinct deep “notch” in the glenoid, as opposed to the relatively smooth curve present in others. The angle of the glenoid relative to the blade is also variable, with some taxa falling consistently on one end of the spectrum.

A more concerted effort should be made to thoroughly describe and examine hadrosaurid scapulae so that a more rigorous analysis of intraspecific variability may be possible. If robust diagnostic characters based on large sample sizes can be found, these can be used to support the diagnoses of hadrosaurid taxa. This increase in quantity and quality of characters pertaining to the scapula would give us a more robust dataset with which to identify both articulated skeletons and isolated hadrosaurid bones. Restricting ourselves to cranial material when choosing diagnostic characters for hadrosaurid dinosaurs only functions to prevent any potentially useful postcranial characters from coming to light.

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# The nature of cranial developmental divergence at the base of Galloanserae: combining comparative ontogeny with the avian fossil record

Bassel Arnaout<sup>1,2,3</sup>, Guillermo Navalon<sup>2,4</sup>, Olivia Plateau<sup>5,6</sup>, Stephan Lautenschlager<sup>7,8</sup>, Benjamin Steventon<sup>3</sup>, and Daniel Field<sup>2,9</sup>

<sup>1</sup>Cell Biology and Anatomy, University of Calgary, Calgary, AB, Canada

<sup>2</sup>Earth Sciences, University of Cambridge, Cambridge, UK

<sup>3</sup>Genetics, University of Cambridge, Cambridge, UK

<sup>4</sup>Department of Life Sciences, Universidad de Alcalá, Madrid, Spain

<sup>5</sup>The Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

<sup>6</sup>Naturhistorisches Museum Bern, Bern, Switzerland

<sup>7</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK

<sup>8</sup>Lapworth Museum of Geology, Birmingham, UK

<sup>9</sup>Museum of Zoology, University of Cambridge, Cambridge, UK

One of the oldest and deepest divergences within crown birds is the split at the root of Galloanserae (fowl) into Galliformes (landfowl) and Anseriformes (waterfowl). This ancient divergence led to the evolution of two clades with distinct cranial morphologies: the galliform skull is characterised by a short deep beak and relatively large and round braincase, while the anseriform skull is generally characterised by wide and elongate bills and a short, deep braincase. Underlying these distinct adult morphologies is an evolutionary divergence in skull development between Galliformes and Anseriformes, which remains poorly understood. To date, previous research has focused only on the early embryonic differences among three galloanseran species. Here, we built upon this prior work with a dataset of  $\mu$ CT scans of hatchlings and adults belonging to thirty species of extant galloanserans, covering the phylogenetic breadth of the clade, along with two early galloanseran fossil skulls. We quantitatively analysed ontogenetic disparity among these species using 3D geometric morphometric methods, revealing that interclade divergence at post-hatching stages is about ~40% greater than at pre-hatching stages. We also found that anseriform cranial ontogeny is both more disparate and peramorphic relative to that of galliforms, underlined by two heterochronic mechanisms—an ontogenetic shift, and hypermorphosis. Incorporating the reconstructed skulls of the fossil taxa *Asterornis*, a putative stem galloanseran, and *Presbyornis*, a putative stem anseriform, show that galliform-like cranial morphology appears to be plesiomorphic for crown Galloanserae, indicating that the iconic cranial morphology characterising most anseriforms likely evolved from an ancestral state exhibiting more galliform-like morphology and ontogeny.

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## You should look at a gift horse in the mouth: using the Patterning and Inhibitory Cascade Models to study the evolution of molarization in hoofed mammals

Austin J. Ashbaugh<sup>1</sup>, Heather A. Jamniczky<sup>2</sup>, and Jessica M. Theodor<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Calgary, Calgary, AB, Canada, T2N 1N4; austin.ashbaugh@ucalgary.ca; jtheodor@ucalgary.ca

<sup>2</sup>Department of Cell Biology and Anatomy, University of Calgary, Calgary, AB, Canada, T2N 4N1; hajamnic@ucalgary.ca

Cheek teeth are filled to the cusp with information about mammalian evolution. Studying the evolution of mammalian cheek tooth crown complexity has benefited our understanding of mammalian evolution in developmental, morphological, and ecological contexts. Most work is focused on individual cheek tooth loci as opposed to considering the premolars and molars as serial homologues. This focus on individual tooth loci has left the exploration of inter-regional phenomena understudied. One such phenomenon is the molarization of premolars across hoofed mammals; some have simple unicuspid premolars while others have premolar crowns that are equal in complexity to their molars. Many developmental models have been proposed to understand cheek tooth evolution, but minimal work has been done to synthesize these models into a holistic understanding of cheek tooth crown complexity evolution. We investigated if applying a synergized theoretical framework of the inhibitory and patterning cascade model to artiodactyl and perissodactyl taxa could be used to study the evolution of molarization in hoofed mammals. We applied an existing 2D landmarking scheme for the upper and lower premolar molar boundaries of hoofed mammals to capture the morphology across this important identity boundary. Shape data were analyzed through phylogenetically informed modularity analyses to capture the covariation structure at

the upper and lower premolar-molar boundaries. A priori modularity hypotheses were proposed based on developmental models including the patterning cascade model and the inhibitory cascade model. Both artiodactyl and perissodactyl results showed support for modularity across the upper and lower premolar molar boundary but showed more variation in the upper premolar molar boundary. Artiodactyls show consistency in support for modularity hypotheses between upper and lower premolar molar boundaries where perissodactyls show significant differences in support for modularity hypotheses between upper and lower premolar molar boundaries. Our results illustrate that the covariation structure at the premolar molar boundary has convergent and divergent elements that both have consequences for our understanding of the evolution of molarization within and between artiodactyls and perissodactyls.

## A frill a minute: new material informs cranial morphology and intraspecies cranial variation in *Pachyrhinosaurus lakustai* from the Campanian (73 Ma) Pipestone Creek Bonebed, Wapiti Formation, northwest Alberta

Emily L. Bamforth<sup>1,2,3</sup>, Jackson Sweder<sup>1</sup>, Aidan Kerr<sup>1</sup>, and Alexander Baxter<sup>1</sup>

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

<sup>2</sup>Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK, S7N 5A2, Canada

<sup>3</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2R3, Canada

The Pipestone Creek Bonebed (PCB), located near Grande Prairie, Alberta, is one of largest and densest dinosaur bonebeds in North America, having produced close to 10 000 specimens of the centrosaurine dinosaur *Pachyrhinosaurus lakustai*. Representing a single large herd of animals from a snapshot of time, the PCB provides significant insight into the paleobiology, ontogeny, and paleoecology of *Pachyrhinosaurus* specifically, and ceratopsians in general. One evolving area of research regarding the PCB material is the assessment of individual morphological variation that exists within this single species of ceratopsians.

Like other centrosaurines, *P. lakustai* had an elaborate cranial frill comprised of squamosal and parietal bones. The partial portion of the frill features two large parietal fenestrae separated by a parietal bar, a small set of parietal horns (P2s) along the distal edge of the midline that point medially, and a larger set of partial horns (P3s) that faced distally. In the past five years, fifteen complete parietals have been collected from the PCB. Analyses of these specimens, as well as a review of parietal specimens collected prior to 2022, has revealed a significant range of variation within this generalized parietal morphology. For example, some parietals have robust P2s that overlap medially, while other specimens almost lack P2s entirely. The width of the parietal margins and parietal bar can vary threefold, from 7 cm to 26 cm, even among specimens of similar overall size. Counterintuitively, parietal specimens that are smaller in overall size tend to have longer P3 horns. It has been proposed that these variations may relate to ontogeny, sexual dimorphism, or simply phenotypic plasticity, hypotheses are currently being explored.

Another autapomorphy of *P. lakustai* is a midline ‘unicorn’ spike on the parietal bar, which is also a variable character (Currie et al. 2008). The midline spike(s) vary in number from one to three and vary greatly in size among individual skulls. In some cases, the unicorn spike(s) appear to be fused osteoderms, while in other cases, they appear to be outgrowths of a midline parietal swelling (Currie et al. 2008). A new skull collected in 2024,

PCB2024.666, was notable for having an extremely reduced or absent midline spike despite being a large, mature individual, calling into question the use of the character as an apomorphy for *P. lakustai*. Future histological work on the midline spike may lead to a better understanding of its origin, ontogenic development, and taphonomy, helping to elucidate why this character may be so notably variable.

One of the challenges associated with studying the frill of *P. lakustai* is the disarticulated nature of the PCB material, such that no frill of *P. lakustai* has yet been found still in articulation with the rest of the skull. Until very recently, the midline spike had always been found in articulation with the cranium, making it difficult to understand the position of the spike relative to the parietal bar and parietal horns. In 2025, a specimen (PCB2025.700) was discovered that comprised an isolated parietal with the parietal bar, parietal horns, and midline spike in articulation. In this specimen, almost 100 cm separates the midline spike and the distal end of the parietals, suggesting that the *P. lakustai* frill may have been far more distally expanded than previously thought. Future work on defining features in isolated parietal bars to determine their proximity to the midline spike may help to elucidate the true morphology of the whole *P. lakustai* skull.

### Literature Cited

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## Interspecies variation of the nasal airways in Ankylosauria from Upper Cretaceous deposits of southern Alberta

Ollie Barnett<sup>1</sup>, Darla K. Zelenitsky<sup>1</sup>, Jared T. Voris<sup>1</sup>, Jordan Mallon<sup>2</sup>, and François Therrien<sup>1,3</sup>

<sup>1</sup>Department of Earth, Energy and Environment, University of Calgary, AB, T2N 1N4, Canada

<sup>2</sup>Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature, Ottawa, ON, Canada

<sup>3</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada

Ankylosauria is a speciose clade of herbivorous dinosaurs characterised by their bony, dermal armour. Even though ankylosaurs are known to have unique nasal airways that vary in complexity, interspecific variation remains poorly understood due to limited computed tomography (CT) reconstructions. CT allows for comparison of these structures among the highly diverse ankylosaur species from the Upper Cretaceous Dinosaur Park and Horseshoe Canyon formations of Alberta, Canada. Here we reconstruct these structures for five species (14 specimens) of ankylosaurs from these strata. These include the ankylosaurids *Anodontosaurus lambei*, *Euoplocephalus tutus* and *Scolosaurus cutleri* and the nodosaurids *Edmontonia rugosidens* and *Panoplosaurus mirus*.

Our results show that the airway morphology of the ankylosaurids *Anodontosaurus* (CMN 8530, TMP 1979.014.0747, TMP 1997.132.0001, TMP 1998.083.0001), *Euoplocephalus* (TMP 1991.127.0001 and AMNH 5405) and *Scolosaurus* (TMP 2001.42.19) are nearly identical. From the naris, the airway in each taxon initially takes a dorsomedial course of the rostral loop that then makes multiple turns into the caudal loop before exiting through the choana. Significant differences were found in the paranasal structures between the nodosaurids *Edmontonia* (TMP 1991.036.0507, TMP 1998.074.0001, TMP 2000.012.0158) and *Panoplosaurus*

(ROM 1215, CMN 2759, TMP 1983.025.0002, TMP 1998.067.0001), although both have a simplified airway relative to the ankylosaurids. *Edmontonia* has a simple, funnel-shaped airway with a rostral-caudal-running paranasal sinus. Thus, the airflow followed a more direct, posteriorly directed route from the naris to the choana. This differs from *Panoplosaurus* in which the rostral loop twists laterally and then continues to the caudal loop before exiting ventromedially through the choanae.

Here we confirm prior nasal airway reconstructions of *Euoplocephalus* and *Panoplosaurus*, while providing reconstructions for three additional taxa. Furthermore, we show interspecific variation between closely related taxa appears high in nodosaurids, but low in ankylosaurids. Additional reconstructions of ankylosaur species and specimens will help us further understand interspecies variation and contribute data for taxonomic and phylogenetic studies.

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## Unlocking the Lockhart Pit: further investigations into a new Plio-Pleistocene(?) vertebrate locality in southeastern Alberta

Christina I. Barrón-Ortiz<sup>1</sup>, Katherine K. Bramble<sup>1</sup>, René W. Barendregt<sup>2</sup>, Dale A. Leckie<sup>3</sup>, Christopher N. Jass<sup>1</sup>, Serhiy Burak<sup>4</sup>, Britta Jensen<sup>5</sup>, Fatima Iftikhar<sup>6</sup>, and Kelsey Martin<sup>7</sup>

<sup>1</sup>Quaternary Studies Program, Royal Alberta Museum, Edmonton, AB, T5J 0G2, Canada; christina.barron-ortiz@gov.ab.ca; katherine.bramble@gov.ab.ca; chris.jass@gov.ab.ca

<sup>2</sup>Department of Geography and Environment, University of Lethbridge, Lethbridge, AB, T1K 3M4, Canada; barendregt@uleth.ca

<sup>3</sup>Department of Earth, Energy, and Environment, University of Calgary, Calgary, AB, T2N 1N4, Canada; Leckied@shaw.ca

<sup>4</sup>Department of Physical Sciences, MacEwan University, Edmonton, AB, T5H 1C2, Canada; buryaks@macewan.ca

<sup>5</sup>Department of Earth and Atmospheric Science, University of Alberta, Edmonton, AB, T6G 2E3, Canada; bjensen@ualberta.ca

<sup>6</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; fiftikha@ualberta.ca

<sup>7</sup>Special Areas Board, Hanna, AB, T0J 1P0, Canada; Kelsey.Martin@specialareas.ab.ca

The Lockhart Pit, located approximately 75 km southeast of Hanna, Alberta, is a gravel pit operated intermittently since the 1980s. The pit is located on a terrace remnant approximately 300 m below the highest surface of the Hand Hills and we interpret it to be geologically younger than the Hand Hills Formation. We initially found vertebrate fossils at the locality in 2019 and conducted additional fieldwork at the site in 2023, 2024, and 2025. Collectively, our data suggest that the Lockhart Pit may preserve a unique vertebrate fauna from timeframes not represented in the geologic record elsewhere in Alberta.

The Lockhart Pit is divided into fossiliferous north and south pits. The south pit has the longest stratigraphic section and most of our work focused in this area, including sampling to establish a paleomagnetic sequence for the deposit. The top of the section (~3 m) is capped by glacial till. An approximately 7-metre sequence of gravels/conglomerates and sand/sandstone with lenses of marl and silt occurs below the till. The gravel succession shows upward fining. Most fossil vertebrates were eroded out of the pit wall, but the few specimens we collected in situ were found in the gravels. Fossil-bearing deposits below the glacial till likely formed in a coarse-grained meandering river system that was only a few metres deep.

Of the identifiable vertebrate fossils, horse remains are the most abundant, represented by a partial skull, two teeth, several tooth fragments, a third phalanx, and other fragmentary postcranial remains. The more complete teeth, an upper third premolar (P3) and an upper second molar (M2), are identified as *Plesippus* sp. based on their degree of hypsodonty, relatively short protocones, simple fossette plications, and features of the ectoloph. We also recovered camelid remains, including a partial lower third molar (m3), distal and proximal metapodial fragments, and an entocuneiform. The m3 is identified as *Hemiauchenia* cf. *H. blancoensis* based on its size, the presence of a distinct “llama buttress,” and degree of hypsodonty. A partial lower dentary with the roots of three teeth could represent a peccary (Tayassuidae), but further study is necessary to determine its taxonomic identity. Small mammal remains recovered from the site include a partial lower jaw of a rodent (Sciuridae) and a weathered partial skull that has yet to be identified. *Plesippus* sp. and *Hemiauchenia* cf. *H. blancoensis* are characteristic of Blancan age (ca. 4.9 – 1.8 Ma; early-mid Pliocene to early Pleistocene).

Samples for palaeomagnetic analysis were collected from four sites within the sedimentary sequence below the surface glacial till. Three of the sites from the gravel and sand sequence are reversely magnetized and only one site, collected from a silt lens immediately above the lowest sampling site in the pit, is normally magnetized. Given the estimated biochronology for the collected fossils, our initial interpretation was that the polarities may indicate that the sedimentary sequence, excluding the till, falls within the middle-late Gilbert or early Matuyama Magneto Chrons.

To further evaluate the age of the vertebrate assemblage, we obtained U-Pb dates on dental enamel of two horse teeth collected from the south pit. One of the teeth was collected from the upper section (finer gravels and sand) of the pit. The mean U-Pb date of this horse tooth is  $4.8 \pm 0.3$  Ma. The second tooth was recovered out of context. It produced a U-Pb date of  $5.2 \pm 0.9$  Ma. If these dates are correct, it would suggest that the fossil assemblage and the sand and gravel deposits are earliest Blancan in age and within the middle Gilbert Magneto Chron. Additional testing of that age hypothesis will be conducted via radiometric dating of a bentonite recovered from the site and, ideally, the recovery of additional fossils.

Although the vertebrate fossil assemblage at the Lockhart Pit is not extensive, the preserved specimens, palaeomagnetic data, and U-Pb dates on dental enamel are significant. Collectively the faunal elements recovered from the site record a unique assemblage. Additional work to refine age hypotheses will help us better place that assemblage within a robust chronological framework.

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## Predicting Species Interactions and their Eco-evolutionary Consequences in the Fossil Record

Louis-Philippe Bateman and Hans Larsson

Department of Biology, McGill University, Montreal, QC, Canada; louis-philippe.bateman@mail.mcgill.ca, hans.ce.larsson@mcgill.ca

Species interactions are responsible for many of the emergent properties of ecosystems, such as their dynamics, response to perturbation, and ecosystem services. They are effectively what make ecosystems complex. Yet, despite their high importance in recent and fossil ecosystems, species interactions have been difficult to explicitly quantify and integrate into paleontological research, simply because they can only very rarely be observed in the fossil record. This has sometimes made it difficult to test fundamental hypotheses on ecological and evolutionary change, such as the Red Queen and Court Jester theories of evolution.

The rise of increasingly accurate models to predict species interactions in the neoecological world presents a remarkable opportunity for palaeobiologists. Here, we trained a deep learning model that uses phylogenetic,

body size, diet, habitat, and locomotory traits to predict interactions amongst extinct mammals. Our model had a strong performance, with precision-recall area-under-curve = 0.76, receiver operating characteristic area-under-curve = 0.93, and true skill statistic = 0.80. The architecture and assumptions of deep learning models and other models used to predict species interactions in the past are discussed. In particular, their ability to accurately interpolate or extrapolate interactions amongst extinct taxa, to uncover the mechanisms behind species interactions, and to accurately predict community structures are compared. We also explore strategies to propagate uncertainty through such models, assess their robustness, and improve their performance.

These models are used to predict trophic networks of over 250 North American Cenozoic mammalian communities. Changes to the trophic networks and their properties in this continental-sized time series are correlated with abiotic and biotic factors, such as climate and species turnover. The Paleocene-Eocene Thermal Maximum and the spread of grasslands are associated with some network property changes, suggesting those metrics may have broad explanatory power of ecosystems through time. These results draw broad implications for both theories of ecological and evolutionary change and develop baselines for expanding work on palaeoecological networks as a new frontier for ancient ecosystem research.

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## A possible pachycephalosaur supraorbital from the Frenchman Formation, southwest Saskatchewan

Mollie K. Black<sup>1</sup>, Jack R. Milligan<sup>2</sup>, and Jordan C. Mallon<sup>3,4</sup>

<sup>1</sup>University of Saskatchewan, Department of Geological Sciences, Saskatoon SK, S7N 5E2, Canada; ciz097@usask.ca

<sup>2</sup>University of Alberta, Department of Biological Sciences, Edmonton, AB, T6G 2E9, Canada; jmillig1@ualberta.ca

<sup>3</sup>Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; jmallon@nature.ca

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

Despite their popularity in public media, pachycephalosaurs are an enigmatic group of dinosaurs, especially in Saskatchewan, with only two partial specimens currently described. Here we report on a probable pachycephalosaur anterior supraorbital from a microsite in the Frenchman Formation of southwest Saskatchewan, Canada. The Frenchman Formation is of Late Cretaceous (Maastrichtian) age and contemporaneous to the American Hell Creek Formation. Its depositional environment is interpreted as a meandering fluvial dominated floodplain. The bone is wedge shaped and has an external surface covered in irregularly spaced tubercles. By contrast, the orbital surface is smooth and exhibits several small foramina. We compare the morphology of this element to contemporaneous taxa including *Sphaertholus*, which has been previously reported from the Frenchman Formation. Though no current *Sphaertholus* material has an anterior supraorbital preserved, this specimen is within the size range of contacts between the anterior supraorbital and adjacent cranial elements. However the proportions of these contacts on this specimen do not fit those of *Sphaertholus*, which are consistent throughout the ontogeny of the genus. As the contemporaneous and geographically adjacent Hell Creek Formation possesses multiple pachycephalosaur species, it should be expected that a similar diversity exists in the Frenchman Formation of Saskatchewan. Describing isolated elements such as this highlights Saskatchewan's hidden fossil diversity and its contribution to the latest Cretaceous dinosaur fauna.

# Etiology of colour banding in Cretaceous marine reptile teeth

Kirstin S. Brink and Virginia K. Gold

Department of Earth Sciences, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada; Kirstin.brink@umanitoba.ca, vkgold792.5@gmail.com

Banding and other colouration patterns in the dentine and enamel of fossilized teeth are relatively common in vertebrate non-mammalian carnivores. However, it is unknown if these colourations are due to the fossilization process (i.e., diagenesis) or if they formed during tooth development. In mammals, colour changes associated with other defects (e.g., enamel hypoplasia) have biological significance, marking life history events or periods of stress, however, this has not been demonstrated in reptiles. In this study, we examined teeth with banded dentine from extinct Cretaceous-aged marine reptiles, mosasaurs, to determine if they formed through fossilization or before the death of the animal and have biological significance. To do so, transmitted light microscopy, electron probe microanalysis, scanning electron microscopy, and transmission electron microscopy analyses were used to determine chemical, morphological, and textural features of normal and banded dentine. Results show that the banded dentine is translucent in thin section, has infilled dentine tubules with a similar elemental composition to the surrounding intertubular dentine, and has smaller intratubular crystals than the surrounding intertubular dentine. Counts of von Ebner Lines suggest the banded dentine formed over 30 days. We interpret this band as sclerotic dentine, formed during the life of the animal. However, the etiology of this patterned dentine remains unknown, as no similar occurrences have been described for humans or other animals. This study emphasizes the use of the fossil record to understand the deep homologies of modern tooth tissues and the diversity of occurrences in vertebrates.

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# Characterizing dromaeosaurid (Theropoda; Paraves) feeding traces, and repeated occurrence on azhdarchid (Pterosauria) bones

Caleb Brown

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

Feeding traces (i.e., tooth/bite marks) on fossil bone provide direct evidence of ancient trophic interactions and feeding behaviour of extinct animals. Despite a considerable and growing body of research on dinosaur feeding traces from the Late Cretaceous of North America, the vast majority of reported occurrences are attributed to Tyrannosauridae and largely occur on the bones of Ornithischia and, to a lesser extent, other Tyrannosauridae. Tyrannosaurids as tracemakers are largely supported by the large size and spacing of the traces, precluding smaller taxa. Conversely size overlap with other small theropods lineages (i.e., Dromaeosauridae, Troodontidae) with very young tyrannosaur individuals, often limits confident referral of smaller-scale tooth marks. As a result, while dromaeosaurids likely occupied important carnivorous niches in these ancient ecosystems, definitive dromaeosaurid feeding traces are rare.

A major exception to this is the holotype of the azhdarchid pterosaur *Cryodrakon boreas* (TMP 1992.083.0002), an associated specimen of which the tibia preserves a series of small bite marks as well as an imbedded tooth which can be referred to the dromaeosaurid *Saurornitholestes langstoni*. As such this specimen provides the rare opportunity to characterize the scale and features of dromaeosaurid tooth marks. A redescription of the marks on TMP 1992.083.0002 reveals a total of nine traces. Traces are largely orthogonal to the long axis of the bone, and are characterized as very thin linear furrows, ranging from 1.7 to 16.7 mm in length and from 0.4 to 0.8 mm in width. Traces show redirection of bone fibers, indicating direction of tooth travel across the bone surface which, when combined with the position of the embedded tooth, suggests marks were caused during caudal retraction of the skull relative to the bone. Several marks also show a raised rim of plastically displaced bone tissue lateral to the trace long axis. Similar, but less distinct, traces are also seen on the proximal third of metacarpal IV, but not on the other associated elements (humerus, pteroid, rib, metatarsal, cervical vertebra). Length and width metrics of the marks on the tibia fall well within the data for actualistic feeding traces of *Varanus komodoensis*, as does the dominance of linear furrows, suggesting Varanidae may be reasonable extant proxy for feeding in Dromaeosauridae.

An exhaustive survey of pterosaur material from the Belly River Group identifies eight other isolated azhdarchid specimens with similar small-scale tooth marks (including a femur, metacarpal IV, ulna, and unidentified elements). Some of these also preserve denticle drag marks and parallel tooth spacing, both consistent with a dromaeosaurid trace maker. Combined with reported occurrence of azhdarchid bones as stomach contents within sauronitholestines, this suggests azhdarchids may have been a common food source of dromaeosaurids. Small scale traces such as those described here are likely underrecognized relative to the larger, more obvious, traces generally attributed to Tyrannosauridae.

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## Theropod tracks at the Nîsôtêw Nimisêw Wacy Tracksite, Gething Formation (Early Cretaceous), northeastern British Columbia

Dakota Camarena<sup>1</sup> and Victoria Arbour<sup>1, 2</sup>

<sup>1</sup>School of Earth and Ocean Sciences, University of Victoria, Victoria, BC, V8W 2Y2, Canada; djcama@uvic.ca

<sup>2</sup>Royal BC Museum, Victoria, BC, V8W 9W2, Canada; VArbour@royalbcmuseum.bc.ca

The theropod ichnogenus *Irenesauripus* was first described from abundant tracks in the Peace River Canyon, in the Aptian-Albian Gething Formation. The original diagnoses of the three ichnospecies of *Irenesauripus* lack sufficient detail in a modern ichnotaxonomic context and rely on common features found in many theropod dinosaur tracks. The recently excavated Nîsôtêw Nimisêw Wacy Tracksite (formerly referred to as the Six Peaks Tracksite), located near Carbon Creek to the southwest of the original Peace River canyon sites, preserves dozens of theropod prints tentatively referred to *Irenesauripus*. These tracks provide a unique opportunity to revisit assumptions of the ichnogenus with a new set of data. Measurement and photogrammetric data collected during 2023 and 2024 fieldwork by the Royal BC Museum are used to understand variation within medium to large-sized theropod tracks. Preliminary results suggest that *Irenesauripus* prints in the Nîsôtêw Nimisêw Wacy Tracksite are larger than those previously described from the Peace River Canyon, but smaller than comparable specimens from Utah and Texas. Prints with narrow digits and angular heels compare well with *I. acutus*, but most lack asymmetrical toe divarication. Prints with toe pad impressions compare well with *I. mclearnii*. The presence/absence of diagnostic *Irenesauripus* features shifts along a continuum within some trackways containing successive footprints left by

a single individual. The presence of multiple *Irenesauripus* morphotypes on the same track surface suggests that the morphological variation is not driven by substrate alone. The currently accepted species of *Irenesauripus* do not fully capture the full range of shape variation.

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## A rare juvenile mosasaur provides potential insights into ontogenetic change within the subfamily Plioplatecarpinae (Squamata, Mosasauridae)

Amy A. Cameron<sup>1</sup>, Takuya Konishi<sup>2</sup>, and Michael W. Caldwell<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada; aacamer1@ualberta.ca, mikec@ualberta.ca

<sup>2</sup>Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio, United States of America; konishta@ucmail.uc.edu

Due to a lack of juvenile and subadult specimens preserved in the fossil record, very little is known about mosasaur ontogeny. In 1974, a potential juvenile mosasaur specimen, M 74.09.03, was recovered in Morden, Manitoba from the Pembina Member of the Pierre Shale Formation (approx. 80 Ma). This specimen is composed of a few disarticulated cranial elements, as well as some ribs and vertebrae, and currently resides in the collections of the Canadian Fossil Discovery Centre. Based on a few cranial features, it appears to belong to the mosasaur subfamily Plioplatecarpinae. Due to its relatively small size and the uncommon lack of fusion between the main elements that comprise the skull roof, it is assumed that this specimen had not yet reached skeletal maturity prior to its death. Qualitative and quantitative comparisons conducted between the likely juvenile and adult plioplatecarpine specimens provide potential insight into the changes the plioplatecarpine skull may have undergone over ontogeny. These include a general widening and thickening of the cranial elements, particularly of the premaxilla, frontal, and parietal. The spacing between the maxillary teeth also increases with size. Fusion of the elements of the skull roof, primarily the frontal and parietal, appears to be incomplete until later in ontogeny. The angle at which the suspensorial rami of the parietal diverge appears obtuse in the smaller specimen compared to larger specimens. The suspensorial rami also thickens lateromedially. The two aforementioned changes imply an increase in size of the supratemporal fenestrae over ontogeny, likely correlated with an increase in size of the adductor jaw musculature. The descensus processus parietalis appears relatively more exposed in dorsal aspect in the younger specimen than in adults, so it is likely that the cranial depth also increases with age. Overall, this small mosasaur specimen provides valuable insights into how the plioplatecarpine mosasaur cranium may have changed during growth, as well as how those skeletal changes may have resulted in dietary changes over ontogeny.

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# Historical confusion and the evolution of the dinosaur pelvis

Leon P.A.M. Claessens

Maastricht Science Programme, Faculty of Science and Engineering, Maastricht University, Maastricht, The Netherlands; leon.claessens@maastrichtuniversity.nl

The original subdivision of the Dinosauria into two clades, the Saurischia and the Ornithischia, was, to a large extent, based on pelvic morphology. When the order Ornithischia was erected, the presence or absence of a prepubic skeletal element was not part of the diagnosis. The later identification of a ‘prepubis’ in ornithischian dinosaurs is the result of misidentification confounded by later misinterpretation. Many historical descriptions of the archosaur pelvis recognized a fourth element located anterior to the pubis. This element, the prepubis (= praepubis, epipubis, or marsupiale), was well known to many 19th century anatomists, and used to build elaborate classification schemes. However, the homology of these different elements was poorly understood. Historical contingencies of new fossil discoveries, different interpretations and misinterpretations of pelvic anatomy in tetrapods, and more than a century of taxonomic revisions have resulted in an interpretation of ornithischian pelvic anatomy that is confusing in a broader phylogenetic context and technically inaccurate. Although outdated phylogenetic interpretations have long been discarded, some of its inaccuracies persist in pelvic anatomical nomenclature and it is time that these are put to rest.

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## Reexamination of hypothesized sexual dimorphism in the Early Permian non-mammalian synapsid *Dimetrodon limbatus*

Nathan Cochran<sup>1</sup> and Jason S. Anderson<sup>2</sup>

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

<sup>2</sup>University of Calgary, Calgary, AB, T2N 1N4, Canada; janders@ucalgary.ca

Sexual dimorphism, a phenotypic difference between the sexes of an organism, occurs commonly in extant taxa and previous authors hypothesized its occurrence in extinct taxa. Previous literature proposed the presence of sexual dimorphism in the Early Permian stem-mammal *Dimetrodon limbatus* due to the presence of two sympatric morphotypes differing in neural spine length, mandibular tooth count, “exaggeration” of the maxillary step, length of the temporal region, length of the postorbital skull, limb bone robusticity, length of the dorsal vertebrae, elongation of the upper dentition, reduction in precanine length, and tooth count anterior to the canines. However, the hypothesized sexual dimorphism was not tested statistically, nor were there controls for stratigraphic or ontogenetic variation in anatomy. We tested whether *D. limbatus* exhibited sexual dimorphism by examining proposed dimorphic character for bimodality. We used an electronic slide caliper to measure mature specimens at the Field Museum of Natural History. We limited the sample to single bonebeds to control for time and mature specimens to control ontogenetic variation in anatomy. The measurements were log transformed then subjected to a Shapiro Wilk’s test and Hartigan’s dip test because a bimodal distribution must be non-normal

and multimodal. Dimorphism was then tested independently using agglomerative hierarchical clustering and gap statistic analysis to find the most significant number of clusters and identify which cluster each specimen belonged. Our analysis supports unimodal, normal distributions for all characters previously reported as dimorphic. Agglomerative hierarchical clustering and gap statistic analysis found the sample was best explained with a single cluster, therefore we reject sexual dimorphism as a hypothesis. These results suggest that the sail height of *D. limbatus* is not a result of sexual selection, although future work must increase the statistical strength of the results by expanding the sample.

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## A specimen of *Gorgosaurus libratus* from the Wapiti Formation of northeastern British Columbia, Canada

Colton C. Coppock<sup>1</sup>, Hans C.E. Larsson<sup>2</sup>, and Philip J. Currie<sup>1</sup>

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

<sup>2</sup>Department of Biology, McGill University, Montréal, QC, H3A 1B1, Canada; hans.ce.larsson@mcgill.ca

Tyrannosaurid dinosaurs are well represented throughout Campanian-aged rocks of southern Alberta. However, little is known about the taxonomic diversity of the clade at latitudes north of this region. A natural mold of a partial tyrannosaurid rostrum (TMRF 2017.01.01) was collected from the Wapiti Formation of the Tumbler Ridge region in British Columbia, Canada. The impression consists of a complete right maxilla and parts of the right lacrimal and jugal from a juvenile individual. Although the precise stratigraphic position remains uncertain due to the proximity of an orogenic belt, preliminary stratigraphic interpretations indicate that the specimen is from the Upper Campanian section of the Wapiti Formation. The well-preserved natural mold provided an opportunity to produce a highly detailed cast (UALVP 63805) that preserves minute features of the original specimen and permits taxonomic identification. The combination of cranial characteristics present in the specimen supports a referral to *Gorgosaurus libratus*. The preserved region of the maxilla indicates the presence of incisiform teeth occupying alveoli one and two. While immature specimens of *Gorgosaurus* from the Dinosaur Park Formation share this anatomy, mature specimens possess a single incisiform tooth restricted to the first alveolus, suggesting an ontogenetic shift in feeding behaviour. Although limited, the cranial material indicates little variation in morphology across the extensive biogeographic distribution of contemporaneous specimens of *Gorgosaurus*, which now spans from northern Montana to northeastern British Columbia. The convex hull formed by occurrences of *Gorgosaurus* indicates a minimum geographic range of approximately 198,000 km<sup>2</sup> for the taxon. Geographic ranges of extant terrestrial apex predators are much larger, indicating that either the distribution of *Gorgosaurus* was controlled by factors not present today, its range is greatly underestimated, or a combination of both. This novel occurrence, together with additional occurrence data for *Gorgosaurus* and the contemporaneous tyrannosaurine *Daspletosaurus*, supports previous hypotheses regarding spatially disparate distributions of Laramidian tyrannosaurid taxa. These patterns elucidate the complex ecological interactions of tyrannosaurid taxa and the faunal diversity throughout Campanian ecosystems.

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# Filter-feeding evolutionary trends in Late Cretaceous lamniform sharks

Bruno P. Costa, Ricardo L. Silva, and Kirstin S. Brink

Department of Earth Sciences, Clayton H. Riddell Faculty of Environment, Earth, and Resources, University of Manitoba, Winnipeg, MB, R3T 2M6, Canada; costab@myumanitoba.ca; ricardo.silva@umanitoba.ca; kirstin.brink@umanitoba.ca

The evolution of planktivorous filter-feeding among marine vertebrates is scarcely known, partly due to the rarity of species in the fossil record that suggest this feeding strategy and the fact that filter-feeding is an uncommon, highly specialized niche. Throughout geological history, filter-feeding has been observed in elasmobranchs (i.e., sharks and rays), actinopterygians (e.g., Pachycormiformes), and marine mammals, specifically cetaceans, the only unambiguous case of planktivory in marine amniotes.

The oldest records of filter-feeding habits among elasmobranchs date to the Cenomanian–Turonian (early Late Cretaceous), including *Pseudomegachasma comanchensis*, *Cretomanta canadensis*, and *Aquilolamna milarcae*. The Coniacian–Campanian aged putative elasmobranch *Platylithophycus cretaceus* is also interpreted to have possessed a planktivorous lifestyle. However, the fossil record shows a lack of transitional elasmobranch species providing evidence for the initial adaptations associated with the acquisition of a filter-feeding lifestyle. Moreover, recent literature suggests that planktivorous filter-feeding in marine vertebrates evolved from large/gigantic pelagic predatory (e.g., lamniform sharks) or suction-assisted raptorial feeding (e.g., cetaceans) ancestors.

A near-complete skeleton of a new Campanian-aged lamniform shark (S.75.02.06) from southern Manitoba, Canada, indicates anatomical characteristics suitable for a planktivorous feeding strategy, despite initially being described as a macrophagous predator. In fact, this specimen appears to combine predator traits, i.e., high precaudal vertebral count suggesting high maneuverability, with filter-feeder traits, i.e., mandibular arch with high aspect ratio and microscopic teeth. The combination of predatory and filter-feeder anatomical traits in S.75.02.06 suggests a transitional species between macrophagous pursuit predators and more derived planktivorous filter-feeding lamniform sharks that evolved later in the early Paleogene, and does not fit with the predicted trends in the evolution of filter feeding vertebrates.

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## New research at the early Miocene site of Tonde Bridge (formerly “Meswa Bridge”), Kenya

Susanne Cote<sup>1</sup>, Kieran P. McNulty<sup>2</sup>, Daniel Peppe<sup>3</sup>, Alan Deino<sup>4</sup>, Michelle Wanjiru Kioko<sup>5</sup>, Cliff Ochieng<sup>5</sup>, Kirsten Jenkins<sup>6</sup>, Abigail Hall<sup>1</sup>, Jason Head<sup>7</sup>, and Joshua Siembo<sup>8</sup>

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

<sup>2</sup>College of Biological Sciences, University of Minnesota, St. Paul, MN, USA

<sup>3</sup>Department of Geosciences, Baylor University, Waco, TX, 76798, USA

<sup>4</sup>Berkeley Geochronology Centre, Berkeley, CA, USA

<sup>5</sup>Earth Sciences Department, National Museums of Kenya, Nairobi, Kenya

<sup>6</sup>Tacoma Community College, Tacoma, WA, USA

<sup>7</sup>Department of Zoology, University of Cambridge, Cambridge, UK

<sup>8</sup>Rusinga Island Prehistory Organization, Mbita, Kenya

The Early Miocene site of “Meswa Bridge”, Kenya is associated with the extinct Tinderet Volcano. Fieldwork in 1977–1980 recovered vertebrate fossils from a channel, including abundant anthracotheres, proboscideans, a large hyaenodont, limited small mammals, and the ape *Proconsul meswae* (Pickford and Andrews 1981). With an often-inferred age of ~22–23 Ma, Meswa Bridge has long been considered the oldest Miocene site in eastern Africa, and *P. meswae* the oldest known hominoid.

As part of a larger paleontological project at Tinderet, we re-located the site and renewed excavations. The site is next to the Tonde River, not the Meswa River, as reported by geologists and paleontologists previously. Community consultations determined that the most appropriate name for the site is Tonde Bridge, a recommendation adopted by the National Museums of Kenya. Fossils will remain accessioned at the National Museums of Kenya under the accession code KNM-ME for consistency in the literature (Siembo et al. 2025). We excavated fossils from multiple channel fills, one of which is the continuation of the original channel excavated in 1979, described the stratigraphy, and dated the site using <sup>40</sup>Ar/<sup>39</sup>Ar geochronology. We also analyzed the entire mammalian fauna from our excavation and the original excavations.

Significant fossil finds included three isolated teeth of *Proconsul meswae*, a modest number but doubling the number of adult teeth of this species, which was known only from juvenile individuals (Harrison and Andrews 2009). These new adult teeth provide further information on the morphology of *P. meswae* and solidify its status as an early proconsulid. A surprising finding is that one of the original specimens included in the hypodigm as the m1 of *P. meswae* (KNM-ME 3; Harrison and Andrews, 2009) in fact belongs to a second, unnamed species of fossil ape characterized by taller and less voluminous cusps, leading to a more open taloned basin, broader mesial and distal foveae, and narrow distal moiety. This insight that two fossil apes are present at Tonde was only possible because of the recovery of additional specimens.

The mammalian assemblage from Tonde Bridge is small and clearly size-biased towards large mammals. The channels effectively represent anthracothere bone beds, and we recovered many more anthracothere fossils. These new remains clarify the degree of canine sexual dimorphism found in the Tonde anthracothere and some aspects of its dental and mandibular anatomy, which was poorly represented in the original collections. Several recovered specimens found in the original channel belong to individuals whose remains were collected in the 1979 excavation. A new canine of *Simbakubwa* (Hyaenodonta) likely belongs to the holotype, and a lower m3 of *Eozygodon* (Mammutidae) also likely belongs to the existing partial skeleton. The most impressive material is a set of associated upper and lower teeth of the proboscidean *Prodeinotherium hobleyi*, a new taxon for the site. Other new taxonomic occurrences include a medium-sized springhare (Pedetidae), a small aardvark (*Myorycteropus*), an unidentified amphicyonid (bear-dog), and a hyracoid (hyrax).

An ash located within the fossil-bearing strata produced a <sup>40</sup>Ar/<sup>39</sup>Ar age of 21.4 Ma, substantially younger than previous age estimates for Tonde Bridge. This result is congruent with the biochronology of the mammalian fauna. It remains the oldest of the Tinderet localities, but is similar in age to Moroto, Uganda (21 Ma; MacLachy et al., 2023). The Tonde Bridge fauna and its revised age have important implications for faunal turnover in eastern Africa during the earliest Miocene. Afrotherians and early arriving laurasiatherians are more common at Tonde Bridge than at slightly later Miocene sites at Tinderet. For example, the only artiodactyl collected is the anthracothere and perissodactyls are absent. Rodents are present, but all represent groups with clear Oligocene African antecedents. Ultimately, the new age for Tonde Bridge contributes to the growing evidence that the shift from afrothere-dominated to laurasiatherian-dominated faunas took place well after the Oligocene-Miocene boundary.

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## 2.5 million years of variation in trophic community structure during a marine transgression across the Late Cretaceous (Campanian) Belly River Group of Dinosaur Provincial Park

Alexandre V. Demers-Potvin<sup>1</sup>, Louis-Philippe Bateman<sup>2</sup>, André S. Mueller<sup>2</sup>, and Hans C.E. Larsson<sup>2</sup>

<sup>1</sup>Department of Bioengineering, McGill University, Montréal, QC, H3A 0E9, Canada; alexandre.demers-potvin@mail.mcgill.ca

<sup>2</sup>Department of Biology, McGill University, Montréal, QC, H3A 1B1, Canada; louis-philippe.bateman@mail.mcgill.ca; andre.mueller@mail.mcgill.ca; hans.ce.larsson@mcgill.ca

Ecological network reconstructions provide biodiversity indicators which are often more indicative of community stability since they account for interspecific interactions. Trophic networks built on consumer-resource interactions (i.e., food webs) are a specific category of ecological networks that are increasingly implemented in palaeoecology, notably to assess the persistence of palaeocommunity structure in response to major species turnover events. Although trophic network time series before and after mass extinction events are known from a few well-sampled localities, there remains a significant shortfall in this respect for periods of “background” extinction rates, which encompass most of life’s history on Earth.

This state of knowledge led us to ask whether the Late Cretaceous (Campanian) Belly River Group (BRG) of the Dinosaur Provincial Park (DPP) biota can be studied as a baseline for the rate of (mostly) non-marine community structure variation in response to environmental change at times of “background” extinction rates. This ancient ecosystem displays a combination of taxonomic diversity, high spatiotemporal resolution, and precise individual fossil specimen quarry locations, unmatched in our planet’s pre-Quaternary fossil record. Moreover, its geological record reveals a gradual palaeoenvironmental transition from the alluvial facies-dominated Oldman Formation to the paralic/coastal facies-dominated Lethbridge Coal Zone (LCZ) in the uppermost Dinosaur Park Formation.

We compare the food web structure of five successive palaeocommunities at the species level, distributed over ~2.5 million years of the BRG and defined by a combination of dominant lithological facies types and biostratigraphic distributions. The taxonomic lists underlying these successive food webs have been recently revised following new fish occurrences in the LCZ’s marine Johnson Unit and new (and ongoing) insect species descriptions from wing impression fossils. All these food webs encompass terrestrial and aquatic organisms, with some nodes split by observed and predicted ontogenetic dietary shifts (e.g., some insects and dinosaurs). Preliminary network statistics suggest that the DPP biota’s structure remained relatively stable in terms of connectance, mean trophic level, mean food chain length, generality and vulnerability, even during the increase in marine transgression frequency characteristic of the LCZ. The stem alligatoroid *Leidyosuchus canadensis* and the elasmosaurid *Fluvionectes*

*sloanae* are revealed as “keystone” species for energy flow within their ecosystem since they have a relatively high estimated prey diversity across land, freshwater and marine environments.

This trophic time series for the Dinosaur Provincial Park biota currently accounts for taxon occurrences but not abundances. We predict that greater variation will be detected in the series’ network properties over time if the strength of at least some trophic links is weighted based on relative or rank taxon abundances from vertebrate microfossil localities. However, this analysis must account for taphonomic biases affecting preservation state and fossil taxon abundance differently across terrestrial, freshwater and marine depositional palaeoenvironments of the Belly River Group. More refined biostratigraphic distributions are also necessary and will be developed from a high-resolution drone mapping effort of all outcrops of the BRG within DPP. Once complete, a detailed, temporally controlled palaeoecological perspective of the DPP biota can be used to address specific questions about biotic responses to environmental change.

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## Evolution of early primate vision: insights from petrosal lobule size in *Dryomomys szalayi* (late Paleocene, Wyoming)

Eri C. Dixon<sup>1</sup>, Jonathan I. Bloch<sup>2</sup>, and Mary T. Silcox<sup>3</sup>

<sup>1</sup>Department of Anthropology, University of Toronto, Toronto, ON, M5S 2S2, Canada; Eri.dixon@mail.utoronto.ca

<sup>2</sup>Florida Museum of Natural History, University of Florida, Gainesville, FL, 32611-7800, USA; Jbloch@flmnh.ufl.edu

<sup>3</sup>Department of Anthropology, University of Toronto Scarborough, Scarborough, ON, M1C 1A4, Canada; Mary.silcox@utoronto.ca

The petrosal lobules are part of the cerebellum, the portion of the brain that fills the subarcuate fossa of the cranium. As part of the follicular-parafollicular complex they regulate smooth-pursuit eye movement. As such, their size may relate in part to the visual adaptations of a particular taxon. Previous work has shown changes through time in the size of petrosal lobules, with an increase in their relative size through the Paleogene.

To study neuroanatomical changes occurring in the primate stem, the petrosal lobules of *Dryomomys szalayi* were examined. *Dryomomys szalayi* is a plesiadapiform primate belonging to the Micromomyidae, a family that branched very early from the primate stem. The species is significant in being one of the most primitive primates known from cranial remains. The volume of the right petrosal lobule of *D. szalayi* was obtained from high-resolution micro-CT data. The lobule endocast was compared to those from a broad range of fossil mammals, including other plesiadapiforms.

Compared to other Paleogene mammalian endocasts, those of *D. szalayi* and the microsomyid plesiadapiform *Niptomomys* cf. *N. doreenae* from the late Paleocene have among the highest petrosal lobule percentages when scaled against body mass (0.0274 % and 0.0326 % respectively) values that are unexpectedly large for their time period. Notably, with respect to plesiadapiforms, *D. szalayi* has a larger petrosal lobule than that in both the paromomyid plesiadapiform *Ignacius graybullianus* (0.0195 %) from the later occurring early Eocene, and *Microsomyops annectens* (0.002 %) from the middle Eocene.

These findings suggest that expansion of the cerebellar petrosal lobules in Euarchontoglires did not follow a single, linear trajectory. The data point to a mosaic pattern of evolution, with different lineages exhibiting variation in lobule size at different times. With respect to *D. szalayi* specifically, these findings may suggest a change in the relative importance of the visual system, such that it was adept at tracking moving items such as prey.

# Discovering fish and fish lizards: fieldwork along the mid-Cretaceous riverbanks of the Hay River, Northwest Territories, Canada

Joshua A. Doyon, Luke E. Nelson, Meghan E. Dueck, Mondo Miyazato, and Alison M. Murray

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; jdoyon@ualberta.ca; lenelson@ualberta.ca; medueck@ualberta.ca; mondo@ualberta.ca; ammurray@ualberta.ca

Gently meandering through the boreal forest of Alberta and the Northwest Territories, the Hay River flows northward into Great Slave Lake. Just north of the Alberta–Northwest Territories border, a single river bend exposes a dense concentration of mid-Cretaceous (Albian; ~105 Mya) marine fossils. Settled within the muddy riverbanks are abundant remains of bony fishes and ichthyosaurs.

The last significant fossil collecting effort at Hay River occurred in 1972. In August 2025, our research team returned to the locality and collected more than 150 specimens. Several fossils represent additional material of previously recognized taxa from the site, including the actinopterygians *Foreyclupea loonensis* (Clupeomorpha) and *Erichalcis arcta* (Teleostei indet.). Conversely, many specimens represent taxa not previously reported from the locality, including aspidorhynchid elements, ichthyodectid scales, and elopomorph vertebrae, all of which are actinopterygian fishes. These finds suggest a greater diversity of large-bodied bony fishes within the ecosystem than previously recognized. One of the most notable discoveries of our fieldwork is a nearly complete ichthyosaur skull, likely attributable to *Maiaspondylus*. This specimen is the most complete skull known of the taxon and provides insight into some of the last ichthyosaurs to persist into the Cretaceous.

Within the broader context of the Western Interior Seaway, these new discoveries offer a unique glimpse of a northern marine ecosystem prior to the Cretaceous Thermal Maximum (CTM) and Oceanic Anoxic Event 2 (OAE2) intervals marked by profound global climate change. Comparisons with younger marine ecosystems, particularly the Cenomanian–Turonian locality of Lac des Bois (94 Mya) in the Northwest Territories, will provide an opportunity to examine ecological shifts leading up to these major climatic events. Furthermore, understanding how these prehistoric marine faunas responded to environmental stressors may help guide efforts to mitigate climate change impacts on marine ecosystems today.

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# Using ichnology to improve the understanding of Cenomanian palaeoecology of northeastern British Columbia: insights from ichnofossil sites near Tumbler Ridge, B.C.

Eamon T. Drysdale<sup>1</sup>, Roy Rule<sup>2</sup>, Charles W. Helm<sup>1,3</sup>, and Victoria A. Arbour<sup>4,5</sup>

<sup>1</sup>Tumbler Ridge Museum, Tumbler Ridge, BC, V0C 2W0, Canada; eamon.drysdale@trmf.ca

<sup>2</sup>Tumbler Ridge UNESCO Global Geopark, Tumbler Ridge, BC, V0C 2W0, Canada; roy.rule@tumlerridgegeopark.ca

<sup>3</sup>African Centre for Coastal Palaeoscience, Nelson Mandela University, Gqeberha, 6031, South Africa; helm.c.w@gmail.com

<sup>4</sup>Department of Research & Collections, Royal BC Museum, Victoria, BC, V8W 9W2, Canada; victoria.arbour@gmail.com

<sup>5</sup>School of Earth and Ocean Sciences, University of Victoria, Victoria, BC, V8P 3E6, Canada

The Aptian to Turonian, informally referred to as the mid-Cretaceous, represents a time of significant change in terrestrial ecosystems, including major transitions occurring in dinosaurian faunas, the emergence of flowering plants, and increased global temperatures and sea levels. However, compared to the well studied environments of the Campanian and Maastrichtian, the mid-Cretaceous vertebrate record is relatively poorly sampled, especially in northern latitudes. The basal portion of the Kaskapau Formation in northeastern British Columbia preserves several Cenomanian-aged ichnofossil sites that provide insight into the mid-Cretaceous palaeoecology of the region. The vertebrate ichnofossils found at these sites include traces of small- to medium-sized theropod and ornithopod dinosaurs, both nodosaurid and ankylosaurid dinosaurs, and large crocodylians. When comparing the vertebrate species present at these sites to those found in Late Cretaceous localities, stark differences are observed in both the faunal composition and body size. However, the palaeoecological data provided by these northeastern BC ichnofossil sites is still dwarfed by what is available for the Late Cretaceous, and thus additional data is always welcome. Here we discuss the basal Kaskapau Babcock Creek site near Tumbler Ridge, BC, and its implications for understanding the palaeoecology of the region.

The Babcock Creek site consists of interbedded layers of rippled mudstones and fine-to-medium-grained sandstones, and preserves a variety of invertebrate burrows and other traces. These traces, along with the observed sedimentological features, suggest that it represents a shallow, coastal, deltaic environment. Vertebrate traces present at this site include ornithopod, theropod, and ankylosaurid footprints. All of these tend to be small (150–200 mm in length) in comparison with other representatives of their respective clades, a trend which is observed throughout basal Kaskapau Formation sites. Unique to the Babcock Creek site is a possible large pterosaur trackway, consisting of three complete and one partial manus-pes pairs, all preserved in epirelief. While these tracks do not preserve the morphology in extreme detail, the general track morphology is evident. The pes tracks are tetradactyl, and approximately 340 mm in length. Three of the digits are pointed and extend anteriorly, similar to *Pteraichnus*, with the more triangular fourth digit extending anteromedially, which is more akin to *Haenamichnus*. The pes is constricted posteriorly, and has a rounded heel, with a slight, rounded indentation on the posteromedial margin. The manus exhibits tridactyl morphology, similar to that seen in *Haenamichnus*, with two digit impressions at the anterior end of the track and a single long digit extending posteriorly. Interestingly, the manus impression is located in front of that of the pes in this trackway, similar to *Haenamichnus*, which is unusual amongst pterosaur trackways. The trackway has a large stride length (1650 mm), indicating that the trackmaker was quite large, significantly larger than that of other trackways found at the site. Based on the observed morphology, we believe the most likely trackmaker is a large pterosaur, although which pterosaur lineage is represented is unknown. Other potential trackmakers can be ruled out based on the following: the tetradactyl nature of the pes prints rules out either ornithopod, ankylosaurid, or theropod dinosaurs, while the shape of both the

manus and pes excludes nodosaurid footprints. It is possible that the tracks could have been created by a crocodilian trackmaker, but the tracks differ in several respects from other more definitive crocodilian tracks observed elsewhere in the Kaskapau Formation. The large size of this trackmaker may suggest that it occupied the niche of a large predator that otherwise appears to be missing from the ichnological record in the area.

The Babcock Creek site, along with other basal Kaskapau Formation localities, provides potential insights into the palaeoecology of the Cenomanian in northwestern Canada. The vertebrate footprints found at these sites suggest that the majority of dinosaur species present were small to medium-sized ornithopods, ankylosaurs, and theropods. However, the presence of possible large pterosaur footprints at the Babcock Creek site, and crocodilian footprints at other basal Kaskapau sites, suggests that the niche of large predators was filled by other vertebrate groups rather than by the large theropods seen during other time periods. However, this dataset is still limited, and more exploration of these sites is needed to further test this hypothesis.

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## Paleoenvironmental reconstructions of the Dinosaur Park Formation: insights from sedimentology and stratigraphy

Paul R. Durkin

Department of Earth Sciences, University of Manitoba, Winnipeg, MB, Canada

Despite the vast amount of research published on dinosaur specimens from the Dinosaur Park Formation (DPFm), detailed sedimentological characteristics remain largely overlooked beyond basic descriptions of host lithology, and stratigraphic positions rely on a problematic lithostratigraphic datum. However, detailed sedimentology and stratigraphy provide critical insights into the depositional environment and precise specimen ages, with important implications for habitat reconstruction, taphonomy, and biostratigraphy. This presentation will demonstrate how comprehensive sedimentological and stratigraphic studies conducted in Dinosaur Provincial Park (DPP) offer essential spatiotemporal context for both existing and future dinosaur specimens.

Over the past decade, our fieldwork at DPP has produced hundreds of meters of measured stratigraphic sections, thousands of paleoflow and lateral accretion measurements, samples for geochemical analysis, and survey data through remotely piloted aircraft systems used to create digital outcrop models. These data have enabled detailed reconstructions of depositional environments, paleohydraulics, and a novel tephrostratigraphic framework that refines our understanding of DPFm paleoenvironments.

The DPFm records a meandering fluvial channel-belt system, comprising point-bar, counter-point-bar, and abandoned-channel deposits, interbedded with floodplain deposits representing levee, backswamp, and proximal-to-distal floodplain sub-environments. Paleohydraulic analysis reconstructs river widths of 165–250 m and bankfull channel depths of 6–8 m, with a channel slope of  $1 \times 10^{-4}$  m/m. The rivers had a backwater length of 38–66 km, placing them well above the backwater zone when contemporaneous shoreline environments existed in southwestern Saskatchewan around 75 Ma. This interpretation is supported by exclusively terrestrial palynological assemblages recovered from lower DPFm floodplain deposits, refuting earlier hypotheses of tidal influence during this period.

Recent bentonite geochronology and geochemical fingerprinting have established a tephrostratigraphic framework that constrains the chronology and precise stratigraphic position of dinosaur specimens. Integrating sedimentological observations from specimen localities with this framework improves the accuracy of biostratigraphy and should become standard practice. Finally, this work will outline actionable strategies for paleontologists to contextualize specimens using our field-based approach and stratigraphic framework.

# Multiple forms of dental pathology in a *Brachychampsa montana* (Eusuchia; Alligatoroidea) from the Upper Cretaceous (Maastrichtian) Hell Creek Formation

Aaron D. Dyer<sup>1,2</sup> and David C. Evans<sup>1,2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, M5S 3B2 Canada; aaron.dyer@mail.utoronto.ca

<sup>2</sup>Department of Natural History, Royal Ontario Museum, Toronto, ON, M5S 2C6, Canada; d.evans@utoronto.ca

Dental pathologies are increasingly used to study the paleobiology and palaeoecology of extinct animals. Here, we describe a variety of dental pathologies in ROM 68491, an individual of *Brachychampsa montana* from the Upper Cretaceous (Maastrichtian) Hell Creek Formation of South Dakota (USA). ROM 68491 comprises a mostly complete skull and mandible, including in situ dentition for most of the left side. Multiple types of abnormal surficial defects of the enamel are present on most of the dentition, and are hypothesised to represent enamel hypoplasia (EH). These indicate sustained, nonspecific systemic stress throughout the individual's recent life history. In histological sections, transverse linear grooves and large pits are associated with incremental bands of globular dentine, and the former with bends in the dentine-enamel junction. This demonstrates developmental disturbances across multiple dental tissues from individual stress events.

A single occurrence of dental caries (cavity) occurs on the apex of a molariform dentary tooth, and represents the second occurrence in a fossil reptile. Finally, a single occurrence of compound odontoma (a benign odontogenic tumor) occurs on the 11th left maxillary tooth, and represents the first occurrence in a reptile.

The number and variety of dental pathologies in ROM 68491 are noteworthy due to the scant literature on reptilian dental pathologies, although an ongoing survey of extant *Alligator mississippiensis* shows that dental pathologies are common. Enamel hypoplasias, dental caries, and compound odontomas, impact broader phylogenetic groups than previously recognised. The occurrences of these dental pathologies are loosely related to the alternating pattern of tooth replacement, with the compound odontoma and severe enamel hypoplasia on the newer cohort of erupted teeth, potentially indicating a period of increasing systemic stress during the individual's recent life history. Continuous tooth replacement likely results in the shedding of pathological teeth before detrimental effects manifest (e.g., caries resulting in bacterial colonization of the pulp cavity and forming a dental abscess). Continued exploration of dental pathologies in fossil reptiles may provide a unique insight into the trade-offs of tooth replacement rates and dental pathologies in the evolution of mammalian diphyodonty.

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## Stable isotope geochemistry of Cretaceous vertebrate enamel in comparison to amber

Ben Egan<sup>1,2</sup>, Maria Velez<sup>1</sup>, Ryan McKellar<sup>2,3</sup>, and Leslie Robbins<sup>1</sup>

<sup>1</sup>Earth Science Department, University of Regina, Regina, SK, S4S 0A2, Canada; ben238@uregina.ca; maria.velez.caicedo@uregina.ca; Leslie.Robbins@uregina.ca

<sup>2</sup>Royal Saskatchewan Museum, Regina, SK, S4P 4W7, Canada; Ryan.McKellar@gov.sk.ca

<sup>3</sup>Biology Department, University of Regina, Regina, SK, S4S 0A2, Canada

The isotopic composition of enamel has been used to reconstruct various obscure aspects of animal biology in groups such as dinosaurs, crocodiles, and cartilaginous fishes. When using carbon isotopes to reconstruct animal diets, Cretaceous vertebrates consistently reported anomalously enriched carbon isotope values for animals that lived within an ecosystem dominated by C<sub>3</sub> plants. To reconcile this issue, it has been hypothesized that C<sub>3</sub> plants during the Mesozoic potentially had higher carbon isotope values than previously reported. In our study, we measured carbon isotopes within fossil tree resins (amber) to show that the C<sub>3</sub> baseline is more enriched in <sup>13</sup>C. Amber is known to preserve the primary isotopic signature of plant carbon due to its complex chemical structure; we argue this makes it a better representation than other geochemical proxy records of C<sub>3</sub> plants. Despite this enriched baseline, the difference between the carbon isotope values of enamel and amber were still larger than modern trophic enrichment factors (TEFs) and hypothesized dinosaur TEFs. A better quantification of the multiple factors impacting the carbon isotope values of Cretaceous enamel is required. We also reconstruct the ecosystem present with the Campanian fossil assemblage at Unity, Saskatchewan using hydrogen, oxygen, and strontium isotopes. Through hydrogen and oxygen isotopes we were able to support prior interpretations that the Unity assemblage represents a coastal ecosystem. Strontium isotopes values deviate from prior studies finding a reduced isotopic range for hadrosaurs when compared to tyrannosaurs. This potentially indicates Unity hadrosaurs were less mobile when compared to other sampled assemblages, although this could be a result of limited sampling. This study represents the first time Cretaceous vertebrates have been geochemically studied within Saskatchewan. Continued isotopic study of Mesozoic vertebrates from different periods and ecosystems will ideally allow for the identification of the factors responsible for anomalous carbon isotope values within dinosaurs.

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## The first record of Rhizodontida (Tetrapodomorpha, Sarcopterygii) from the Upper Mississippian (Serpukhovian) Tar Springs Formation of Indiana, U.S.A., and a review of global *Strepsodus* occurrences

Adam I. Eliezer<sup>1</sup>, Ryan Shell<sup>2</sup>, Caleb P. Bohus<sup>3</sup>, and Charles N. Ciampaglio<sup>4</sup>

<sup>1</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, Canada; adameliezer@cmail.carleton.ca

<sup>2</sup>Department of Vertebrate Paleontology, Cincinnati Museum Center, Cincinnati, OH, USA; ryanshell501@gmail.com

<sup>3</sup>Department of Organismal Biology, Uppsala University, Uppsala, Sweden; caleb.bohus@ebc.uu.se

<sup>4</sup>Science, Math and Engineering Unit, Lake Campus, Wright State University, Celina, OH, USA; chuck.ciampaglio@wright.edu

Recent fieldwork in the Mississippian (Serpukhovian)-aged Tar Springs Formation near Eckerty, Indiana, has produced a partial cleithrum of a rhizodontid fish. This fossil represents the first known occurrence of a Paleozoic vertebrate from the site and the first rhizodontid fish to be reported from the state of Indiana. The specimen, referred to here as the Eckerty Form, is attributable to Rhizodontida based on the diagnostic reverse overlap of the clavicle and cleithrum and the presence of a depressed posterior flange. The Eckerty Form shows some similarity to cleithra from the Foulden site of Scotland the shape of the depressed posterior flange, and notably, the Ducabrook localities of Queensland, Australia, in features like the shape of the dorsal lamina. Cleithra from both localities have been attributed to *Strepsodus sauroides*, but the absence of autapomorphic characters precludes species-level assignment to the Eckerty Form. However, cleithral morphology, such as the presence of a strong-

ly developed posterior flange that does not reach the dorsal margin, supports provisional referral to the genus *Strepsodus*. While further comparison is limited due to the incompleteness of the ventral lamina, it is notable that the Eckerty Form is unusually robust and thick amongst known *Strepsodus* cleithrum. Isolated elements such as this cleithrum are particularly valuable for studying rhizodontids, as complete specimens are rare and identification often depends on distinct, anatomical characters that differentiate genera. This discovery expands the known geographic range of *Strepsodus* into the Illinois Basin and, when considered alongside global occurrence data, refines the biostratigraphic and biogeographic framework of the genus while clarifying its distribution throughout the Carboniferous. This study also reevaluates a historical misassignment of *Strepsodus* from the Bear Gulch Limestone of Montana, which lacks diagnostic features of the genus. Recognition of *Strepsodus* in the Tar Springs Formation highlights the potential for additional vertebrate discoveries in Mississippian carbonate successions of the North American midcontinent and emphasizes the importance of isolated pectoral girdle elements for documenting Carboniferous rhizodontid diversity and biogeographic patterns.

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## Environmental influences on dinosaur assemblages in the Horseshoe Canyon and Upper Wapiti Formations

Sebastian Feng and Philip J. Currie

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; zfeng9@ualberta.ca; pjcurrie@ualberta.ca

The Upper Cretaceous Horseshoe Canyon Formation and equivalent beds of the Wapiti Formation have been sampled in Alberta for fossils for more than a century. However, dinosaur microfossils are relatively sparse in comparison with the abundant isolated bones, bonebeds and associated/articulated skeletons of larger dinosaurs. This contrasts with the beds of the Dinosaur Park Formation of southern Alberta, the ecological interactions of which are better documented and understood. This ongoing study examines the distribution of different dinosaur families in the Horseshoe Canyon and Wapiti formations as determined by macrosite analyses across different lithologies.

The current data have generalized sandstone units with fluvial/channel depositional environments, whereas mudstone units are generally associated with interfluvial/floodplain settings. Minimum Number of Individuals (MNI) analyses were conducted on specimens from the Royal Tyrrell Museum of Palaeontology and the University of Alberta Laboratory of Vertebrate Palaeontology. After limiting the sites to those with a minimum of two individuals and 50 elements, 26 localities were selected with an MNI of 211. Chi-square analysis and Fisher's Exact Test were performed at the family level, revealing a moderate significance ( $p = 0.012$ ;  $p = 0.036$ ). Bray-Curtis Polar Ordination (BCPO) and Non-Metric Multidimensional Scaling (NMDS) were also conducted on the count number and relative percentage of each family on each site, respectively. Overall, both methods revealed no significant community differences between lithologies and formations. Similar analyses conducted on the absolute number of elements at each site yielded comparable results. The outcome of this study supports a homogenous community of dinosaur fauna in the Late Cretaceous Western Interior of North America on a finer lithological, temporal and geographical scale compared to other studies. This study also expands the understanding of the faunal makeup of the Horseshoe Canyon and Upper Wapiti Formations.

This ongoing project looks forward to expanding and refining the current dataset, retrieving further lithological and stratigraphic information, conducting additional ecological tests to limit taphonomic interferences, and revealing faunal patterns in the Upper Cretaceous of northern Laramidia.

# The validity of *Nodosaurus textilis*, Nodosauridae, and Nodosauria

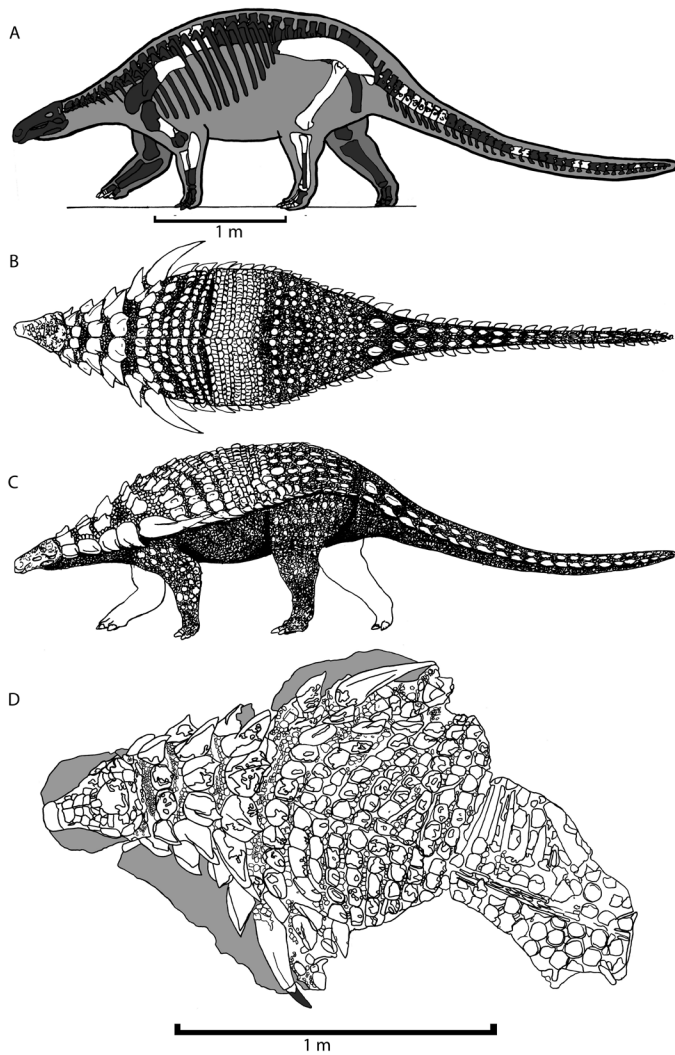
Tracy L. Ford

Dino Hunter, P.O. Box 1171 Poway, CA 92074; dino.hunter@cox.net

Marsh (1889) was the first to describe *Nodosaurus textilis* from early Late Cretaceous marine deposits of Wyoming. A year later, he referred it to its own family, Nodosauridae. Originally, *Nodosaurus* was suggested to be from the Benton sands (Lull 1921). Based on the marine invertebrates associated with the skeletal material, it was then placed in the middle Cenomanian (early Late Cretaceous) Belle Fourche Member of the Frontier Formation. The type specimen of *Nodosaurus textilis* (YPM 1815) is a partial skeleton of a small armored dinosaur. The only other nodosaurid with similar thoracic/body and pelvic osteoderms is *Borealopelta markmitchelli* (TMP 2011.033.0001), also from marine deposits of Alberta, Canada, though from the older (Albian) Clearwater Formation. The holotype of *Borealopelta* is a partial, but well-preserved, anterior half of the skeleton, including the posterior pelvic osteoderms. The osteoderms are well preserved, and some retain traces of the keratinous covering with skin preservation (Brown et al. 2017).

Both *Nodosaurus* and *Borealopelta* have bands of rectangular tertiary body osteoderms (Ford 2000) near their pelvis and a pelvic shield with oval osteoderms surrounded by smaller osteoderms (Fig. 1). *Nodosaurus* has only a few osteoderms preserved, consisting of caudal osteoderms, partial cervical spine(?), one of the pair of median cervical osteoderms, bands of rectangular osteoderms, and a partial pelvic shield. Lull (1921) illustrated a skeleton with bands of thin osteoderms on the lower posterior edge of the body but with no other osteoderms. This illustration has been used for decades, showing *Nodosaurus* with just bands of osteoderms and no larger pointed osteoderms along its sides. This would be unusual since most other nodosaurs have three cervical bands with 3 pairs of osteoderms, a single shoulder band, thoracic/body osteoderms either in bands (such as seen in *Nodosaurus* and *Borealopelta*) or osteoderms sporadically placed (*Sauropelta* and *Edmontonia*), a pelvic shield, and caudal osteoderms in two rows (Ford, 2000). The thoracic/body osteoderms are arranged in several transverse vertical rows of elongate osteoderms (taller than wide), tightly packed with small osteoderms. Part of the pelvic shield is preserved, with large octagonal (though with more rounded edges than in *Borealopelta*) osteoderms surrounded by small osteoderms (Fig. 2).

The names *Nodosaurus* and Nodosauridae have been used for over 100 years, but their validity has been questioned due to the incompleteness and scarcity of *Nodosaurus* osteoderms (Raven et al., 2023). Panoplosauridae has been suggested as a replacement for Nodosauridae for the overall clade typified by Nodosauridae (Panoplosaurinae emend. to Panoplosauridae Raven et al., 2023). Nodosauridae has recently been suggested to be paraphyletic, with ‘polacanthid’ ankylosaurs, ‘panoplosaurid’-group typified by *Edmontonia* and *Panoplosaurus*; and a ‘struthiosaurid’ group typified by *Struthiosaurus* and *Hungarosaurus*. Finding different genera with the same osteoderm morphology is important and helps to establish that these genera belong to the same clade/family. The inclusion of *Borealopelta* in Nodosauridae strengthens the validity of Nodosauridae. It is suggested that suborder Nodosauria be used instead to refer to the group of armored dinosaurs typically called Nodosauridae (Ford in prep). Suborder Nodosauria includes the family Nodosauridae (Ford in prep), the family Edmontoniidae (emend subfamily Edmontoniinae), the family Panoplosauridae (via Raven et al. 2023), but excludes Polacanthidae and Struthiosauridae (as per Raven et al. 2023), but within the Order Ankylosauria.



**Figure 1.** A–C) *Nodosaurus textiles*; A, reconstruction of the skeleton with known skeletal elements in white (modified from Lull, 1921), B, C, new life reconstruction based on *Borealopelta markmitchelli*, in B, dorsal and C, left lateral views; D) *Borealopelta markmitchelli* in dorsal view after Brown et al. (2017).

**Literature Cited**

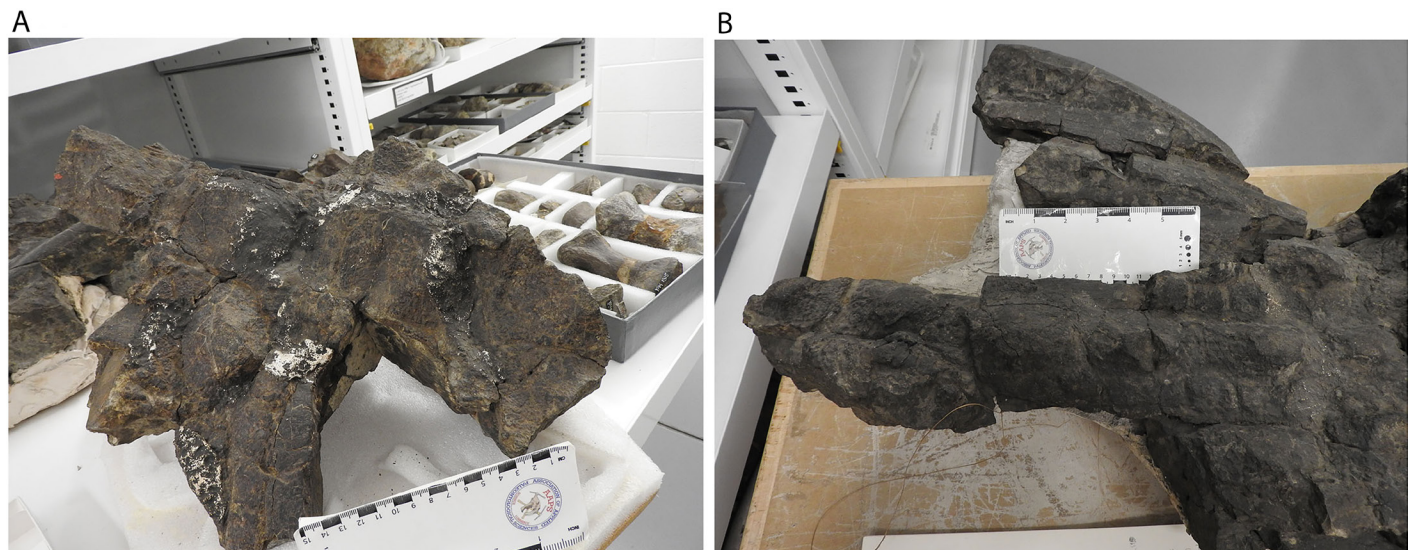
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**Figure 2.** A–C) *Nodosaurus textiles*; A, reconstruction of the skeleton with known skeletal elements in white (modified from Lull, 1921), B, C, new life reconstruction based on *Borealopelta markmitchelli*, in B, dorsal and C, left lateral views; D) *Borealopelta markmitchelli* in dorsal view after Brown et al. (2017).

# Life history filters in mammalian extinction at the end of the Cretaceous

Gregory F. Funston<sup>1</sup>, Elis Newham<sup>2</sup>, David C. Evans<sup>3,4</sup>, and Gregory P. Wilson–Mantilla<sup>5,6</sup>

<sup>1</sup>Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY, USA

<sup>2</sup>School of Engineering and Materials Science, Queen Mary University of London, London, UK

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

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

<sup>5</sup>Burke Museum, University of Washington, Seattle, WA, USA

<sup>6</sup>Department of Life Sciences, University of Washington, Seattle, WA, USA

Life history traits, like reproductive strategy, pace of development, and lifespan, are suggested to impact extinction risk. However, testing this assumption across past extinctions remains challenging because resolving both life history and stratigraphy on fine scales is difficult in the fossil record. Here, we overcome this barrier by leveraging advances in conventional and synchrotron palaeohistology, and an exceptional sample of mammals across the end-Cretaceous extinction boundary in eastern Montana. We demonstrate that propagation phase-contrast synchrotron  $\mu$ CT, in addition to annual cementum annulations, can reveal daily growth marks in the enamel of fossils, via cross-calibration with conventional thin sections. This supports a non-destructive, high-throughput pipeline for collecting life history data from isolated teeth. Using these dental growth records, we show distinctly shorter lifespans and faster developmental schedules between latest Cretaceous and earliest Paleocene taxa. Of the three major clades, eutherians show the least drastic shifts in developmental pacing across the boundary, and metatherians the strongest, suggesting some taxon-specific effects possibly attributable to reproductive strategies. Ongoing work includes increasing the sample and involving additional beamlines around the globe. The advantages offered by synchrotron approaches open an exciting new avenue into virtual palaeohistology, and opportunities to test fundamental questions about the responses of organisms to environmental change.

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## Histology and $\mu$ CT scanning allow detailed diagnoses of multiple pathologies in a large *Gorgosaurus* (Theropoda: Tyrannosauridae)

Christiana W. Garros<sup>1</sup>, Henry S. Sharpe<sup>1</sup>, Jared Voris<sup>2</sup>, Kyla Beguesse<sup>3</sup>, François Therrien<sup>4</sup>, and Philip J. Currie<sup>1</sup>

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

<sup>2</sup>Department of Earth, Energy, and Environment, University of Calgary, Calgary, AB, T2N 1N4, Canada; jared.voris@ucalgary.ca

<sup>3</sup>Department of Biological Sciences, North Carolina State University, Raleigh, NC, 27695, USA; kabegues@ncsu.edu

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

Pathologies provide a unique window into the behaviours and ecology of extinct animals by capturing specific moments in an animal's lifetime. While pathologies are well-known in large theropods, especially tyrannosaurids, specimens rarely receive full, detailed palaeopathological descriptions. Here, a well-preserved partial skeleton of *Gorgosaurus libratus* (TMP1994.012.0602) exhibiting numerous pathologies throughout its skeleton was surveyed in detail. Two caudal vertebrae and the left metatarsal II exhibit signs of trauma and chronic stress resulting in exostoses. Four dorsal ribs (three right and one left) present healed fractures, two of which feature evidence of complications during healing (including malunion and inflammation). TMP1994.012.0602 also has 19 tooth-strike lesions on the snout, a larger number than typically reported in tyrannosaurid individuals. The right fibula also exhibits significant diaphyseal expansion suggestive of fracture callus. While numerous tyrannosaurids are known with pathologic fibulae, TMP1994.012.0602 is only the second to be studied radiologically. X-ray computed microtomography (microCT) revealed several oblique fractures resulting in four separate fragments (comminuted fracture) that spiral around the long axis of the fibula with a right-handed twist (spiral fracture). The most noteworthy pathology on TMP1994.012.0602 is the missing left half of the nuchal crest bordered by a rim of irregularly rough reactive bone suggestive of trauma. While damage or absence of bone in this region implies impaired functions of the attaching muscles, the presence of reactive bone further distally along the left side of the sagittal crest provides a rare example of functional response to injury. This is interpreted here as a compensatory response to shifting stresses imparted by the *m. adductor mandibulae externus* group. Additional lines of evidence in the form of osteohistology and macrowear on the in situ teeth suggest this animal survived for at least a few months following this injury; TMP1994.012.0602 joins the ranks of large theropods with numerous healed pathologies. Through this study, TMP1994.012.0602 demonstrates how detailed diagnosis beyond gross morphological observation is critical for providing insights into the specific causes of traumatic events encountered by these large predators, and for better understanding their physiological capability to withstand them.

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## We're all ears: a comparison of five merycoidodontid petrosals

Jay M. Gegner<sup>1</sup>, S.V. Robson<sup>2</sup>, and Jessica M. Theodor<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4, Canada; jay.gegner@ucalgary.ca, jtheodor@ucalgary.ca

<sup>2</sup>Hamburg, Germany; svrobson.paleo@gmail.com

Oreodonts are a group of North American artiodactyls which experienced a notable radiation during the Paleogene and Neogene periods. Despite being common in the fossil record, their taxonomic relationships within Oreodontoidea and with other artiodactyls has remained a contentious issue. This is in part due to specimens being misinterpreted as separate species based on taphonomic deformation. The group is divided into the early diverging agriocherids and the more speciose merycoidodontids. This study describes and compares the previously undescribed petrosals of four merycoidodontid genera: *Aclistomycter*, *Limnenetes*, *Miniochoerus* and *Bathygenys*. *Merycoidodon*, described previously in the literature, is also included in this comparison.

In life, the petrosal bone houses the series of hair-lined membranous channels responsible for an animal's sense of balance and hearing. The petrosal forms early in development with little subsequent change and may provide valuable information for phylogenetic analysis. Using  $\mu$ CT scanning, we produced high-resolution reconstructions of both the petrosals themselves and the hollow channels of the bony labyrinth within to make detailed comparisons between genera. All taxa have relatively square petrosals, with similar width and height. The sub-

arcuate fossa, which is bordered by the anterior semicircular canal and cups part of the cerebellum in life, shows notable variation in both shape and depth. *Aclistomycter* is the only genus to lack a true subarcuate fossa, instead having a shallow, cone-shaped depression on the endocranial surface with no association with the anterior canal. All others, including the odd shallow, notch-shaped fossa in *Limnenetes*, show a close association between the semicircular canal and subarcuate fossa. *Bathygenys* and *Merycoiododon* share some interesting features, including a pronounced basicapsular groove bordered by two ridges, an inferior petrosal venous sinus walled by both the basicapsular groove, and an indentation on the basioccipital bone. Observations of the petrosal and associated bony labyrinth of each specimen will be used to create a taxon-character matrix, which will allow us to conduct a more in-depth phylogenetic analysis of the merycoiododontids.

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## Stable oxygen isotopes of mosasaur teeth from the Pierre Shale, Manitoba: separating diagenetic and physiologic signals

Virginia K. Gold<sup>1</sup>, Gina Bilic<sup>1</sup>, Ryan Sharpe<sup>1,2</sup>, Mostafa Fayek<sup>1,2</sup>, and Kirstin S. Brink<sup>1,3</sup>

<sup>1</sup>Department of Earth Sciences, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada; goldv@myumanitoba.ca; bilicg@myumanitoba.ca

<sup>2</sup>Manitoba Isotope Research Facility, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada; Ryan.Sharpe@umanitoba.ca; Mostafa.Fayek@umanitoba.ca

<sup>3</sup>Canadian Fossil Discovery Centre, Morden, MB, R6M 1N9, Canada; Kirstin.Brink@umanitoba.ca

Diagenesis is a pervasive obstacle in interpreting stable oxygen isotope ratios in fossilized materials. As such, it can be difficult to interpret perceived physiological patterns, e.g., animal migration or stress responses, without a thorough understanding of the diagenetic history of the sample material. As a case study, we performed a series of analyses to evaluate the diagenetic alteration of mosasaur teeth from the Millwood member of the Pierre Shale in Manitoba.

First, scanning electron microscopy (SEM) and electron microprobe (EPMA) analyses were performed on sectioned teeth to characterise the partitional patterns based on their chemical compositions. Next, we took multiple transects at differing sampling densities through the dentine using laser ablation inductively coupled plasma mass spectroscopy (LA-ICP-MS) and secondary ion mass spectrometry (SIMS) to examine changes in elemental and isotopic composition, respectively, throughout the tooth. Our results show significant variations in  $\delta^{18}\text{O}$  values along transects taken in different areas of the teeth. Two transects in one sample produced ranges from +12.8‰ to +17.2‰, and +15.7‰ to +20.6‰. Initially, we interpreted these variations as an indicator that mosasaurs were migrating between saltwater and freshwater environments. However, when these transects were compared to the images obtained by the SEM and EPMA, we noted that many dentine tubules showed diagenetic barium-rich infillings. These infillings could be skewing interpretations if the transects are sampling infilled tubules instead of unaltered dentinal apatite, both through potential matrix effects and  $^{18}\text{O}$  enrichment of barite.

The combination of techniques used in this study allows for a comprehensive assessment of the mode and degree to which diagenesis affected these samples and indicates that detailed spot sampling is needed before undertaking isotopic analyses. This information also contributes to our growing understanding of the taphonomic history of fossils from the Pierre Shale of Manitoba.

# Preparation, analysis and description of sub-adult *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the Bearpaw Formation, Late Cretaceous, western Canada

Corbin G. Gomez

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; cggomez@ualberta.ca

In recent years, southern Alberta has had a boom in mosasaur discoveries in large part due to the ammolite mining excavations. This specimen originates from the Bearpaw Formation, Late Cretaceous in age. Mosasaur remains are frequently discovered, displaying good preservation. One such specimen is TMP 2013.045.0001, a subadult *Mosasaurus missouriensis* discovered in 2013 in an ammolite mine managed by the company Korite Ltd. The fossil was collected in three jackets, one of which contain the skull and anterior half of the body, which are the parts described in this study. Then marginal dentition of the specimen has low faceting teeth. This is similar to other larger specimens of *M. missouriensis* and different from smaller specimens, having deeper faceted marginal dentition. The specimen only has 56% of its visible teeth intact, which is unusual in well preserved mosasaurs from the Bearpaw Formation. The missing teeth and empty tooth sockets are correlated with depressions in the premaxilla, maxilla, and dentary. Partial calcified cartilaginous sternum is also preserved with intact and broken margins suggesting scavenging by sharks.

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## Fossil dermal denticles as a tool for understanding the ecology of subrecent and ancient (pre- and post-human impact) shark communities across the Isthmus of Panama

María M. Gómez<sup>1,2</sup>, Erin Dillon<sup>3</sup>, Irene García<sup>3</sup>, Brígida De Gracia<sup>3</sup>, and Aaron O’Dea<sup>3</sup>

<sup>1</sup>Facultad de Ciencias de la Vida, Escuela Superior Politécnica del Litoral, Guayaquil, Guayas, Ecuador; mercedes.gomez@ucalgary.ca

<sup>2</sup>Smithsonian Tropical Research Institute, Balboa, 0843, Panama City, Panama; dillone@si.edu; irenegarcia.ig798@gmail.com; DeGraciaB@si.edu; odeaa@si.edu

Sharks are a group of elasmobranchs that inhabit the majority of marine ecosystems. As apex and mesopredators, they play a crucial role in maintaining ecosystemic health and are essential components of multiple food webs. Despite their importance, shark populations worldwide have declined drastically due to the growing anthropogenic presence in the oceans. Coastal ecosystems, particularly coral reefs, have been significantly disturbed by human influence and face the threat of potential extinction. Panama is home to significant shark diversity due to its unique positioning within the Eastern Tropical Pacific; however, some degree of shark fishing is allowed, and fishing regulations are not strictly enforced.

Multiple conservation projects have been implemented to protect sharks, but the current baseline of shark recovery efforts is based on studies conducted after the rise of industrial fishing. As such, the state of shark communities preceding human presence in the oceans is poorly understood. A long-term perspective is therefore needed to understand the historical variation in shark communities, recognize the extent of the impact of human pressures on shark functional diversity, and refine future conservation efforts. Here, we use fossil dermal denticle (shark scale) accumulations in coral reef sediment cores to identify regional variation in shark communities. Dermal denticles from pre-human impact (mid-Holocene, ~7–3 Ma) and post-human impact (last 100 years) sections of sediment cores were collected from the Pacific (Gulf of Panama) and Caribbean (Bocas del Toro) coasts of Panama. These sites are characterized by distinct oceanographic conditions, nutrient availability, and degrees of anthropogenic activity.

By using a purpose-built reference collection of regional shark denticle morphometrics, we first ground-truthed the ecological significance of the metrics by testing them against known shark ecologies. Then, we grouped fossil denticles into functional morphotypes and collected measurements to 1) record the morphological diversity of shark communities across time and region and 2) quantify changes in the relative abundance of ecologically-significant traits in shark assemblages through time. Preliminary results suggest that the relative abundance of pelagic morphotypes in the Pacific coast and the existence of subtle variations within functional morphotypes that could indicate changes in ecological diversity within the group. Our findings suggest that shark communities across the Isthmus of Panama may have responded differently to the increasing anthropogenic presence in the ocean. This study highlights the potential of the use of fossil dermal denticles to understand shark functional diversity before and after human presence in the oceans.

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## Morphology of trionychid shell material of the Scollard Formation

Madeline E. Groat and Corwin Sullivan

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; megroat@ualberta.ca; corwin1@ualberta.ca

Cretaceous softshell turtles (family Trionychidae) have been observed across an expansive range, including much of southern Alberta; however, in more northern environments, their fossil record is sparse. This study focuses on partial shells from two previously unidentified individuals, now known to belong to the genera *Hutchemys* and *Atoposemys*. The *Hutchemys* specimen (TMP 93.94.01) includes a mostly complete carapace and plastron, while the *Atoposemys* (TMP 90.52.9) is represented by only the anterior elements of the carapace. Generic identification was done using diagnostic characteristics such as surface ornamentation and shape of the neural and nuchal plates. Both individuals are Maastrichtian in age, and were excavated from the Scollard Formation of northern Alberta. This identification of the specimens will allow greater understanding of the lives and potential environmental tolerances of the turtles which, when taken in tandem with geologic evidence, will give greater information about the paleoenvironment of the Scollard Formation.

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# Mammalian communities preserved at Mfangano Island and Rusinga Island, Kenya, provide a crucial framework for understanding early Miocene ape evolution in Eastern Africa

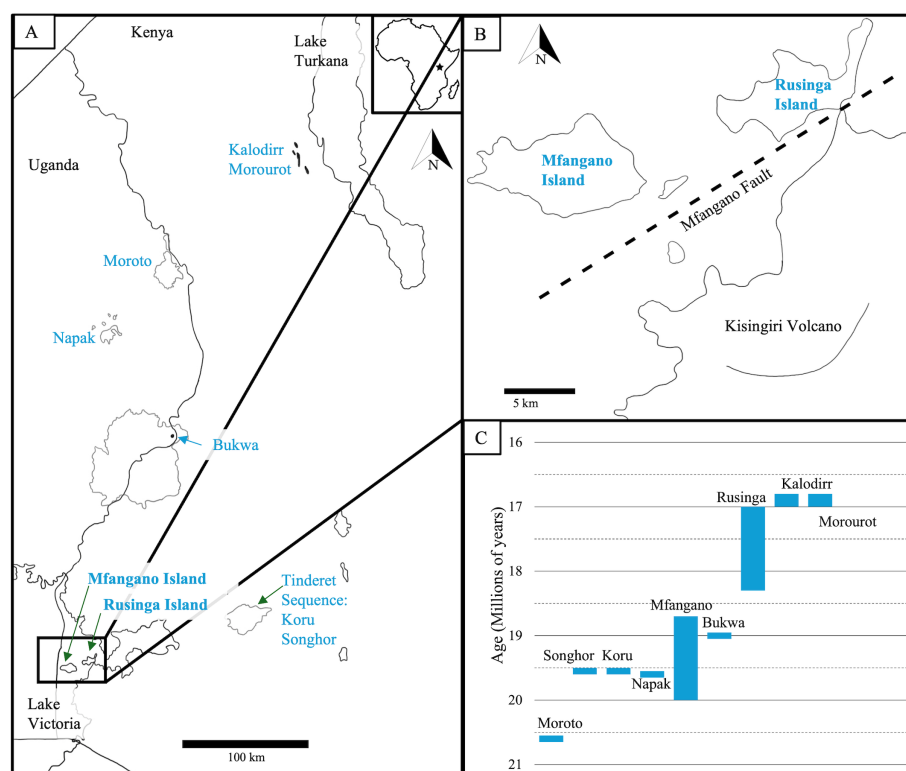
Abigail S. Hall

Department of Anthropology and Archaeology, University of Calgary, Calgary, AB, T2N 1N4, Canada; ashall@ucalgary.ca

The Early Miocene fossil sites in eastern Africa have produced some of the most important assemblages for understanding early ape evolution. The highly fossiliferous Kisingiri sequence sites Mfangano Island and Rusinga Island, Kenya (Fig. 1), are arguably the most important of these early Miocene assemblages, producing fossils from more than one hundred species of plants and animals. Critically, the diversity and abundance of fossils representing the early apes *Ekembo*, *Nyanzapithecus*, and *Dendropithecus* make these assemblages touchstones for understanding the early evolution and diversification of apes. Although extensive efforts have been made to characterize the taxonomy and morphology of these early apes, the broader mammalian communities to which these primates belonged remain poorly understood.

Unlike the majority of early Miocene sites in Kenya and Uganda, which likely accumulated in a geologically short amount of time (e.g., Bishop et al. 1969), the Kisingiri sequence was deposited over a longer time span of approximately 3 million years from 20–17 Ma (Peppe et al. 2017). This geochronological framework means that Mfangano and Rusinga are known to be coeval with several other sites in eastern Africa (Fig. 1).

In this study, I present the first comprehensive analysis of mammalian assemblages from all localities at Mfangano and Rusinga, integrating new geochronological, taxonomic, and abundance data. Here, I re-evaluate all mammalian fossils from these sites to reconstruct the community structure present within each assemblage.



**Figure 1.** A) Geographical locations of the early Miocene sites considered in this study. Kisingiri Sequence sites Mfangano Island and Rusinga Island are bolded. B) Relative geographical locations of the Kisingiri sites considered here and their approximate relationships to the Mfangano Fault and the extinct Kisingiri volcano. C) Chronology of the sites included in this study.

Critically, I place these Kisingiri assemblages within the context of other eastern African assemblages, producing the first faunal analysis of over 30 distinct early Miocene fossil localities from sites in Kenya and Uganda (Fig. 1). Further, I test the hypothesis that a significant faunal turnover event took place approximately 20–19.5 Ma in eastern Africa (Cote et al. 2018).

Overall, the faunal assemblages from Mfangano and Rusinga closely resemble one another, although the oldest assemblages from Mfangano, the Makira Series, also share many similarities with the older comparative assemblages considered in this study. Both the taxonomic occurrence and abundance structure of these mammalian assemblages reveal that changes in community structure during the early Miocene correlate with both temporal and geographical distance between sites. Additionally, differences between the youngest assemblages in the dataset highlight the importance of spatial distance and likely environmental factors in patterning faunal differences between these mammalian communities. Further, specific faunal characteristics of the Mfangano assemblages, including the presence of lagomorphs, large suids, and the ape *Ekembo*, support the hypothesis that a major faunal turnover event took place in eastern Africa and help refine the timing of this event to about ~19.5 Ma. Ultimately, the results of this study provide an updated temporal and ecological framework for understanding the origins and diversification of early Miocene apes and help to clarify the characteristics and timing of a major faunal turnover event in eastern Africa.

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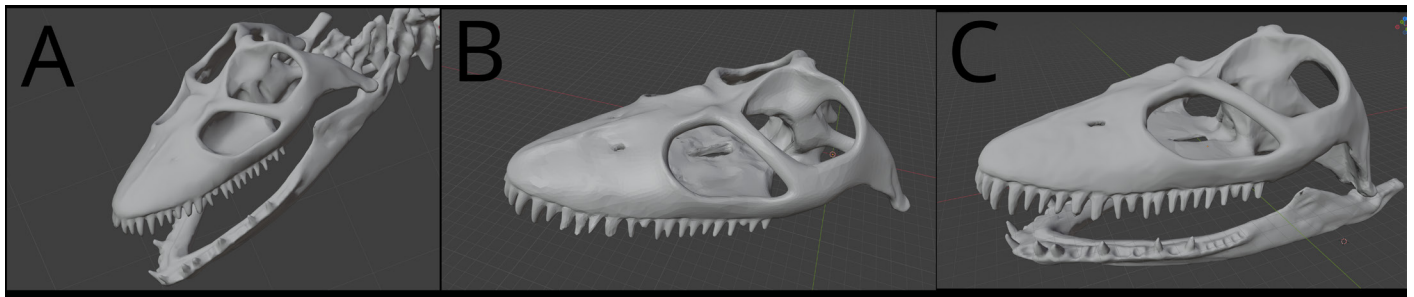
## Reconstruction of a plesiosaur skull using low-resolution scan data and comparative anatomy

Gillian C. Halliday and Hallie P. Street-Sampson

Department of Biological Sciences, MacEwan University, Edmonton, AB, Canada; hallidayg2@mymacewan.ca; streeth@macewan.ca

The reconstruction of the skeletal anatomy of fossil organisms is a challenging task, particularly when working with incomplete or fragmentary specimens. We attempted to reconstruct the skull of the plesiosaur *Cryptoclidus eurymerus* using a low-polygon scan of a partial specimen (IGPB R 324) from the Goldfuss Museum. The specimen's skull is primarily made of plaster, and therefore provides a low resolution of accurate anatomical detail. Other specimens of *C. eurymerus* with cranial material are all fragmentary, the most complete being NHMUK R 3730, consisting of a crushed complete premaxilla, incomplete pterygoids, maxillary fragments, a complete right ramus, and broken left dentary. Using the open-source program Blender, we increased the quality of the original scan and sculpted the model to take into account anatomical details from specimens NHMUK PV R3730,

NHMUK PV R8621, and NHMUK PV R2860. To reconstruct the remaining anatomy, we utilized cranial materials of *Kimmersaurus* (NHMUK PV R8431), *Muraenosaurus* (NHMUK PV R2421, NHMUK PV R2678), *Ophthalmothule cryostea* (PMO 224.248), *Callawayasaurus colombiensis* (UCMP:V:38349, UCMP:V:125238) and *Libonectes morgani* (SMUSMP 69120). Anatomical data was prioritized based on phylogenetic proximity to *C. eurymerus* according to recent phylogenetic interpretations. The software allowed for precision manipulation of the scan data, incorporating inferred features while maintaining anatomical consistency. This methodological approach has provided a more detailed and accurate reconstruction of the *C. eurymerus* skull, in a format which allows for both sharing without compression and for 3D printing. This underscores the utility of combining digital modeling tools with comparative anatomy to overcome challenges posed by incomplete data in paleontological reconstructions, providing a case study for future work on incomplete fossil specimens.



**Figure 1.** Incomplete workflow diagram. A, Original scan, unmodified; B, Isolated cranium with nasal cavity sculpted, external nares opened, and interpterygoid vacuity opened; C, Cranium further modified with new posterior palatine vacuity, rotated exoccipital, opisthotic, squamosal and quadrate. Rami, separate from cranium, has alveoli sculpted.

## Latest Middle Triassic tetrapod footprints from the Brown Hill section, Williston Lake, British Columbia, Canada

Kendra Harrington, Mahdiyeh Gholizadeh, Ryusuke Kimitsuki, Ciara Stewart, and John-Paul Zonneveld

Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB, T6G 2E3, Canada; kharring@ualberta.ca; gholiza1@ualberta.ca; kimitsuk@ualberta.ca; ciara3@ualberta.ca; zonnevel@ualberta.ca

The diversity and ecology of early Mesozoic tetrapods have received far less attention from scientists while their more charismatic, late Mesozoic counterparts are well studied and documented. Evidence of early Mesozoic tetrapod life on land is known from the east coast of Canada, northeastern United States, and southwestern United States, but Triassic rocks in western Canada comparatively lack palaeontological data supporting their presence. Prior to the present work, the only report of terrestrial tetrapods from northwestern Pangaea (now western Canada) consists of the enigmatic archosaur *Sikannisuchus huskyi* from the Norian Pardonet Formation. Here we examine a set of tetrapod trackways from British Columbia from the Middle Triassic (late Ladinian) beds of the Charlie Lake Formation. These trackways, assigned to *Procolophonichnium* and *Rhynchosauroides*, extend the geographic range of these ichnotaxa into western Canada and support their interpretation as emplaced by foragers and hunters along transitional marine environments. While more research is necessary to provide specific identification, the study of these early tetrapods highlights evidence of their presence in Canada's western provinces, and bolsters knowledge surrounding the early evolution and ecology of diapsids and synapsids in the Triassic.

# Secondarily aquatic tetrapod twins: *Crassigyrinus* and *Vancleavea* — an example of convergent evolution

Donald M. Henderson

Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada

*Crassigyrinus scoticus* is a primitive tetrapod from the Early Carboniferous of Scotland, and is assumed to have evolved from a terrestrial ancestor. *Vancleavea campi* is an early archosauriform from the Late Triassic of the western United States. Despite the great temporal, geographic and phylogenetic distance between these taxa, they share a remarkable degree of convergence to life as secondarily aquatic tetrapods, as either pursuit predators or perhaps as sit-and-wait predators. Cranial convergences include large eyes positioned towards the top of the skull; short faces; expanded cheek (posterior to orbit) regions; elongate, straight mandibles; and extensive marginal dentitions with congruent arrangements of large fangs (or fang groups) on both the upper and lower jaw margins. Both taxa show reduction in the robustness and length of the limbs, and in each case the forelimbs are more reduced than the hind limbs. However, both animals retain substantial pelves that remain connected to the spine. *Vancleavea* preserves a tail with a pronounced dorsal fin uniquely supported by osteoderms and demonstrates the potential for a tail-propelled, anguilliform mode of swimming. Although the tail of *Crassigyrinus* is not known, its elongate presacral body and reduced limbs suggest that it too would have had a similar mode of locomotion.

# Using teiid lizards to understand tooth attachment and resorption in extinct mosasaurs

Fatima Iftikhar<sup>1</sup>, Michael W. Caldwell<sup>1</sup>, and Aaron R. H. LeBlanc<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2M9, Canada; [fiftikha@ualberta.ca](mailto:fiftikha@ualberta.ca); [mikec@ualberta.ca](mailto:mikec@ualberta.ca)

<sup>2</sup>Faculty of Dentistry, Oral & Craniofacial Sciences, King's College London, London SE1 1UL, UK; [aaron.leblanc@kcl.ac.uk](mailto:aaron.leblanc@kcl.ac.uk)

Modern tegu lizards (Teiidae) possess tooth crowns surrounded by significant masses of bony tissue and large external replacement pits, unique tooth attachment morphologies that are very similar to those observed in numerous clades of extinct mosasaurs. Some studies have contended that mosasaurs have a mammal-like thecodont (socketed) tooth attachment with a calcified periodontal ligament (PDL); this contention contrasts with the conventional view that mosasaurs present a form of pleurodont implantation and attachment to the jawbone via a “bone of attachment.” The peculiar nature of mosasaur dental morphology raises questions around the development of the attaching tissues and how the giant bony bases were removed and the teeth were shed. *Tupinambis* and *Dracaena* in particular are large extant tegus where tooth development can actually be observed, not just inferred from preserved bony evidence as in mosasaurs. These tegus are thus ideal modern analogs to study mosasaur tooth attachment and replacement. We therefore histologically sampled several extant tegu species with teeth at different ontogenetic stages.

Our histological data are the first to reveal that tegu lizards have bony tooth bases that initially consist of a large, vascularized alveolar bone that mineralizes centrifugally from the tooth root surface in a web-like fashion around preexisting vasculature, a process that explains the spongy nature of the mosasaur PDL. These data also

reveal that tegu and mosasaur osteoclast (bone resorbing cell) activity is extensive and concentrated lingually in order to resorb the large amount of calcified tissue under a shedding tooth, even revealing secondary resorption fronts in both taxa that were not visible externally. This contrasts with more typical ‘pleurodont’ squamates that lack resorption pits, like pythons and varanids, and those that do, like pleurodont iguanids, but target much less mineralized tissue. Considering this, our tegu histological data provides a developmental model for mosasaur tooth attachment and shedding due to similar ankylosed modes of attachment, attachment tissue mineralization and resorption. We can therefore characterize a “teiid-” and “mosasaur-type” of tooth resorption that has not been reported previously.

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## Variability of soft tissue preservation in a juvenile hadrosaurid dinosaur from the Dinosaur Park Formation of Alberta, Canada

Tristan Joubarne<sup>1</sup>, Caleb M. Brown<sup>1,2</sup>, Paul Durkin<sup>1</sup>, and Kirstin S. Brink<sup>1</sup>

<sup>1</sup>Department of Earth Sciences, University of Manitoba, Winnipeg, MB, R3T 2M6, Canada; joubarnt@myumanitoba.ca; Paul.Durkin@umanitoba.ca; Kirstin.Brink@umanitoba.ca

<sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, T0J 0Y0, Canada; caleb.brown@gov.ab.ca

Although typically rare in the fossil record, exceptionally well-preserved soft tissues are relatively common in hadrosaurid dinosaurs. Valuable information can be gained from these specimens, specifically as it relates to their external anatomy, such as integument patterns (Bell et al. 2012; Bell 2014; Joubarne et al. 2023), fleshy “mittens” around the hands (Osborn 1912; Joubarne et al. 2023), soft tissue cranial crests (Bell et al. 2014; Sharpe et al. 2025), and keratinous sheaths forming nails and hooves (Drumheller et al. 2022; Sereno et al. 2025). However, despite the relative abundance of these hadrosaur soft tissues in the fossil record, the processes and conditions leading to their preservation are still poorly understood. Our research project aims to better understand the processes that can lead to soft tissue preservation in hadrosaurs. To do so, we examined an indeterminate hadrosaurid dinosaur (TMP 2003.011.0001) with associated fossilized integument recovered from the upper Campanian Dinosaur Park Formation near the hamlet of Irvine (Alberta, Canada). Soft tissues associated with the hands of this specimen were found to form a single, fleshy “mitten” around digits II–III–IV, and vertical bands formed of two different types of scales were observed on its anterior torso (Joubarne et al. 2023). As part of our study, we re-examined these different tissues under UV light. Our preliminary analyses revealed the presence of a hoof-like structure extending from the terminal phalanx (ungual) of digit IV on the left foot, and possibly of digit III on the right foot, reminiscent of the pedal structures reported in *Edmontosaurus annectens* mummies from the Lance Formation of Wyoming (Sereno et al. 2025). These hoof-like structures become apparent and produce a bright yellow fluorescence under UV light. Preliminary UV fluorescence analyses on this specimen also reveal a bright orange fluorescence of the integument associated with the limbs (arms, hands, and feet), but not of the three integument patches located on the anterior torso of this individual, suggesting differences in chemical composition of these soft tissues, likely indicative of different modes of preservation. Future directions for our project include conducting further sedimentological and geochemical analyses to determine the pathways that led to the preservation of soft tissues on this juvenile hadrosaurid specimen.

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## Possible osteosarcoma on the neural spine of *Edmontosaurus regalis* from the Danek Bonebed, Edmonton, Alberta, Canada

Kaiki Kobayashi and Philip J. Currie

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; kaiki@ualberta.ca; pjcurrie@ualberta.ca

Bone tumours are rare in the fossil record, and only a few samples have been previously reported. In particular, osteosarcoma is a rare, malignant neoplastic tumour, which has only once been reported in Dinosauria. UALVP 61048 is a disarticulated partial neural spine of *Edmontosaurus regalis* collected from the upper Campanian to lower Maastrichtian (71.8 Ma to 71.5 Ma) Horseshoe Canyon Formation at the Danek Bonebed, Edmonton, Alberta, Canada. The specimen exhibits two severe proliferative pathological lesions covering both lateral surfaces with pseudoarthrosis at the posterior side of the spine. Macroscopically, lesions are similar in morphology to the later reparative to early remodelling phase of a fracture callus. The lesions, however, are asymmetrical and heterogeneous. A smaller lesion is a well-circumscribed, lobulated mass with a broad pedicle attached to the outer surface. A larger lesion is a broadly spread, flatter mass extended into the cortical bone. Detailed diagnosis was performed using plain radiography,  $\mu$ -Computed Tomography ( $\mu$ CT), and histology of a ground thin section. With plain radiography, the small lesion exhibits a characteristic cauliflower-like mass attached to the underlying bone. Moreover, a radiolucent cleavage line between the lesion and cortex (“string sign”), and sharply marginated erosion (“cortical saucerization”) are present. The large lesion is ivory in appearance. Neither the lesions nor the

host bone shows any lytic parts.  $\mu$ CT images show cortical bone resorption and intramedullary extensions underlying the lesions. Histologically, both lesions exhibit parallel lamellar bone trabeculae, some of which are interconnected and partially contain woven bone. Moreover, severe trabecular destruction underlies the lesions. The results suggest the possibility of parosteal osteosarcoma (PO). Parosteal osteosarcoma is a low-grade, slow-growing tumour, and one case was reported in the temnospondyl *Metoposaurus* in the fossil record. Although the osteological structure shows similarity to PO, we cannot observe any cellular material; therefore, other diagnoses remain possible.

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## The epaxial ossified tendon lattice and musculature of *Centrosaurus apertus* (Ornithischia: Ceratopsidae)

Kaiki Kobayashi and Corwin Sullivan

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; kaiki@ualberta.ca; corwin1@ualberta.ca

An epaxial ossified tendon trellis is a common feature in ornithischian dinosaurs. This character has long been known but has been the subject of only a few studies. Ossified tendons can provide direct evidence of the fibre orientations of some key epaxial muscles in ornithischian dinosaurs and are essential for a more accurate understanding of their locomotor system. Here we examine the epaxial ossified tendons of an adult *Centrosaurus apertus* specimen (UALVP 55261) from the Upper Cretaceous (Campanian) Dinosaur Park Formation of White Rock Coulee, southeastern Alberta. Most of the skeleton is articulated, and the tendon arrangement is preserved nearly in situ, albeit with some loss and displacement of tendon bundles. Previous studies have suggested that sets of epaxial ossified tendons in ceratopsians and iguanodontoids corresponded to *m. transversospinalis* in Crocodylia and *m. longus colli dorsalis*, pars thoracica in Aves. We describe the ossified tendons in the trunk and tail of UALVP 55621 and propose identifications for the muscles with which the tendons were associated, based on similarities in structure and attachment sites to avian and crocodylian muscle groups. Earlier authors concluded that the ossified tendons preserved in various ornithischians formed a three-layered lattice, but the present study reveals evidence that the epaxial tendons of *C. apertus* form four distinct, laterally successive lattice-like layers with clear regionalization. The tendons in each layer originate and terminate at different sites on the vertebrae, and the spatial relationships of the tendon layers to the vertebral column and to each other imply that the layers represent, from medial to lateral, *m. multifidus*, *m. spinalis*, the medial part of *m. articulospinalis*, and the lateral part of *m. articulospinalis*. Moreover, the lateral part of *m. articulospinalis* in the caudal region shows structural similarities with *m. levator caudae* in birds. The epaxial muscles of *C. apertus* appear to have exhibited a crocodylian-like arrangement in the sacral region and a bird-like arrangement outside the sacral region, suggesting the gradual emergence of the avian condition among Dinosauria.

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# The strongest fossil evidence of intraspecific face-biting demonstrated by an adult *Mosasaurus missouriensis* (Squamata: Mosasauridae) specimen from Alberta, Canada

Takuya Konishi<sup>1</sup>, Maximillian Scott<sup>2</sup>, Caleb Brown<sup>3</sup>, Kirstin Brink<sup>2</sup>, and Donald Brinkman<sup>3</sup>

<sup>1</sup>Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221, USA; konishta@ucmail.uc.edu

<sup>2</sup>Department of Earth Sciences, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada; scottm7@myumanitoba.ca; Kirstin.Brink@umanitoba.ca

<sup>3</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; caleb.brown@gov.ab.ca; Don.Brinkman@gov.ab.ca

Recovered from the upper Campanian Bearpaw Formation exposed in southern Alberta, TMP 2012.010.0001 is a virtually complete adult skeleton of *Mosasaurus missouriensis* (Mosasauridae: Mosasaurinae). Measuring about 6.5 m in total body length with a 90-cm-long, well-preserved skull, the mandibles of TMP 2012.010.0001 preserve lesions that exhibit a wide range of morphology and different stages of healing. One such lesion is an unequivocal bite mark on the lateral surface of the left surangular, represented by an oval puncture wound that measures 38.0 mm tall and 23.6 mm wide, with a tooth fragment of another mosasaur lodged inside. The slightly raised rim of the puncture, representing an active site of bone remodeling, is smooth and beveled, where CT imaging reveals a higher bone density compared to the surrounding, healed surangular bone. The lodged tooth fragment is much smaller in size than the puncture, its maximum dimensions measuring 12.76 mm wide and 12.86 mm long. The tooth is broken at both the basal and apical ends, indicating high impact force when it punctured the surangular.

Anterior to the puncture, the long posterior border of the intramandibular joint formed by both the surangular and the angular shows an irregular, jagged (but beveled) edge. Along the anterior border of this joint, the posterior end of the splenial is swollen with rugosity but showing no smaller-scale pathological features. Another elongate lesion about 3 cm long with a raised rim is located on the lateral side of the right dentary, extending horizontally under the fourth and fifth tooth positions. The right dentary lesion appears older than the ones on the left side of the skull, likely representing a separate episode of bone injury experienced by the mosasaur. Of all the mosasauroid taxa known to date from the Bearpaw Formation exposed across southern Alberta, the set of morphological traits exhibited by the embedded tooth fragment best agree with that of a mature *Mosasaurus missouriensis*, the only species of this genus thus far reported from the province. This indicates that TMP 2012.010.0001 was involved in intraspecific, non-predatory face-biting aggression with another mature mosasaur individual. While non-lethal intraspecific aggressions among extinct vertebrates have been hypothesized for other mosasaurs, ichthyosaurs, dinosaurs, crocodylians and synapsids, in no cases is the specific identity of the trace maker demonstrably conspecific with the trace bearer, and/or does the lesion show any signs of healing. We argue that TMP 2012.010.0001 represents the strongest case in the vertebrate fossil record of a non-lethal, intraspecific aggression.

# First Saskatchewan Paleocene amber — geochemistry and bioinclusions

Katie D. Kreutzer<sup>1,2</sup>, Kaitlin T. Lindblad<sup>2</sup>, Ben M.J. Egan<sup>1,2</sup>, Lauren Lindsay<sup>1,2</sup>, Seyed Samaei<sup>3</sup>, Jinkai Xue<sup>3</sup>, Maria I. Velez<sup>1</sup>, Ryan C. McKellar<sup>2,4</sup>, and Leslie J. Robbins<sup>1</sup>

<sup>1</sup>Department of Earth Sciences, University of Regina, Regina, SK, S4S 0A2, Canada; kreutzerkatie12@gmail.com

<sup>2</sup>Royal Saskatchewan Museum, Regina, SK, S4P 4W7, Canada; Ryan.McKellar@gov.sk.ca

<sup>3</sup>Cold-Region Water Resource Recovery Laboratory (CRWRRL), Environmental Systems Engineering, Faculty of Engineering and Applied Science, University of Regina, Regina, SK, S4S 0A2, Canada; ssw067@uregina.ca; jinkai.xue@uregina.ca

<sup>4</sup>Department of Biology, University of Regina, Regina, SK, S4S 0A2, Canada.

Amber's unique chemical structure provides excellent preservation of primary environmental isotopic signatures and fossil arthropods. Amber deposits are poorly represented from the latest Cretaceous into the Paleocene, obstructing our understanding of how insects and other terrestrial organisms with low preservation potential adapted during the end-Cretaceous extinction event. Here we present a newly discovered amber deposit in the Estevan coalbeds (Ravenscrag Formation, Paleocene, ~63 Ma) of southern Saskatchewan. This new deposit helps fill in the Cretaceous–Paleogene Amber Bioinclusions Gap (72.1–55 Ma). Four coal seams are found at the site, three are amber-producing, and only one has produced amber with bioinclusions. The botanical and arthropod inclusions found represent some of the earliest Paleocene insects in amber, demonstrating the potential to uncover important evolutionary information with further collection and preparation. The deposit is also described using stable isotopes of carbon and hydrogen ( $\delta^{13}\text{C}$  and  $\delta\text{D}$ ), and Fourier Transform Infrared (FTIR) spectroscopy.  $\delta^{13}\text{C}$  values suggest the amber-producing trees were stressed, while  $\delta\text{D}$  values indicate a significant coastal influence during the early Paleocene, likely reflecting the receding Western Interior Seaway. FTIR results demonstrate chemical similarities with modern resins and indicate the resin source as Cupressaceae conifers. This multi-proxy approach of ecosystem reconstruction provides a vital window into arthropod recovery after the K–Pg extinction event and the conditions under which these animals persisted. Future work will examine an additional amber deposit in southern Saskatchewan, ~64 Ma, to explore broader ecological patterns during the early Paleocene.

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# Finally! The most complete hind paddle of *Plioplatecarpus* (Squamata, Mosasauridae) from the Bearpaw Formation, Late Cretaceous, Alberta

Marilyn C. Laframboise

Royal Tyrrell Museum of Palaeontology, Drumheller, AB, Canada; marilyn.laframboise@gov.ab.ca

The Cretaceous marine lizard *Plioplatecarpus* (Squamata, Mosasauridae) is well known from numerous partial skeletons from Europe and North America. While there are many descriptions of the skull and most of the axial skeleton, there are few descriptions of the elements from the hind paddles. An almost complete skeleton of *Plioplatecarpus primaevus* (TMP2022.043.0001) recovered from the Bearpaw Formation (Fm) of southern Alberta has the best preserved hind paddle to date.

The Bearpaw Fm in Alberta comprises marine sediments that are best exposed around Lethbridge and Manyberries. Outcrops of Bearpaw Fm are visible in Dinosaur Provincial Park, near Brooks, Finnegan, Dorothy, and north of Drumheller. The Bearpaw Fm also extends into southwest Saskatchewan. The Bearpaw Fm unit known as Muddy Unit 1 crops out on the St. Mary River just south of Lethbridge with many mosasaur specimens recovered from within the same 10 m stratigraphic section. The Muddy Unit 1 is underlain by the Lethbridge Coal Zone. The specimen of *Plioplatecarpus primaevus*, TMP2022.043.0001, was found about 0.5 m above a 10-inch bentonitic layer. Many ammonites, three genera of mosasaurs, as well as plesiosaurs, turtles, fish, and a few dinosaurs have been collected from the same area in the last two decades.

The right hind paddle of TMP2022.043.000 is the focus of this work. This is the most complete hind paddle of *Plioplatecarpus primaevus* known to date. Except for the femur and fibula, all the elements of TMP2022.043.0001 were collected in one field jacket. The second and third digits have a few missing or damaged phalanges.

This description includes how the identity of the elements was determined, phalangeal arrangement, and phalangeal formula. Comparisons with *Mosasaurus missouriensis* and *Prognathodon overtoni* from the Collections of the Royal Tyrrell Museum were the primary source in determining the arrangement of the elements in the hind paddle. The phalangeal formula of the new hind paddle was determined by comparing known forepaddles of *Plioplatecarpus primaevus* which have a phalangeal formula of 6-8-8-6-4. The thirty-five elements from a single field jacket were assumed to be from the same paddle, even though not preserved in full articular position. The phalangeal formula of the hind paddle as reconstructed here is 6-6?-6?-6?-4. The forepaddle elements are consistently larger in size than the hind paddle elements.

A visual study of each element for surface details, and measurements for total length, proximal and distal length and width and mid-shaft width, was used to determine orientation. Phalanges of almost similar length could be arranged in rows from proximal to terminal. The arrangement and number of phalanges per digit was determined by comparing their size and shape with those of specimens of *Mosasaurus* and *Prognathodon*.

Based on literature, the tarsal series in *Plioplatecarpus* and most mosasaurids typically includes the astragalus, calcaneum, tarsal 3, tarsal 4. The tarsal arrangement in TMP2022.043.001 mirrors that of *Platecarpus* specimens available in the scientific literature and comparisons with *Mosasaurus* and *Prognathodon*.

Some elements from the left hind paddle of TMP2022.043.001 show spectacular abnormalities. These abnormalities are currently under study, and any speculation on the type or cause will not be addressed in this work.

The study of the most complete *Plioplatecarpus* hind paddle will continue to provide key insights and understanding of this mosasaur.

# Collapse of the mammoth steppe and the late Pleistocene decline of eastern Beringian horse populations: insights from stable isotopes and body mass modeling

Zoe Landry<sup>1,2</sup>, Joshua Miller<sup>3,4</sup>, Clément Bataille<sup>1,5,6</sup>, and Danielle Fraser<sup>2,3,7,8</sup>

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

<sup>2</sup>Department of Palaeobiology, Canadian Museum of Nature, Ottawa, ON, Canada; dfraser@nature.ca

<sup>3</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; Josh.Miller@uc.edu

<sup>4</sup>Department of Geosciences, University of Cincinnati, Cincinnati, OH, USA

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

<sup>6</sup>Department of Forestry & Natural Resources, West Lafayette, IN, USA; cbataill@purdue.edu

<sup>7</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, Canada

<sup>8</sup>Department of Biology, Carleton University, Ottawa, ON, Canada

The collapse of the mammoth steppe biome during the late Pleistocene deglaciation and the subsequent extinction are well-documented yet poorly understood phenomena. There is, as of yet, no consensus regarding the primary driver(s) of the ecosystem collapse and the following extinction. At present, three primary drivers have been proposed: 1) end-Pleistocene global warming, 2) human hunting and subsequent overkill, and 3) cascading ecological effects due to other abiotic factors and population declines of megafauna. While it is arguably most likely that the actual ecosystem collapse and extinction were caused by an interplay among multiple abiotic and biotic factors, it is also likely that individual species were affected differently by such factors, and in turn, had different causes of extinction — which must be investigated at the species level. Here, we present novel isotopic and body mass data of eastern Beringian caballine (*Equus* sp.) and stilt-legged (*Haringtonhippus francisci*) horses, which suggest that changes in nitrogen dynamics linked to cascading effects of ecosystem-scale changes likely contributed heavily to the extinction of horses at the end of the Pleistocene. Nitrogen ( $\delta^{15}\text{N}$ ) isotopes reveal a precipitous decline beginning ~20 ka, at the end of the Last Glacial Maximum and well before major climatic reorganization at the onset of the Bølling–Allerød Interstadial. This early decline in  $\delta^{15}\text{N}$  baseline values reflects a fundamental restructuring of steppe vegetation and nutrient cycling on the mammoth steppe, which suggests that the mammoth steppe of eastern Beringia was changing thousands of years before the terminal Pleistocene extinction. Concurrently, horse body size and  $\delta^{15}\text{N}$  decreased steadily through deglaciation, consistent with increased nutritional stress and shrinking habitat suitability as grasslands were replaced with boreal forest environments. Taken together, our findings of ecological deterioration inferred from isotopic and body mass proxies provide compelling support for cascading ecosystem effects as the best explanation for horse extinction in eastern Beringia at the end of the Pleistocene. These lines of evidence demonstrate that eastern Beringian horse populations experienced sustained ecological stress linked to the degradation of the mammoth steppe, rather than abrupt extinction or local extirpation associated with climate forcing alone. Our results highlight the dominant role of ecosystem transformation, particularly nutrient regime collapse, in shaping megafaunal vulnerability during the late Pleistocene deglaciation.

# The ace of spades? A new anuran from the late Campanian (Late Cretaceous) of North America illuminates early diversification of spadefoot toads (Pelobatoidea)

Alfred J. A. Lemierre<sup>1</sup>, Amy C. Henrici<sup>2</sup>, David J. Varricchio<sup>3</sup>, Jianye Chen<sup>4</sup>, and James D. Gardner<sup>1</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; alfred.lemierre@gov.ab.ca; james.gardner@gov.ab.ca.

<sup>2</sup>Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, PA, 15213, USA; HenriciA@CarnegieMNH.org.

<sup>3</sup>Department of Earth Sciences, Montana State University, Bozeman, MT, 59717-3480, USA; djv@montana.edu.

<sup>4</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; chenjianye@ivpp.ac.cn.

Spadefoot toads (Pelobatoidea, Anura) are a clade of Holarctic anurans composed of four families, each of them occurring, mostly, on a single continent today, despite wider geographical ranges indicated by their Cenozoic fossil record. Molecular clock analyses place the emergence of spadefoot toads during the Late Jurassic–Early Cretaceous, but the early diversification and evolution of Pelobatoidea are still poorly understood. Here we present a new anuran fossil taxon from the late Campanian (Late Cretaceous) of North America belonging to a new genus and species. The designation is based mainly on a nearly complete articulated skeleton from the Two Medicine Formation (Montana, USA) with additional disarticulated skeletons from the same formation, and isolated bones from several localities within the Dinosaur Park Formation (Alberta, Canada). Comparisons among extinct and extant anurans reveal strong similarities to members of Pelobatoidea, including a combination of key osteological features (e.g., presence of a spiral groove on the ilium; sacral transverse process expanded distally; anomocoelous vertebrae), that are only recovered within the clade. The similarity to members of Pelobatoidea was further confirmed in our preliminary phylogenetic analyses that recovered our new taxon within Pelobatoidea. The new Campanian anuran is the oldest unequivocal pelobatoid and pushes the record of the clade in North America back to more than 25 my. The presence of a pelobatoid within the Late Cretaceous of western North America is consistent with recent biogeographical analyses placing the emergence and early diversification of spadefoot toads in North America.

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# The devil is in the details: a new stem iguanian from the Late Cretaceous of Alberta, Canada

Alfred J. A. Lemierre<sup>1</sup>, Ilaria Paparella<sup>1</sup>, François Therrien<sup>1,2</sup>, and Darla K. Zelenitsky<sup>2</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; alfred.lemierre@gov.ab.ca; ilaria.paparella@gov.ab.ca; francois.therrien@gov.ab.ca

<sup>2</sup>Department of Earth, Energy, and Environment, University of Calgary, Calgary, AB, T2N 1N4, Canada; adkzeleni@ucalgary.ca.

Iguanian lizards (Squamata: Iguania) are one of the most diverse groups of squamates around today. Modern representatives of this clade are divided into two main lineages, the Acrodonta and Pleurodonta. Pleurodontan iguanians encompass almost half of the modern-day lizard diversity of North America; however, their Mesozoic

fossil record on the North American continent is restricted to a single unequivocal occurrence, *Magnuviator ovimonsensis*, from the Egg Mountain locality (between 77.9 – 76.3 Ma) in the Two Medicine Formation (Upper Cretaceous, Campanian) of Montana. Here, we report on disarticulated cranial elements of a new iguanian lizard from the Devil's Coulee locality (~75 Ma) in the upper Campanian Oldman Formation of Alberta, approximately ~1.3–3 million years younger than *Magnuviator*. The new taxon shares key similarities with the 'Gobiguania', a group of stem-iguanian lizards more closely related to the Pleurodonta, including taxa from the Late Cretaceous deposits of the Mongolian Gobi Desert. Preliminary phylogenetical analyses place the Devil's Coulee lizard in a polytomy with *Magnuviator* and the Mongolian 'gobiguanians' as the sister group to the Pleurodonta. The phylogenetic and geographic context of this new lizard is consistent with the iguanians spreading from Asia into North America during the Late Cretaceous, likely via a northern land connection. Furthermore, our study reveals that the Devil's Coulee specimen is the northernmost Mesozoic occurrence of a pleurodont-related fossil iguanian in North America, as well as the oldest overall iguanian from Canada, pushing back the presence of the clade on our continent by more than 30 million years.

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## Bergmannian body size trend in *Triceratops* (Dinosauria, Ceratopsia)

Caelan Libke<sup>1</sup>, Landon Burgener<sup>2</sup>, Hillary C. Maddin<sup>1</sup>, and Jordan C. Mallon<sup>1,3</sup>

<sup>1</sup>Department of Earth Sciences, Carleton University, , Ottawa, ON, K1S 5B6, Canada; caelan.libke@gmail.com; hillary.maddin@carleton.ca

<sup>2</sup>Department of Geological Sciences, Brigham Young University, Provo, UT 84604, USA; landon.burgener@byu.edu

<sup>3</sup>Beaty Centre for Species Discovery and Paleobiology Section, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; jmallon@nature.ca

*Triceratops* is a ceratopsid dinosaur genus that was geographically widespread across the Western Interior of North America during the latest Cretaceous. The stratigraphy, taxonomy, and ontogeny of *Triceratops* are well understood, making it an excellent candidate for comparative studies. The large size of some northern individuals may indicate that *Triceratops* exhibits a pattern of increasing body size with latitude, consistent with Bergmann's rule. This pattern is well-documented across numerous extant homeotherms, but no clear example has been reported in dinosaurs. Here, we reevaluate the relationship between paleolatitude and body size in *Triceratops*, using basal skull length and six additional cranial dimensions as body size proxies. We expand on prior work by using more precise geographic, taxonomic, and ontogenetic constraints to control for potential confounding effects. We also test the relationship between body size and climatic variables using two different paleoclimate estimates. This represents one of the most comprehensive assessments of body size–environment relationships within non-avian dinosaurs.

We find that *Triceratops* conforms to Bergmannian body size patterns, which predict larger individuals in cooler, higher-latitude localities. Adult basal skull length increases significantly with paleolatitude and decreases significantly with mean annual temperature (MAT) and warmest-month mean temperature (WMMT). In contrast, coldest-month mean temperature (CMMT) and mean annual precipitation (MAP) show no significant relationships to body size. The other cranial dimensions exhibit similar overarching patterns but weaker statistical support. The strong relationship between body size and temperature-related variables suggests a thermoregulatory basis for the observed pattern and aligns with the hypothesis that *Triceratops* was homeothermic. This pattern may have been driven by an uncharacteristically steep latitudinal temperature gradient across the Western Interior during the Late Cretaceous. Notably, statistical support for the patterns varies between *Triceratops horridus* and

*T. prorsus*; body size in *T. prorsus* consistently exhibits a stronger, statistically significant relationship with temperature variables such as MAT and WMMT. This disparity may reflect the effects of global climate change associated with the Latest Maastrichtian Warming Event, which coincides with the appearance of *T. prorsus*.

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## Spot the difference: comparisons of dentition and postcrania of *Leidyosuchus* (Campanian) and *Borealosuchus* (Maastrichtian, Paleocene)

Kaitlin T. Lindblad<sup>1,2</sup> and Jack R. Milligan<sup>3</sup>

<sup>1</sup>Department of Earth Sciences, University of Regina, Regina, SK, Canada; lindblak@uregina.ca

<sup>2</sup>Royal Saskatchewan Museum, Regina, SK, Canada

<sup>3</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; jmillig1@ualberta.ca

*Leidyosuchus* and *Borealosuchus* are medium-sized mesorostrine eusuchians known from Late Cretaceous and Paleogene North American terrestrial faunal assemblages. Once synonymous, *Borealosuchus* arose from the revision of several species initially assigned to *Leidyosuchus*. Only one valid species of the latter remains, *Leidyosuchus canadensis* from the Campanian of Alberta. Both genera have a similar skull shape, but *Borealosuchus* is a stem-crocodylian, and *Leidyosuchus* is a basal member of the crown clade Alligatoroidea.

Despite extensive comparisons of their cranial characters, the postcranial material of *Leidyosuchus* is poorly known, and the dental morphology and postcrania of the two genera have not been compared in detail. Our preliminary examination of this anatomy shows notable minor differences.

Both *Borealosuchus* and *Leidyosuchus* show similar tooth forms along the toothrow; however, *Leidyosuchus* possesses globular molariform teeth similar to the ‘button’ teeth of more derived relatives (e.g., *Albertochampsa*) as well as more varied enamel texturing. By comparison, the posterior teeth of *Borealosuchus* are homogeneous and pointed. Proximal limb elements of *Borealosuchus* are characterized by a ‘slim’ appearance, which is also noted to be present in *Leidyosuchus*. *Borealosuchus* dorsal osteoderms lack anterior-posterior keels, have rectangular mid-line and equant/triangular lateral elements, and have minimal or no osteoderm coverage along the limbs and tail. *Leidyosuchus* armour remains poorly sampled, but a couple undescribed associated specimens (e.g., UALVP 53766) and microsite material show a comparable armour with low keels on dorsal osteoderms.

The similarities in the dentition, osteoderms, and limbs between *Leidyosuchus* and *Borealosuchus* are likely synapomorphies, a consequence of their positions as basal/stem crocodylians. Both have been suggested to fill the ‘generalist crocodile’ niche in their respective habitats, but differences in dentition may be best explained by *Leidyosuchus* being an alligatoroid, rather than any substantial dietary differences.

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# *Pachyrhinosaurus* pathologies from Pipestone Creek

Kai O. MacFarlane<sup>1</sup>, Angela R. Lieverse<sup>2</sup>, and Emily L. Bamforth<sup>1,3,4</sup>

<sup>1</sup>University of Saskatchewan, Department of Geological Sciences, Saskatoon SK, S7N 5E2, Canada; oec038@usask.ca

<sup>2</sup>University of Saskatchewan, Department of Anthropology, Saskatoon SK, S7N 5E2, Canada; angela.lieverse@usask.ca

<sup>3</sup>Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 0C0, Canada; curator@dinomuseum.ca

<sup>4</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada

The Pipestone Creek Bonebed (PCB) (Campanian, 73 Ma) located near Grande Prairie, Alberta, has had a recent upsurge in interest thanks to recent media attention. Despite this, the bonebed remains understudied. The PCB represents a single mega-herd of the ceratopsian species *Pachyrhinosaurus lakustai*, which provides a unique and rare opportunity to study ecological aspects pertinent to gregarious ceratopsians. Here, we focus on the prevalence of pathologies found within the 302 specimens comprising the PCB collection housed at the Philip J. Currie Dinosaur Museum. Through a lesion-based approach focusing on the morphology of the bones, 11 pathologies of varying types were identified and recorded. This approach identifies lesions based on bone structure and morphology which requires an in depth understanding of bone biology and formation. Despite the extensive taphonomic changes the bonebed has undergone, bone formation is a key indicator because it can only occur during life. The size and extent of these lesions were also noted to understand the severity and distribution of the pathological conditions. The most common pathologies were identified on rib fragments and vertebrae. These included mainly fractures and button lesions. The presence of healed fractures and age-associated degenerative changes allows us to discern the herd's demographic structure. Understanding the processes contributing to lesion formation and recovery provide insight into how the herd lived and what ecological and physiological factors may have influenced their lives. These are key indications needed to help determine the herd's cause of death and deepen our overall understanding of the bonebed. Although pathological studies such as this have been applied to other herbivorous dinosaurs such as hadrosaurs, it is less commonly applied to ceratopsians making this study a further development of the field.

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# Filling in the gaps in the insect fossil record before the end-Cretaceous extinction event

Ryan C. McKellar<sup>1,2</sup>, Kano Sasaguchi<sup>3</sup>, and Ben Egan<sup>4</sup>

<sup>1</sup>Royal Saskatchewan Museum, Regina, SK, S4P 2V7, Canada; ryan.mckellar@gov.sk.ca

<sup>2</sup>Biology Department, University of Regina, Regina, SK, S4S 0A2, Canada

<sup>3</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; sasaguch@ualberta.ca

<sup>4</sup>Earth Sciences Department, University of Regina, Regina, SK, S4S 0A2, Canada; ben238@uregina.ca

The limited number of amber and compression fossil deposits between 78 Ma and 50 Ma that have been available for study has significantly impacted our knowledge of insect evolution. This time interval is important for understanding the evolutionary history of modern insects, because some of the most diverse insect orders underwent adaptive radiations or faunal turnovers as flowering plants rose to dominance in the Cretaceous. Near the end-Cretaceous extinction event we also appear to lose some insect families that were widespread and abundant throughout much of the Cretaceous period. If we want to assess the relative importance of extinction events and

floral shifts on insect lineages—as well as the downstream effects on terrestrial food webs and groups like insectivores—we need to improve sampling within this time window.

Over the last decade, new amber assemblages in the Horseshoe Canyon and Wapiti formations of Alberta, as well as the Battle, Frenchman, and Ravenscrag formations of Saskatchewan, have begun to fill in this gap. Here we will focus on some of the initial findings from Cretaceous assemblages in these formations, and how the improved resolution that these new deposits are providing is allowing us to better constrain the timing of evolutionary events and extinctions among insects. Even with the few inclusions that have been recovered and described to date, interesting patterns are beginning to emerge. Throughout the relatively warm and equable Cretaceous, researchers have proposed the Baeomorpha Realm for warm temperate northern areas where parasitoid wasps of the family Rotoitidae are found alongside an abundance of aphids. The Baeomorpha Realm was thought to lack significant ecological pressure from Formicidae (ants); however, ants seem to undergo a faunal turnover and a boost in abundance within newly discovered Maastrichtian amber deposits in western Canada. We also seem to lose some of the most conspicuous families of parasitoid wasps (e.g., Serphitidae) as we head into newly discovered amber deposits that occur slightly earlier in the Maastrichtian.

Previous inferences about changes in insect faunas have relied on amber deposits that are separated by tens of millions of years and thousands of kilometers. The growing number of amber deposits in the Late Cretaceous of Laramidia allows us to fine-tune diversity observations and faunal associations within a relatively narrow geographical area, and against a relatively consistent ecological backdrop.

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## Comparative body size distributions of Pleistocene and Recent Canadian wolves (*Canis lupus*)

Logan Micucci<sup>1</sup>, Zoe Landry<sup>2,5</sup>, Kamal Khidas<sup>3,4</sup>, and Danielle Fraser<sup>1,5,6,7</sup>

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

<sup>2</sup>Department of Earth Sciences, University of Ottawa, Ottawa, ON, K1N 6N5, Canada; zland032@uottawa.ca

<sup>3</sup>Vertebrate Zoology, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; kkhidas@nature.ca

<sup>4</sup>Biology, Laurentian University, 935 Ramsey Lake Rd., Sudbury, ON, P3E 2C6, Canada

<sup>5</sup>Palaeobiology, Canadian Museum of Nature, Ottawa, ON, K1P 6P4, Canada; DFraser@nature.ca

<sup>6</sup>Biology, Carleton University, Ottawa, ON, K1S 5B6, Canada

<sup>7</sup>Department of Paleobiology and Evolution of Terrestrial Ecosystems Program, Smithsonian Institution, Washington DC, 20560-0121, USA

During the late Pleistocene (129–11.7 ka), strong competition drove evolution of the Beringian wolf ecotype, a morphologically robust form found in Beringia. Relative to Recent counterparts, Beringian wolves possessed robust jaws, wide carnassial teeth, and short snouts, which enhanced carcass utilisation and enabled niche partitioning with other late Pleistocene carnivores. Body mass differences may also have enabled this. We selected 32 Pleistocene grey wolves (*Canis lupus*) specimens from eastern Beringia, and 106 Recent Canadian specimens. To statistically compare body masses, we used lengths and widths of the upper and lower carnassial teeth (P4 and m1 molars) and estimated body mass using published regressions. We also compared published values for Alaskan, Siberian, and European Pleistocene wolves. When accounting for sample size differences using subsampling, significant differences in the distributions of carnassial and body size estimates between Yukon Pleistocene and Recent Canadian forms were not found, though they did differ significantly in m1 lengths and P4 widths (P-value < 0.05). Yukon Pleistocene forms were significantly smaller than their Alaskan and Siberian conspecifics (P-value < 0.05), but similar to European forms. We suggest that Yukon Pleistocene wolves belonged to the same

ecotype as Recent Canadian wolves, were driven by specialization on large ungulates, but not genetic relatedness. We further hypothesize that Alaskan and Siberian Beringian wolves evolved larger bodies due to specialization on larger herbivores, or relying on scavenging and deterring kleptoparasites.

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# Taphonomy and palaeoecology of the Deadfall Hills Bonebed of the Wapiti Formation, northern Alberta

Jack R. Milligan<sup>1</sup>, Taia Wyenberg-Henzler<sup>1</sup>, Jordan Stock<sup>1</sup>, Henry S. Sharpe<sup>1</sup>, Emily L. Bamforth<sup>1,2</sup>, Nicolás Campione<sup>3</sup>, and Corwin Sullivan<sup>1,2</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; jmillig1@ualberta.ca; wyenberg@ualberta.ca; jcstock@ualberta.ca; hssharp@ualberta.ca; corwin1@ualberta.ca

<sup>2</sup>Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 0C0, Canada; Curator@dinomuseum.ca

<sup>3</sup>Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia; ncampion@une.edu.au

Hadrosaurid and ceratopsid bonebeds from the Late Cretaceous of Alberta have been studied for decades, providing insights into the palaeoecology and taphonomy of megaherbivorous dinosaur-dominated communities. However, most studies focus on those from southern Alberta (e.g., Dinosaur Park Formation), with comparatively few reported from northern, palaeoarctic regions. In northern Alberta, most bonebeds typically include a single taxon (hadrosaurid- or ceratopsid-dominated), from the Campanian–Maastrichtian (80–68 Ma) Wapiti Formation. Here, we present observations on the taphonomy and palaeoecology of a new monodominant, multitaxic hadrosaurid bonebed known as the Deadfall Hills Bonebed (DHBB), in which the primary taxon is a large, indeterminate species of *Edmontosaurus*—based on the presence of diagnostic cranial material. Notably, the DHBB is tentatively placed within the underrepresented Unit 5 of the Wapiti Formation (early–middle Maastrichtian), which, if confirmed, makes it one of the youngest dinosaur macro-bonebeds in Alberta. The *Edmontosaurus* material recovered to date consists of skull elements (including two left postorbitals, a nasal, a quadrate, a surangular, and a dentary) and several postcranial elements spanning several ontogenetic stages. Based on 53 prepared specimens, the *Edmontosaurus* specimens from the DHBB are larger than any hadrosaurid from the Wapiti Formation recovered to date. The current minimum number of individuals (MNI) based on right scapulae is 3, represented by two adults and one juvenile. Other remains recovered from this site represent a diversity of theropods, including teeth and body fossils of tyrannosaurids, troodontids, and dromaeosaurids. Elements include a large troodontid pedal phalanx, two dromaeosaurid metatarsals, an albertosaurine tyrannosaurid premaxilla with two unerupted teeth, and numerous shed theropod tooth crowns. Scavenging of the *Edmontosaurus* by theropods is evinced by tooth marks on several specimens, attributable to tyrannosaurids based on tooth mark size and tooth spacing measurements. The skeletal material in the bonebed is disarticulated, with the notable exception of an articulated partial hindlimb of a large *Edmontosaurus* individual, including the femur, tibia, fibula, and tarsal elements, and a series of vertebrae encased within an ironstone concretion. Articulated *Edmontosaurus* material could indicate the presence of soft tissue on the skeletons before and during burial despite scavenging by theropods. Comparing aspects of the DHBB, including the mixed articulation and disarticulation of elements, theropod diversity and palaeobiology with other bonebeds in the Wapiti Formation and other temporal/regional equivalent sites could help elucidate the paleoecologic and environmental factors that helped shape the taphonomic history of this assemblage.

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# Historical contingency of early vertebrate phylogeny: what if and what now

Tetsuto Miyashita

Beaty Centre for Species Discovery, Canadian Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario, K1P 6P4, Canada

Early vertebrate research has made its greatest impact in the literature when forming a phylogenetically informed narrative for the origins of major lineages. Phylogenetic hypotheses are both sensitive to and contingent on taxon and character sampling, whereas sampling mode, intensity, and coverage are all functions of geographical and socioeconomic factors. Vertebrate fossil record is most intensively sampled in densely populated and economically developed regions. For Paleozoic fishes, systematic research began in the United Kingdom, France, and Germany, spread to cover collections from North America, and became established as a scientific enterprise more recently in Asia and Oceania, while there is rising interest but with sparse research centres in Africa and South America. How did this historical contingency affect our phylogenetic understanding of early vertebrates? Would we come to harbour a different set of assumptions, ideas, and interpretations if the order of taxic discoveries was reversed? And what does it tell us about biases in our current consensus and future prospect?

To paraphrase these questions rather whimsically, the scientific community responded with a positive surprise when Chinese researchers reported the taxa *Guiyu*, *Shuyu*, *Entelognathus*, or *Shenacanthus* (in the order of discoveries) because they appeared so different and more ‘primitive’ than the more ‘familiar’ and ‘derived’ forms such as *Cheirolepis*, *Cephalaspis*, *Coccosteus*, or *Acanthodes*. However, if — assuming an alternate line of history where, for the fun of it, the Pax Mongolica took a longer hold and maintained the power balance in favour of the Orient — early vertebrate research began in East Asia, then the former set of taxa would be more familiar to researchers, and the latter set would be the ‘weird’ ones that potentially change our understanding about their relationships. Such historical contingency may have also led us to identifying and defining characters differently.

I took a simple approach to explore these questions by editing the current consensus datasets in early vertebrate phylogeny, removing or re-coding taxa by geographical regions. Then I ran a maximum parsimony analysis on each of these alternate datasets. Results are contrasting between different datasets. Reversing the order of discoveries makes surprisingly little impact to phylogenetic hypotheses on jawless vertebrates. This is partly because jawless vertebrates tend to be highly provincial in their distributions. These historically alternate trees simply depict pruned versions of the current ‘consensus’ topology, except for thelodonts in which characters from isolated scales can associate them with chondrichthyans.

In comparison, historical contingency impacts gnathostome phylogeny to much greater degree. Coding only for Chinese taxa in the current datasets generates consensus trees in which: a) antiarchs form a basal grade from euantiarchs to yunnanolepids; b) the ‘arthrodire’ clade mostly populated by petalichthyiids form a sister group to the gnathostome crown; c) maxillates associate with this ‘arthrodire’ clade instead of the gnathostome crown; d) *Meemania* and *Shenacanthus* each falls outside the Chondrichthyes+Sarcopterygii clade in some of the most parsimonious trees. These trees indicate uneven sampling from major lineages, notably actinopterygians, chondrichthyans, and various placoderm groups. Consequently, the Chondrichthyes are found at the end of a long branch, and by their character coding, it would remain unclear whether ‘antiarchs’ are unequivocally jawed vertebrates.

Expanding the sampling to include Central Asia, Siberia, Australia, and Antarctica (assuming an alternate historical scenario where the Ming Dynasty’s trade policies led to faster economic development in these regions than in Europe), the East Asia-centric framework remains largely stable with weakening clade support, except: a) additions of well-preserved ptyctodonts would support ‘acanthothoracids’ or maxillates to form a sister group to the less resolved gnathostome crown; b) actinopterygians may be nested among ‘sarcopterygians’; and c) viewed in our own timeline, these trees may resurrect the idea that ‘acanthodians’ are stem to both chondrichthyans and osteichthyans.

If, instead, we posited that early vertebrate research began in the Americas by the Indigenous Peoples, then

the initially supported topology would have antiarchs and acanthothoracids at the basal polytomy of jawed vertebrates, arthrodires as sister to crown gnathostomes, and either ‘actinopterygians’ polyphyletic within the Sarcopterygii or ‘sarcopterygians’ paraphyletic within ‘actinopterygians’. As a trade-off to the confusing osteichthyan relationships, the chondrichthyan stem would be richly populated in comparison to Asia- or Austroasia-centric early vertebrate phylogeny. Finally, the Euro-centric dataset would have produced consensus trees most compatible with our current consensus, except with the Actinopterygii being nested within the Sarcopterygii.

Throughout these regionally biased analyses, many of the characters in current usage became either constant or parsimony-uninformative. These characters are useful only when the dataset samples across regions include those concerning major change in the body plan or those discussed extensively in the literature: nasohypophyseal organization, patterning of sensory canals, and articulation of jaw cartilages. With these results, I plan to explore chondrichthyan and osteichthyan relationships in greater detail, and with Youan Zhu at the Institute of Vertebrate Paleontology and Paleoanthropology, expand our scope to then examine the same question using datasets in archosaur phylogeny.

These thought experiments reveal biases inherent to both our current understanding of early vertebrate phylogeny and our current practice in formulating cladistic characters. Although my analyses do not tell us how or where in the tree we are being led astray by such biases at this moment, they suggest plenty are left in this field to generate more surprises. In that regard, I highlight two factors our community can make concerted efforts for: 1) international collaboration is critical not just for general reasons often stated in scientific literature, but also for the real, pressing need to counteract regional biases discussed here; 2) we should support growing local interest and budding centres for early vertebrate research in Africa and South America foremost, and in Central Asia and the homelands of Indigenous Peoples in high latitudes of the Northern Hemisphere. Taking lessons from the rapid growth of early vertebrate research in China since the latter half of the 20th century, my last point comes with a special note: to make training and collaboration not unidirectional or asymmetric, but reciprocal and equitable to the best of our abilities, not only to follow good practice, but also to maximize scientific gains.

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## The histology and biomechanics of ossified tendons

Bryan R.S. Moore<sup>1</sup> and Jason S. Anderson<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4, Canada; bryan.moore@ucalgary.ca

<sup>2</sup>Faculty of Veterinary Medicine, University of Calgary, Calgary, AB, T2N 4N1, Canada; janders@ucalgary.ca

Tendons are a form of connective tissue made primarily of collagen and elastin which connect muscles to bone. In most cases, their primary functions are to transmit muscular force to bones, facilitating joint movement, and to store and release elastic energy during locomotion. In certain cases, however, tendons ossify, becoming rigid, inflexible, and incapable of fulfilling their usual roles. This begs the question, what is the benefit of tendon ossification?

The aim of this study is to determine the potential role(s) of ossified tendons in the animals in which they occur. To accomplish this, we will first survey the paleohistology of ossified tendons across a wide range of extinct archosaurs including ceratopsians, ornithopods, sauropods, pachycephalosaurs, and ankylosaurs. We will then compare the patterns observed in extinct taxa to the histology observed in the only extant taxa known to ossify their tendons, teleost fish and modern birds. Finally, biomechanical tensional stress tests will be conducted on the ossified tendons of extant taxa to determine their mechanical properties and potentially inform those of extinct taxa.

Differing bone textures between taxa could suggest differing, and perhaps unique, functional roles of ossified tendons, as the mechanical properties of bone change based on microstructure and mineral content. Bone with high mineral content has high stiffness, but low toughness, strength, and energy to break. Lamellar and fibrolamellar bone are stronger in tension and more fatigue resistant than Haversian bone. Haversian bone is often developed in

response to an accumulation of structural damage, and so may be representative of age and/or the amount of stress ossified tendons are exposed to throughout life rather than being a direct result of mechanical function.

Preliminary results from our survey show considerable variability in the histology of ossified tendons among extinct taxa. Observed bone textures include standard Haversian bone in ornithopods and ceratopsians, extremely dense Haversian bone in ankylosaurids, porous Haversian bone in nodosaurids, neatly organized lamellar bone in the taxon *Parksosaurus* sp., and a hybrid histology consisting of central Haversian bone which grades exteriorly into woven bone in pachycephalosaurs. Sauropods and extant taxa have yet to be sampled.

These results may indicate that ankylosaurid tendons are subjected to a large amount of stress and damage when compared to their nodosaurid relatives. Ornithopod and ceratopsian tendons may experience some stress to a lesser degree than ankylosaurids, but Haversian bone may also always be a consequence of age. *Parksosaurus* sp. displays a bone texture with higher levels of organization that are usually associated with high mechanical strength, and the tendons sampled from pachycephalosaurs appear to be actively undergoing heavy remodeling and rapid growth rates. Ongoing work continues to refine these interpretations. Future research directions include sampling additional taxa with ossified tendons, including nonavian theropods and nyctosaurid pterosaurs, in order to develop a comprehensive framework for understanding ossified tendon histology and mechanical properties.

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## Craniodental analysis of the oldest fossil lorisid, *Mioeuoticus bishopi* (Strepsirrhini, Primates)

Hiruni N. Mudannayake<sup>1</sup>, Holly E. Anderson<sup>2</sup>, Sergi López-Torres<sup>2</sup>, Laura MacLatchy<sup>3</sup>, and Susanne Cote<sup>1</sup>

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

<sup>2</sup>University of Warsaw, Faculty of Biology, Warsaw, Poland; h.anderson@uw.edu.pl ; s.lopez-torres@uw.edu.pl

<sup>3</sup>Department of Anthropology, University of Michigan, Ann Arbor, MI, USA; maclatch@umich.edu

While lemuriforms are the strepsirrhines of Madagascar, lorisiforms are the strepsirrhines of mainland Africa and Asia. Their existence spans over 66 million years, making them one of the oldest living primate lineages. Sometime in the Paleogene, the two extant lineages emerged: the lorises (Lorisidae) and galagos (Galagidae). Their fossil record is notably sparse, largely because of their low population densities, solitary and arboreal lifestyles, and lack of preservation due to their small body size and tropical forest habitat. Consequently, the paucity of the lorisoid fossil record has made determining evolutionary relationships between extant and extinct taxa difficult. Assignment of fossils into Galagidae and Lorisidae has also been challenging. Their long history and vast biogeographical spread across Africa and Asia, however, is a testament to their deep evolutionary history.

Only seven fossil lorisid species have been named to date. *Mioeuoticus bishopi* is the oldest named fossil lorisid and comes from early Miocene (~18-20 Mya) deposits in Uganda and Kenya. The type specimen of *M. bishopi* is NAP I.3.6/58 from Napak, Uganda. It is the anterior portion of the cranium, with the face and palate consisting of the left P4-M3 and right P2, P4-M2. Previous phylogenetic craniodental character analyses place *M. bishopi* as a lorisid or as a stem lorisiform. We are currently conducting a comprehensive phylogenetic analysis of all lorisiformes, coding over 200 morphological characters. Here, we provide a detailed description of NAP I.3.6/58, using microCT data from a high-quality cast of the specimen. We will code the type specimen for all morphological characters and incorporate the data into the larger phylogenetic analysis. This will provide refined anatomical descriptions of *M. bishopi* and aid in reanalyzing the phylogenetic position of this taxon within Lorisioidea.

# A biodiverse multitaxic bonebed provides insights into megaherbivore assemblage transitions in the Dinosaur Park Formation, Alberta, Canada

André S. Mueller<sup>1</sup>, Alexandre V. Demers-Potvin<sup>2</sup>, Don Brinkman<sup>3</sup>, Caleb M. Brown<sup>3</sup>, Mark Powers<sup>4</sup>, Gabrielle Bonin, Louis-Philippe Bateman<sup>1</sup>, Dirley Cortés<sup>5,6,7</sup>, Olivia Osterreicher<sup>1</sup>, and Hans C.E. Larsson<sup>1</sup>

<sup>1</sup>Department of Biology; McGill University, Montreal, QC, H3A 1B1, Canada; andre.mueller@mail.mcgill.ca; gabrielle-bonin28@gmail.com; louis-philippe.bateman@mail.mcgill.ca; hans.ce.larsson@mcgill.ca

<sup>2</sup>Department of Bioengineering, McGill University, Montréal, QC, H3A 0E9, Canada; alexandre.demers-potvin@mail.mcgill.ca

<sup>3</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; don.brinkman@gov.ab.ca; caleb.brown@gov.ab.ca

<sup>4</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; powers1@ualberta.ca

<sup>5</sup>Smithsonian Tropical Research Institute Tupper Ancon, Panama; dirley.cortes@mail.mcgill.ca

<sup>6</sup>Centro de Investigaciones Paleontológicas, Villa de Leyva, Colombia

<sup>7</sup>Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

The Dinosaur Park Formation biota is currently known to have experienced megaherbivore turnover events, as evidenced by the presence of distinct biostratigraphic zones (MAZ-1 and MAZ-2). However, little is known about the faunal composition at the transition between these zones, and it remains unknown whether this faunal shift was primarily gradual or punctuated. Multitaxic bonebeds provide insight into local paleoecological interpretations and community composition. Over the last eight years, McGill University has conducted fieldwork in Dinosaur Provincial Park (DPP), focusing on systematic excavation of such fossil sites. One such bonebed is Bonebed 190 (BB190), located in the Iddesleigh region of DPP. This bonebed was chosen particularly because it lays at the intersection between MAZ-1 (*Corythosaurus*–*Centrosaurus* spp.) and MAZ-2 (*Lambeosaurus*–*Styracosaurus* spp.). Until recently, BB190's affinity to either zone remained unknown. From this single locality, hundreds of macrofossils and thousands of microfossils were recovered, revealing a unique faunal assemblage for DPP with remarkably high taxonomic diversity. It was determined that this site preserved MAZ-2 fauna, including *Styracosaurus* sp. and cf. *Lambeosaurus* sp., marking one of the lowest known quarries in this zone. We also report the first unequivocal co-occurrence of *Gorgosaurus* sp. (based on associated lacrimal and dentary elements) and *Daspletosaurus* sp. (based on preserved fused nasals) within a single fossiliferous horizon from that bonebed. At one quarry within BB190, a high volume of nodosaurid material, which appears to belong to a single disarticulated individual tentatively referred to *Edmontonia* sp., has been recovered. Other collected dinosaur material includes fossils from tyrannosaurids, ornithomimids, caenagnathids, dromaeosaurids, troodontids, avialans, pachycephalosaurs, thescelosaurids, ankylosaurids, and leptoceratopsids. Bulk-sampled microfossils also include diverse vertebrate assemblages, including squamates, mammals, fish, salamanders, frogs, turtles, crocodylians, champsosaurs, pterosaurs, marine reptiles, as well as invertebrates including gastropods. This high taxonomic diversity makes BB190 one of very few localities within DPP (alongside multitaxic bonebeds 10, 47 and 102) to document a significant proportion of the non-marine vertebrate species richness of the Dinosaur Park Formation through well-preserved macrofossil remains. The study of these fossils will provide insights into faunal dynamics at the MAZ-1/MAZ-2 transition, refine biostratigraphic frameworks within the DPP formation, and improve our understanding of late Campanian ecosystem structure and turnover processes in western North America.

# First large, articulated teleosteomorph fish from the lower Shaftesbury Formation (Albian) of British Columbia, Canada

Alison M. Murray, Luke E. Nelson, and Joshua A. Doyon

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; ammurray@ualberta.ca; lenelson@ualberta.ca; jdoyon@ualberta.ca

The oldest known fishes recovered from the northern part of the Western Interior Seaway of Canada are from Albian deposits; however, very few fish are known from this area at that time. Only three taxa have previously been reported, two species of the euteleost *Erichalcis* and the primitive clupeomorph *Foreyclupea loonensis*. In 2002, a large fish was collected from the lower part of the Shaftesbury Formation near Fort St. John, BC. These layers are below the Albian–Cenomanian Fish Scale Layer, and are Albian in age. The fish material is preserved in two separate nodules, with a head and anterior body in the larger nodule, and a tail in a second, smaller nodule. Because nucleation of concretions can be discontinuous, and the size and morphology of the two parts are congruent, it is quite possible that the two nodules contain parts of the same individual; however, we diagnose the new species using information only from the part preserved in the larger nodule. The fish is identified as a new species of Pachyrhizodontoidei, a stem-group to Teleostei (i.e., within Teleostomorpha but outside Teleostei).

# Structural and functional heterogeneity in epaxial ossified tendons of *Triceratops*

Marco Muscioni<sup>1,2</sup>, Simone A.M. Lemmers<sup>3</sup>, Kaiki Kobayashi<sup>4</sup>, Ilaria Carlomagno<sup>3</sup>, Maurizio Polentarutti<sup>3</sup>, Giorgio Bais<sup>3</sup>, Henning Markotter<sup>5</sup>, Marko Prasek<sup>3</sup>, Paula Sanchez<sup>3</sup>, Lucia Mancini<sup>6</sup>, Diego Dreossi<sup>3</sup>, Giorgia Bacchia<sup>7</sup>, and Federico Fanti<sup>1,2</sup>

<sup>1</sup>Department of Biological, Geological, and Environmental Sciences, Alma Mater Studiorum University of Bologna, Bologna, 40126, Italy; marco.muscioni2@unibo.it; federico.fanti@unibo.it;

<sup>2</sup>Collezione di Geologia ‘Museo Giovanni Capellini’, Alma Mater Studiorum, Università di Bologna, Bologna, 40126, Italy

<sup>3</sup>Elettra-Sincrotrone Trieste S.C.p.A., Basovizza, 34149 Italy; simone.lemmers@elettra.eu; ilaria.carlomagno@elettra.eu; maurizio.polentarutti@elettra.eu; giorgio.bais@elettra.eu; marko.prasek@elettra.eu; paula.sanchez@elettra.eu; diego.dreossi@elettra.eu

<sup>4</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; kaiki@ualberta.ca

<sup>5</sup>Department of Non-Destructive Testing, Abteilung Zerstörungsfreie Prüfung, Bundesanstalt für Materialforschung und -Prüfung (BAM), Berlin, 12205, Germany; henning.markotter@bam.de

<sup>6</sup>Department of Materials, Slovenian National Building and Civil Engineering Institute (ZAG), Ljubljana 1000, Slovenia; lucia.mancini@elettra.eu

<sup>7</sup>Zoic Limited Liability Company, Trieste, 34148, Italy; info@zoic.it

Mineralised tendons are well documented among dinosaurs but are rarely preserved in anatomical connection, limiting investigation of their exact muscular origins, functional roles, and diagenetic histories. As a result, the pathways underlying tendon mineralisation, their interaction with biomechanics and post-burial processes remain poorly resolved. Here, we examine an in-situ network of ossified epaxial tendons associated with the dorso-sacral region of a partial *Triceratops prorsus* skeleton from the Hell Creek Formation (latest Maastrichtian, 66–67 Ma, USA). Three anatomically and mechanically distinct regions of a single tendon were analysed using an integrated multi-scale framework combining traditional histology, laboratory and synchrotron radiation micro-computed tomography ( $\mu$ CT, SR- $\mu$ CT), and synchrotron radiation X-ray fluorescence (SR-XRF) mapping. Histological and tomographic data reveal well-organised ossified tissue, including lamellar bone, developed vascular networks, and extensive secondary osteonal remodelling, further demonstrating a biologically regulated ossification rather than passive calcification. Crucially, distinct microstructural architectures among morphologically different areas in the same element indicate functional heterogeneity linked to differing mechanical regimes, from attachment zones to tensile cable-like structures. Quantitative three-dimensional morphometry further resolves variation in bone volume fraction, porosity, and vascular organisation, consistent with local-scale biomechanical specialisations. Elemental mapping differentiates primary biological mineralisation from secondary diagenetic overprinting: calcium, phosphorus, and strontium are homogeneously distributed within the tendon matrix, consistent with preserved bioapatite. In contrast, iron and associated trace elements are concentrated within pore spaces and along external surfaces, reflecting groundwater infiltration and pore-fill precipitation, while uranium and rare earth elements show unusual surface enrichment possibly indicative of chemically mediated uptake during fossilisation.

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## Taxonomic revision of *Enchodus dirus* leads to the recognition of a new species of *Enchodus* from North America

Luke E. Nelson<sup>1</sup>, Alison M. Murray<sup>1</sup>, and Megan E. Sims<sup>2</sup>

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

<sup>2</sup>University of Kansas Biodiversity Institute & Natural History Museum, Lawrence, Kansas, 66045, USA; megan.sims@ku.edu

Many species within the teleost fish genus *Enchodus* were erected based on isolated remains, including *Enchodus dirus* Leidy, 1857, which was named for a fragmentary dentary. We redescribe this holotype and find it to be nondiagnostic, lacking sufficient characters to separate it from other species of *Enchodus*. A complete skull from the Niobrara Chalk, which was previously referred to *E. dirus*, is designated as the holotype of a new taxon. This new species has a unique character suite, including: sigmoidal palatine teeth lacking postapical barbs, palatine teeth with a symmetrical cross-section and a single cutting edge, no marginal row of teeth on the mandible, no ornamentation on the mandible, and a rostrodermethmoid which is wider than long with lateral wings. The dentary teeth of the holotype lack prominent posterior ridges, unlike the holotype of *E. dirus*, and the two specimens are stratigraphically separated by 10 million years. Previous specimens referred to *E. dirus* are reviewed, and two additional specimens from the Niobrara Formation are referred to the new species. Some *Enchodus* specimens from the Fox Hills Formation, including the holotype of *E. dirus*, may be better referred to *Enchodus gladiolus*, although none are complete enough to be certain. A nearly complete skull from Greece, which was previously identified as *Enchodus* cf. *E. dirus* is not conspecific with our new species.

# Expanded caudalmost sternal ribs in extant pelicans suggest stabilizing function for the morphologically similar ribs of the Cretaceous toothed bird *Jeholornis prima*

Ping Nixon-Hermansen and Corwin Sullivan

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; nixonher@ualberta.ca; corwin1@ualberta.ca

Most extant birds have vertebral and sternal ribs with little disparity among the segments of the thoracic region, with some minor differences in length, and the presence of uncinat processes on some ribs. However, the long-tailed, toothed Cretaceous bird species *Jeholornis prima*, of the Jehol group of Northeast China, has two proximocaudally expanded caudalmost sternal ribs. This unusual feature was initially thought to be unique to *Jeholornis*, lacking any living avian morphological analogue. However, several analogous, undescribed rib adaptations have since been identified

Within the genus *Pelecanus*, the caudalmost sternal ribs are proximally expanded, with a variable convex flange whose exact shape varies inter and intraspecifically. In *Pelecanus erythrorhynchos*, the American white pelican, the flange is bordered by a cartilaginous expansion, which acts as the attachment site for the ventralmost fibres of *M. obliquus internus abdominis* muscle. Given the consistency of location and attachments of the internal oblique muscle across all known extant avian taxa, it is likely that the interaction between the internal oblique and the flanged rib is conserved across the genus *Pelecanus*.

Another expanded caudalmost sternal rib occurs in some Galliformes, such as the chicken (*Gallus gallus domesticus*), and turkey (*Meleagris gallopavo*). The caudalmost sternal rib morphology within these galliformes is somewhat intra- and inter-specifically variable, but still notable for their functional analogy to *Jeholornis*. Unlike in the pelican, the galliform caudalmost sternal ribs have an acute vertice giving rise to a caudally concave margin both dorsally and ventrally. The galliform caudalmost rib expansion is essentially defined by a sharp point, while the pelican rib expansion is defined by a rounded flange.

Electromyographic studies of chicken respiratory movement have found the *M. obliquus internus abdominis* is active during exhalation. In the aforementioned rib-flanged taxa, exhalation may be more forceful due to the extended attachment area provided by the flange. It is possible that the increased moment arm of the caudalmost sternal rib (via the expanded flange) allows the internal oblique to better stabilize the ribcage, preventing craniodorsal displacement of the sternal ribs and sternum. Provided other abdominal or intercostal muscles acted to prevent caudodorsal movement of the proximal ends of the vertebral ribs, activation of *M. obliquus internus abdominis* would drive the caudoventral displacement of the distal ends of the sternal ribs, and thus the sternum. This would exert resistance against forces pushing the sternum dorsally, and preventing depression of the sternum during inhalation. This would be particularly useful in counteracting water pressure on the ribcage during swimming (in pelicans), or a ground reaction force on the sternum of a heavier bird (i.e., the turkey or chicken) while resting prone. A similar function for the sternal rib flanges, based on a similar association with *M. obliquus internus abdominis*, is probably in *Jeholornis prima*.

# Perinate hadrosaur remains and associated eggshells from the Upper Cretaceous Oldman Formation of southeastern Alberta, Canada

Ayari Otomo<sup>1</sup>, Darla K. Zelenitsky<sup>2</sup>, Kohei Tanaka<sup>3</sup>, François Therrien<sup>4</sup>, Corwin Sullivan<sup>1</sup>, and David C. Evans<sup>5</sup>

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

<sup>2</sup>Department of Earth, Energy, and Environment, University of Calgary, Calgary, AB, T2N 1N4, Canada; dkzeleni@ucalgary.ca

<sup>3</sup>Institute of Life and Environmental Science, University of Tsukuba, Tsukuba, Ibaraki, 305-8572, Japan; koheitanaka@geol.tsukuba.ac.jp

<sup>4</sup>Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; T0J 0Y0 and Department of Earth, Energy, and Environment, University of Calgary, Calgary, AB, T2N 1N4, Canada; francois.therrien@gov.ab.ca

<sup>5</sup>Department of Natural History, Royal Ontario Museum, Toronto, Ontario, M5S 2C6, Canada; davide@rom.on.ca

In North America, eggs and perinatal remains of hadrosaurid dinosaurs have primarily been recovered from Upper Cretaceous (Campanian) deposits of the Oldman Formation in Alberta and of the Two Medicine Formation in Montana. Nearly all hadrosaurid eggs and embryos from Alberta are from a locality known as Devil's Coulee, located near Lethbridge in southernmost central Alberta. Here we report on perinatal hadrosaurid remains and associated eggshell from a newly discovered locality in the Oldman Formation of southeasternmost Alberta. The specimen, UC 16624, consists of skeletal elements from at least two individuals associated with large eggshell fragments. All major regions of the skeleton are represented by elements, except for the pelvic girdle. Portions of the skull, hindlimb, manus, and of the vertebral column are preserved in articulation or semi-articulation. Due to the poor preservation and early developmental stage of the remains, it is difficult to determine whether they belong to a lambeosaurine or a saurolophine. The eggshell possesses a stipple-like surface texture similar to lambeosaurine eggs (*Hypacrosaurus stebingeri*) as opposed to the net-like ridges of saurolophine eggs (*Maisaura peeblesorum*). The body mass of one of the perinatal individuals is estimated at 4200 g, a size that could likely be accommodated inside a lambeosaurine egg (3900 – 4190 mL) but not a saurolophine egg (900 mL). As such, the UC 16624 individuals would likely represent either perinatal lambeosaurines or large saurolophine hatchlings. Additional preparation or computed tomographic scanning may assist in further identifying these remains.

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# Estimating the body mass of hadrosaurids in Alberta using the anteroposterior lengths of the alveolar grooves in maxillae and dentaries

Ayari Otomo, Colton Coppock, and Philip J. Currie

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; otomo@ualberta.ca; ccoppock@ualberta.ca; pjcurrie@ualberta.ca

Isolated bones of hadrosaurids are the most commonly seen dinosaur specimens in the western interior region of North America. In Alberta, there are probably millions of fragmentary bones of hadrosaurids from multiple age ranges that are exposed in the badlands at any one time.

The dentigerous jaw bones (maxilla, dentary) can be identified because they possess the unique food-processing structure called the “dental battery.” Each dental battery possesses up to 300 teeth, which are aligned in columns called “tooth families”. Adult hadrosaurids could have 32 or more tooth families in one dentary, depending on the size and age of the animal. In contrast, the babies have only 9-15 tooth families, and it is known that the number of tooth families are added onto the front and back of a tooth row as the animal grows larger. Although hadrosaurid bones are the most common fossils found, the number of well-preserved maxillae and dentaries that are complete enough for counting tooth rows and measuring the height or length are infrequent. In this research, a method of utilizing the numerous fragmentary bones by estimating the body mass of hadrosaurid dinosaurs based on the anteroposterior length of the alveolar groove on fragmentary specimens, is suggested. Body mass is relevant to several aspects of dinosaur biology such as population densities and growth rates.

Twenty-eight specimens of 16 hadrosaurid species and of 3 iguanodontid species were measured. As a result, a strong correlation was found between the body mass estimated using the stylopodial measurements and the average anteroposterior length of alveolar grooves of dentary. The correlation between body mass estimated stylopodial measurements and the average anteroposterior length of maxilla alveolar grooves were not significantly strong. This research suggested a potential ability of estimating body mass of hadrosaurids using the average alveolar groove length of dentary. Further research with a greater number of data points is required for a more precise correlation relationship to be identified.

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# Reassessment of a purported deinocheirid from the Judith River Formation (Campanian) of Montana

Shyong En Pan<sup>1</sup>, Caelan Libke<sup>2</sup>, Gianni Zambonin<sup>2</sup>, and Jordan C. Mallon<sup>1,2</sup>

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

<sup>2</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, Canada; caelanlibke@cmail.carleton.ca, giannizambonin@cmail.carleton.ca;

A recently described pair of partially preserved, large ornithomimosaur dentaries from the Judith River Formation (upper Campanian) of Montana has been suggested to belong to Deinocheiridae, based primarily

on gross morphology. Such an identification would be remarkable, given that nearly all ornithomimosaur fossils from the Upper Cretaceous of North America are attributable to Ornithomimidae; just a single, fragmentary specimen from Mexico has otherwise been identified as deinocheirid. After reconsidering the dentary characters used to differentiate the two families (ventral expansion at symphysis, length:height ratio, dorsal ridge presence, and splenial contact morphology), we find that those characters are unreliable as taxonomic indicators. Consequently, we believe that the Montanan material cannot be confidently assigned to Deinocheiridae. This does not reduce the importance of the Montanan specimen, which may represent a new ornithomimid species or else a rare, senescent growth stage of some already known form.

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## Evolution and reconstruction of the mosasaurian pelvic girdle and pelvic-axial articulation

Ilaria Paparella

Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; [ilaria.paparella@gov.ab.ca](mailto:ilaria.paparella@gov.ab.ca)

Mosasauria (dolichosaurs, aigialosaurs, mosasaurs) represent the only lineage of non-ophidian squamates to have fully adapted to an obligatory aquatic lifestyle. During the Late Cretaceous, they achieved a global distribution and evolved highly derived body plans characterized by streamlined proportions, flipper-like limbs, and a lunate tail. Research on mosasaurs tends to focus primarily on cranial anatomy, while postcranial elements are comparatively understudied. Complete, well-preserved specimens from the Late Cretaceous Bearpaw Formation of southern Alberta provide key anatomical data for reassessing the morphology and evolution of the mosasaurian pelvis, particularly in hydropelvic mosasaurids.

Mosasaurids are commonly divided into plesio pelvic and hydropelvic morphotypes. Plesio pelvic taxa retain a pelvic configuration comparable to that of terrestrial limbed squamates and basal mosasaurians (i.e., dolichosaurs and aigialosaurs), in which the ilium, ischium, and pubis are tightly articulated or fused, and the ilium bears a larger posteriorly directed process, here called the ‘sacral process’ of the ilium. In plesio pelvic forms, a distinct iliosacral joint connects the pelvis to the sacral vertebrae. In contrast, hydropelvic mosasaurs exhibit a substantially modified condition: the sacral iliac process is typically oriented dorsally-anterodorsally, and the three pelvic elements show marked differences in overall morphology and acetabular contribution. The precise nature of the pelvic attachment to the vertebral column in hydropelvic taxa remains unresolved.

Major issues complicating interpretation of pelvic–axial articulation in hydropelvic mosasaurs include: (1) the absence of clearly identifiable sacral vertebrae; (2) the lack of definitive osteological correlates, such as articular facets on the ilium or adjacent vertebrae; and (3) the absence of fossil specimens preserving unequivocal pelvic articulation. Pelvic contact has traditionally been hypothesized at the level of the first pygal vertebra, yet no specimen preserves a clear bony iliosacral joint. Moreover, pygal vertebrae do not exhibit features that unambiguously indicate sacral homology or a firm bony articulation with the ilium.

In phylogenetic analyses, orientation of the sacral iliac process is often the principal character used to diagnose the derived hydropelvic condition. A survey of pelvic variation across Squamata, however, reveals that verticalization of the iliac sacral process has evolved multiple times. Chamaeleonids provide a particularly informative comparative model: in these taxa, the iliac sacral process is elongate and vertically oriented, varying from posterodorsal to anterodorsal. Articular facets for sacral ribs are frequently restricted to the dorsal tip of the ilium, and in some species, pelvic attachment occurs largely via calcified cartilage and soft tissues (ligaments and muscles).

I propose that hydropelvic mosasaurs exhibited a comparable soft-tissue-mediated attachment between a vertically oriented iliac blade and the anterior pygal ribs. Such a configuration would account for the absence of

prominent articular facets and for the frequent postmortem disarticulation of the pelvis observed in articulated skeletons. Functionally, ventral displacement of the pelvic girdle and lateral compression of the sacro-caudal region would be consistent with an enhanced tail-driven swimming mode in which lateral undulation was concentrated in the caudal region, while the anterior trunk remained relatively rigid.

Beyond functional implications, re-examination of mosasaur pelvic anatomy is also important for phylogenetic reconstructions. Postcranial elements such as the ilium, ischium, and pubis appear to be diagnostic at least at the subfamily level. Within a phylogenetic framework, the evolution of the pelvic girdle supports multiple independent origins of hydroplastic morphotypes from plesio pelvic ancestors. Convergence toward a pelvic configuration functionally optimized for aquatic propulsion is more consistently supported in phylogenetic hypotheses than derivation from a single hydroplastic form. The mosasaur pelvis thus provides a key example of repeated evolutionary modification of the squamate body plan, balancing morphological constraints and selective pressures.

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## No metamorphosis in tetrapods across the fin-to-limb transition

Jason D. Pardo<sup>1,2</sup>, Franklin Duffy<sup>3</sup>, and Arjan Mann<sup>1</sup>

<sup>1</sup>Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL, USA; [jpardo@fieldmuseum.org](mailto:jpardo@fieldmuseum.org); [arjanm@fieldmuseum.org](mailto:arjanm@fieldmuseum.org)

<sup>2</sup>Faculty of Chemistry and Geosciences, Vilnius University, Vilnius, Lithuania

<sup>3</sup>Committee on Evolutionary Biology, University of Chicago, Chicago, IL, USA; [fduffy@uchicago.edu](mailto:fduffy@uchicago.edu)

Modern amphibian life history is characterized by a period of rapid endocrinological, morphological, and ecological change, referred to as metamorphosis. Although true metamorphosis is thought to have originated relatively late in the assembly of the lissamphibian body plan, current hypotheses propose that lissamphibian metamorphosis evolved as a condensed version of a protracted ontogenetic trajectory present in the ancestor of all tetrapods, with such a transition facilitating the water-land transition. We here report new fossils of early post-hatching stages of stem tetrapods from the Carboniferous Mazon Creek lagerstätten that challenge this framework. New fossils attributable to early post-hatching stages of an embolomere preserve a fully ossified skull and absence of external gills at the initiation of feeding, indicating an absence of a transitory larval period in tetrapods prior to the divergence of the amphibian and amniote lineages. Similar lack of transitory larval characters is observed in *Esconichthys apopyris*, here recognized as early life history stages of the megalichthyid tetrapodomorph ‘fishes,’ showing that direct development was broadly present across the fin-to-limb transition, albeit with delayed onset of ossification in megalichthyids. Early life history stages of lungfishes from the same locality demonstrate patterns of cranial ossification similar to those observed in modern *Neoceratodus*, with an absence of transient larval characteristics and apparent rapid development of the skull at least post-hatching stages, whereas coeval coelacanths have accelerated development of the skull and postcranium prior to emergence from the chorion. This broad evidence from across many sarcopterygian lineages shows that direct development from a large macrolecithic egg was the norm for Palaeozoic sarcopterygians, including the earliest tetrapods. A transient larval stage is a later innovation emerging either within the lissamphibian stem group or at the base of the tetrapod crown group. Scenarios that appeal to amphibian metamorphosis to make sense of tetrapod terrestrialization should be reconsidered.

# Taxonomic reassessment of juvenile tyrannosaurine specimens reveal large biogeographic ranges in tyrannosaurids

Gorm S. Raun<sup>1</sup>, Colton C. Coppock<sup>1</sup>, Demchig Badamgarav<sup>†,2</sup>, Khishigjav Tsogtbaatar<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; gormskou@ualberta.ca; ccoppock@ualberta.ca; pjcurrie@ualberta.ca

<sup>2</sup>Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar 15160, Mongolia; tsogtbaatar@ipg.mn

The recently named tyrannosaurid *Asiatyrannus xui*, from the Nanxiong Formation of southeastern China, bears a striking resemblance to juvenile specimens of *Tarbosaurus bataar*. Similarly, the long contested *Raptorex kriegsteini* also possesses numerous cranial morphologies that are shared with both juvenile specimens of *Tarbosaurus bataar* and *Asiatyrannus xui*. Thus, a reassessment of Asian tyrannosaurid taxa named based on material with known juvenile characteristics is warranted. Here, the taxonomic affinities of *Asiatyrannus xui* and *Raptorex kriegsteini* are reassessed based on proposed diagnostic characters. Morphological evidence suggests that both “*Asiatyrannus xui*” and “*Raptorex kriegsteini*” are likely junior synonyms of *Tarbosaurus bataar*. The referral of “*Raptorex kriegsteini*” to *Tarbosaurus bataar* is supported by the stratigraphic work of previous authors, the presence of *Tarbosaurus bataar* autapomorphies in “*Raptorex kriegsteini*”, and the widespread occurrence of previously reported *Raptorex kriegsteini* autapomorphies in specimens of *Tarbosaurus bataar*. The referral of “*Asiatyrannus xui*” to *Tarbosaurus bataar* is supported by the presence of *Tarbosaurus bataar* autapomorphies, by morphologies shared in juvenile and adolescent specimens, and by a lack of apomorphies in “*Asiatyrannus xui*” that are not present in *Tarbosaurus bataar*. The identification of a *Tarbosaurus bataar* specimen from the Nanxiong Formation of China drastically expands the known biogeographic range of the species and aligns with the reported ranges of some North American tyrannosaurids. The evidence suggests that the known ranges for many tyrannosaurids are vastly underestimated and likely rivalled ranges of modern carnivorans.

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# Testing the limits of petrosal data and their utility in resolving camelid evolutionary relationships

Selina-Viktor Robson

Veringstraße 77, 21107 Hamburg, Germany; svrobson.paleo@gmail.com

Although living camelids are native to South America (*Vicugna*, *Lama*) and Asia and Africa (*Camelus*), the family originated in North America and was confined to the continent for the first ~40 million years of its evolution. While there are only seven extant species, over 100 extinct species have been described, but most hypothesized camelid relationships have not yet been tested using modern phylogenetic methods. Recent work on perissodactyls has indicated that the internal otic region, particularly the petrosal bone, is useful for resolving within-family relationships. To test whether this is also the case for camelids, I compiled a petrosal dataset of 25 living and extinct camelid species. This dataset includes members from all extinct subfamilies and represents close

to one quarter of all camelid species. Because there was a great deal of intraspecific variation in the petrosals, I coded both a species-level and a specimen-level taxon-character matrix, both with 34 characters. The species-level matrix included the 25 camelid taxa plus the oromerycid *Eotylopus reedi* as an outgroup, and the specimen-level matrix included 41 camelid specimens plus *E. reedi*. I then conducted parsimony and Bayesian phylogenetic analysis on the datasets.

The results of my analyses suggest that, while the petrosal bone can be used to recover some important relationships, additional lines of evidence are needed. In both the specimen-level parsimony and Bayesian analyses, the subfamily Camelinae was recovered as monophyletic, but the known relationships within the subfamily based on the living taxa were not maintained. Indeed, four living species were represented by multiple specimens, and none of these species were found to be monophyletic in either analysis. Of the extinct taxa with multiple representatives, only the species *Stenomylus gracilis* was monophyletic in the parsimony analysis and only *S. gracilis* and *Camelops* sp. were monophyletic in the Bayesian analysis. For the species-level results, not only was the subfamily Camelinae recovered as monophyletic, but the genera *Camelus* and *Vicugna* were also found to be monophyletic by the parsimony analysis, and *Camelus* was monophyletic in the Bayesian analysis. *Stenomylus gracilis* and *Camelops* sp. were coded as single operational taxonomic units so their monophyly could not be tested. None of the analyses supported the currently hypothesized relationships among the extinct camelids. While this could indicate that said hypothesized relationships are incorrect, I suggest that the more likely culprit is the dataset. There are notable differences in petrosal morphology between camelines and earlier camelids, such as an enlargement of the anterior process and reduction of the subarcuate fossa, but most of the non-cameline camelids share the same character states. When differences are present, they are typically found in only one taxon or are variable within taxa. More intensive sampling of the extinct taxa may lead to better results, but based on my current dataset, some aspects of the petrosal are highly conserved while other aspects are extremely variable. Because of this, there may simply be too few characters shared by only closely related taxa to produce meaningful results and I recommend that these data are best used when combined with characters from other parts of the skeleton.

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## A reassessment of referred material supports the validity of *Dromiceiomimus brevitertius*

Declan Rourke<sup>1</sup>, Bradley McFeeters<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; drourke@ualberta.ca; pjcurrie@ualberta.ca

<sup>2</sup>Department of Earth Sciences Carleton University, Ottawa, ON, K1S 5B6, Canada; bradleymcfeeters@cmail.carleton.ca

*Dromiceiomimus* has been an important genus in our understanding of the diversity of ornithomimids in the Campanian–Maastrichtian deposits of the Horseshoe Canyon Formation of Alberta, Canada. It has been known from several partial skeletons. However, the validity of *Dromiceiomimus* has been contested for nearly half a century with some authors (Makovicky et al. 2004; Kobayashi et al. 2006; Xu et al. 2011) considering it synonymous with *Ornithomimus edmontonicus* citing a lack of morphology differences. Recent evidence has argued in favour of the validity of *Dromiceiomimus* based on a relatively complete skeleton referred to *Dromiceiomimus* (UALVP 16182) by Macdonald and Currie (2019).

Here we review all referred material to *Dromiceiomimus* to assess its validity as a taxon and potential synonymy with *Ornithomimus edmontonicus*. Based on our review of referred material, we affirm that *Dromiceiomimus* is a valid taxon. *Dromiceiomimus* can be distinguished from *Ornithomimus* and other ornithomimids by a suite of

cranial and postcranial characters. Cranial differences include different morphologies in the lacrimal, surangular, quadratojugal, and braincase. Moreover, postcranial differences are observed in the scapula and manus that can be considered reliably diagnostic. To assess the relationship of *Dromiceiomimus* to other ornithomimids we conducted a phylogenetic analysis of ornithomimosaur and ornithomimids using an updated character matrix and a variety of new taxa as operational taxonomic units. We recovered *Dromiceiomimus* in the North American ornithomimid clade closely related to *Struthiomimus altus*. The resulting tree topology also suggests a more complex evolutionary history of North American ornithomimids than previously thought. Overall, our results help add to our understanding of the diversity of ornithomimids in North America during the Late Cretaceous period.

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# Applications of reflectance transformation imaging (RTI) to insect compression fossils with implications for vertebrate specimens

Kano Sasaguchi<sup>1</sup>, John Acorn<sup>2</sup>, and Felix Sperling<sup>1</sup>

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

<sup>2</sup>Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada; jacorn@ualberta.ca

Compression fossils often preserve subtle surface topography that is difficult to interpret under conventional lighting. Fine morphological details, critical for taxonomic identification of insects, such as venation patterns, sutures, or delicate surface textures, may remain obscured in two-dimensional preservation. Reflectance Transformation Imaging (RTI) is a technique that captures multiple photographs under varying light angles and computationally models surface reflectance to produce interactive "2.5D" visualizations, plus false-color "normals" composite images. RTI enhances subtle relief and allows re-lighting of specimens with a controllable virtual light source to reveal diagnostic features. Here, we present the application of RTI to Paleocene insect compression fossils from the Paskapoo Formation of central Alberta (ca. 58 Ma). RTI has significantly improved recognition of fine morphological structures strengthening taxonomic resolution. Beyond insect material, the potential applications of RTI extend to other compression fossils common in vertebrate palaeontology. Preliminary trials demonstrate its utility in clarifying subtle bone boundaries in compression-preserved fish, highlighting feeding damage on fossil leaves, and enhancing trace features such as amphibian track impressions. RTI provides a non-destructive tool for refining morphological analysis across a wide range of fossil types. It is increasingly recognized as an adequate substitute for in-person examination of such fossils.

# Marine reptiles from Japanese Upper Cretaceous: progress in the last decade

Tamaki Sato

Faculty of Science, Kanagawa University, Yokohama, Kanagawa 221-8686, Japan; tsato@kanagawa-u.ac.jp

Fossils of various reptilian taxa have been reported from the Mesozoic marine sediments in Japan. Sato et al. (2012) provided a review of the occurrences of plesiosaurs, mosasaurs and marine turtles in Upper Cretaceous deposits of Japan and discussed their significance. More than a decade has passed since then, with new discoveries to add now to the record. This work provides a summary of the studies on marine reptiles from the Late Cretaceous of Japan after the 2012 review.

New mosasauroid taxa, i.e., the halisaurine *Phosphorosaurus ponpetelegans* Konishi et al., 2015, and the mosasaurine *Megapterygius wakayamaensis* Konishi et al., 2023, were described from the uppermost Cretaceous; the former is from the lowermost Maastrichtian of the Yezo Group in Hokkaido, and the latter near the Campanian/Maastrichtian boundary in the Sotoizumi Group in Wakayama Prefecture. Other recently reported occurrences of mosasauroid remains are mostly from the Maastrichtian. In contrast, notable findings of plesiosaurs came from the lower parts of the Upper Cretaceous. A partial skeleton of a polycotyloid, which likely represents a new taxon, and an indeterminate pliosaurid specimen were described from the Turonian of the Yezo Group (Sato et al. 2023). The earliest occurrence of an elasmosaurid in Japan came from the lower Cenomanian of the Goshoura Group in Kagoshima Prefecture (Utsunomiya 2019). *Mesodermochelys* is the most common marine turtle from the Late Cretaceous of Japan, and Jenkins et al. (2017) reported a Campanian specimen from the Yezo Group which retains boreholes and associated small molluscan shells, hinting at the presence of a chemosynthetic community.

A census study based on the collection of local Cretaceous fossil marine reptiles at the Hobetsu Museum in Hokkaido (Sekiguchi and Sato 2020) showed that remains of plesiosaurs are by far the most common in the lower Campanian and older units but none are from the younger strata from which a number of mosasauroids and marine turtle specimens have been collected. The Campanian-Maastrichtian Izumi Group, however, has yielded fragmentary plesiosaurian remains from the contemporaneous unit. There have been reports of Cretaceous marine reptiles from geological units which have no previous records, such as the Taneichi Formation (Santonian–Campanian) in Iwate Prefecture and Nakaminato Group (Campanian–Maastrichtian) in Ibaraki Prefecture (e.g., Kato et al. 2021). Sato et al. (2012) noted that the stratigraphic distribution of Japanese mosasauroids follows the pattern recognized in other parts of the world but chelonoids do not. It is expected that further specimen collection and study on marine reptiles from Japan will test whether the faunal transitions of Late Cretaceous marine reptiles in the northwestern Pacific are comparable with those in other areas such as the Western Interior Seaway.

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# Testing hypotheses of competition between gnathostomes and agnathans based on hydrodynamic performance

Bradley Scott

Department of Biological Sciences, Concordia University of Edmonton, Edmonton, AB, Canada; [bradley.scott@concordia.ab.ca](mailto:bradley.scott@concordia.ab.ca)

The transition from jawless (agnathan) to jawed (gnathostome) vertebrates is one of the most important events in the evolution of vertebrates. It occurred during the Silurian and Devonian periods. Hypotheses of how nearly all agnathans went extinct and gnathostomes dominated vertebrate faunas are highly varied: competition from gnathostomes, environmental changes, and high endemism of agnathans compared to gnathostomes, but remain largely untested. Recent morphometric comparisons have shown that, although some agnathans differ greatly in body form from gnathostomes, other agnathans overlap in morphology with gnathostome groups. This overlap is consistent with the competition hypothesis; however, for competition to be supported, the morphological similarity between taxa must also represent similarity in function, relevant to their ecology. Function was approximated based on biomechanical performance of 3D models in 3 different conditions relevant to habitat use and foraging. The 3D models were created based on measurements from whole body fossils of agnathans and gnathostomes from Silurian and Devonian periods. Effects of differences in morphology on locomotor performance were estimated using computational fluid dynamics. All models were scaled to the same standard length (100 mm) and under the same flow conditions (200 mm/s, 2 standard lengths per second). Forces on the model were simulated for three sets of flow states for each model: 1) Level drag, pitch at 0 degrees; 2) Lift-to-drag ratio, pitch up 10 degrees, and 3) Ground effect (drag at ground flow as a percentage of level drag from 1) with the ventral-most point of each model approximately 1 mm above a wall with flow velocity of zero. Hydrodynamic performance was found to differ across taxa, such that even morphologically similar taxa, like phyllolepid placoderms and heterostracans, varied in at least one of the flow states modelled here. This refutes the competition hypothesis and demonstrates a novel method for testing hypotheses of major palaeoecological transitions using fossil data.

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# The Calgary 2E mammalian local fauna: 100 years later

Craig S. Scott

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

While the remains of mammals of Paleocene age were first discovered in Canada along the Red Deer River in south central Alberta by Barnum Brown in 1910, the first Paleocene mammalian specimen to have been recognized as such—a lower second molar of the taeniolabidid multituberculate *Catopsalis*—was collected from a locality along the banks of the Elbow River in Calgary and subsequently described by Loris Russell in 1926. Though no fewer than 50 additional localities have since been discovered in Calgary and the surrounding area, documenting the remains of mammals of primarily early Paleocene age, the mammalian fauna from this site—dubbed Calgary 2E—has remained very poorly known. Collections made by the Tyrrell Museum since 2009 have significantly improved the sample, and the resulting local fauna now includes no fewer than 40 taxa. Important discoveries include new genera of eucosmodontid and taeniolabidid multituberculates, chriacid and triisodontid “condylarths”, and new species of the ptilodontid *Ptilodus* and the plesiadapiforms *Paromomys* and *Pronothodectes*. The local fauna is taxonomically diverse, but numerically poor, with many taxa known only from single specimens. The mammalian complement is distinct from other broadly coeval faunas in the region, showing closest resemblance to those from the Who Nose? and Bearspaw localities in northern Calgary, but few meaningful resemblances to those outside of southern Alberta. The age of the mammalian fauna at Calgary 2E has long been a source of debate, with estimates ranging from late Puercan (Pu3) to earliest Tiffanian (Ti1), a predicament resulting from small samples, poor age constraint, and uncertainties deriving from magnetobiostratigraphy. While several taxa in the Calgary 2E local fauna are stratigraphically long ranging and uninformative, the presence of the plesiadapid *Pronothodectes* minimally suggests a middle Torrejonian (To2) or possibly a late early Torrejonian (To1) age, despite the occurrence of taxa known from as early as the early part of the Puercan elsewhere. Mammalian local faunas in the Calgary and Cochrane areas document an important record of mammalian evolution during the early Paleocene, but the record is depauperate prior to the middle Torrejonian (To2). The Calgary 2E locality and its mammalian fauna accordingly provide a welcome new data set that will figure importantly in understanding one of the more poorly represented intervals in the early Paleocene of North America.

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## Assessing grasping ability in early bird antecedents, and implications for the origins of avian flight

Parker A. Senger and Corwin Sullivan

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; pasenger@ualberta.ca; corwin1@ualberta.ca

The evolution of powered flight in birds involved a transition from a terrestrial, cursorily adapted theropod ancestor. This required the reintegration of the forelimbs previously freed by the advent of bipedality for non-locomotor behaviors such as predation, back into the locomotory system. This transition has generally been conceptualized according to either the cursorial hypothesis, positing that ground-dwelling theropods flapped incipient wings to increase running speed or scale steeply inclined surfaces, or the arboreal hypothesis positing that small theropods used their forelimbs in an arboreal setting to climb into the canopy and glide from branch to branch. The arboreal hypothesis, but not the

cursorial one, predicts a high level of manual grasping ability in theropods closely related to birds, because of the postulated use of the forelimbs in climbing. To test whether early bird antecedents indeed passed through a locomotory stage characterized by grasping, we used ternary morphospaces to examine the proportions of the manus with a focus on the penultimate phalanges, which have been suggested to become elongate relative to the rest of the hand or foot as a means of improving grasping ability in many lizards, mammals, and birds. Our results indicate that early birds and non-avian theropods exhibit generally conservative proportions of the manual digits, with no clear trend that would indicate an increase in grasping ability preceding the transition to flight. In *Archaeopteryx*, for example, the penultimate phalanx makes up 31% and 28% of the total length of the second and third digits, respectively, and the corresponding values are 33% and 27% in the closely related *Anchiornis*. These proportions results are overall similar to those for the dromaeosaurids *Linheraptor* (34% and 32%) and *Microraptor* (27% and 21%), taxa near the transition to birds, but also resemble those for the much more phylogenetically basal *Allosaurus* (32% and 27%) and *Guanlong* (36% and 32%). However, the lack of evidence for an increase in manual grasping ability in near-avian theropods does not rule out the arboreal hypothesis of bird origins. Maniraptorans, and to some extent other theropods, plesiomorphically possessed a degree of manual grasping ability that evolved in the context of predation, which may have been sufficient for arboreal locomotion in at least a limited capacity without any marked or consistent increase in the length of the penultimate phalanges.

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## Getting our ducks in a row: scientific philosophy in hadrosaurid dinosaur character, taxon, and tree construction

Henry S. Sharpe

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9; Canada; sutherland.sharpe@gmail.com

Hadrosaurids are among the best-known non-avian dinosaur clades, with a rich but often uncritical history of phylogenetic systematic study. The vast majority of recent work concerns alpha taxonomy, with very few examinations of character construction and homology. The ever-expanding suite of hadrosaurid phylogenetic characters is saturated with spurious and undersampled ratio characters, poorly constructed characters with conflated hypotheses of homology, and duplicated characters. The phylogenetic algorithm is often used as a tool for primary homology testing, rather than for secondary homology justification.

There is a strong correlation between hypodigm skeletal completeness and distribution of apomorphic character secondary locators; species known from incomplete skeletons are judged to be distinct based on features that are not considered to be diagnostic in species known from more complete skeletons. Three case studies demonstrate that the current phylogenetic character suite does not adequately accommodate intraspecific variation, that fragmentary taxa are of limited systematic utility, and that, when combined, these factors paint an inaccurate picture of hadrosaurid evolution.

Hadrosaurid systematic studies typically follow a phenetic total evidence program to maximize phylogenetic resolution and the number of named hadrosaurid taxa, regardless of anatomical, taxonomic, or phylogenetic justifications. Suggestions are made towards a new objective of improved phylogenetic cladistic resolution based on robust terminal taxon creation and frequent homology testing, as well as efforts to constrain the rampant and confounding idiosyncratic skeletal variation in these animals.

# A specimen of *Edmontonia* with an unusual cranial pathology

Connor Sievwright and Philip J. Currie

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; sievwrig@ualberta.ca; pjcurrie@ualberta.ca

TMP 1998.074.0001 is a skull of *Edmontonia rugosidens*, collected in 1998 by the Royal Tyrrell Museum from the Dinosaur Park Formation in Alberta. The skull was found isolated and is extremely well preserved, but has gone undescribed until now. This is surprising due to the presence of a highly unusual pathology. On the parietal of the individual, a large circular impression is present just right of the midline. Roughly the size of a golf ball, this pathology appears to have been caused before death and is inconsistent with an unhealed injury. It appears as a smoothly surfaced pit (with no evidence of postmortem surface cracking or flaking) and does not pierce through into the brain case. It is not similar to any described pathologies in ankylosaurs. There is no evidence of predation, and tooth marks are entirely absent.

This pathology is possibly indicative of an unknown or undescribed form of bone disease in ankylosaurs. Pathological pitting has been seen in the skulls and osteoderms of ankylosaurs, but these are not nearly as extreme as is seen here. Similar pathologies have also been found in theropods caused by parasitic protozoans, and resemble a large hole in the skull (typically found in the maxilla). It also is potentially evidence of ontogenetically related (senescence) bone resorption, something that has been noted in ceratopsians. These typically take the form of an additional fenestrae being added to the skull, or the form of a deep impression. This unusual trend has been seen in numerous taxa of ceratopsids, and has never been noted in other groups of dinosaurs, but bears a remarkable resemblance to the pathology found in TMP 1998.074.0001.

This specimen gives a new look at pathologies in ankylosaurs, for which previous studies have been relegated primarily to the osteoderms or the pelvic and caudal vertebrae. Pathologies are an understudied aspect of dinosaur paleontology as a whole, and this description provides a new look into a previously undescribed and highly unusual example.

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# Ecological drivers of biodiversity dynamic shifts of terrestrial amniotes during the Permian-Triassic climatic crises

Tiago R. Simões<sup>1</sup>, Arielli F. Machado<sup>2,3</sup>, Shelley Wang<sup>1</sup>, Voltaire D. Paes-Neto<sup>2,3</sup>, Alexander Farnsworth<sup>4,5</sup>, Felipe L. Pinheiro<sup>2</sup>, and Stephanie E. Pierce<sup>3</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, 08544, USA

<sup>2</sup>Laboratório de Paleobiologia, Universidade Federal do Pampa, São Gabriel, Rio Grande do Sul, Brazil

<sup>3</sup>Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, 02138, USA

<sup>4</sup>School of Geographical Sciences and Cabot Institute, University of Bristol, Bristol, BS8 1SS, UK

<sup>5</sup>State Key Laboratory of Tibetan Plateau Earth System, Environment and Resources (TPESER), Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China

Understanding the impact of environmental shifts on biodiversity across broad taxonomic, geographic, and temporal scales can provide fundamental insights into the drivers for the rise and fall of clades throughout Earth's history. Crucially, they represent a unique historical perspective on how climate change-induced mass extinctions can re-shape global biodiversity dynamics—a timely issue in the face of modern anthropogenic climate change. However, the fate of terrestrial organisms, such as land amniotes, have been challenging to assess relative to marine systems because of their patchier fossil record. Here, we combine an expanded fossil occurrence dataset and recent advances in machine learning to infer diversification dynamics through time for amniotes (reptiles and synapsids) during the largest set of biotic crises of the Phanerozoic: the Permian–Triassic (P–T) mass extinction events. Further, we use ecological niche modeling based on high resolution paleoclimatic data to predict their optimal niche ranges across these events. Our results across all models provide unambiguous support for high extinction rates and a massive drop in net diversification for synapsids during the P–T. However, contrary to long-standing ideas, reptiles and temnospondyls did not undergo a global mass extinction at the end of the Permian. Instead, reptiles underwent massive taxonomic radiation, with highest net diversification rates early in the Triassic, at both regional and global levels. Ecological niche modeling corroborates these findings, indicating suitable niches for reptiles contracted later, and recovered sooner, relative to synapsids. Rate of temperature shift and seasonality were the most important factors influencing niche suitability and extinction rates for all tetrapod clades, despite their incredibly disparate body plans and physiologies, indicating these were the key environmental drivers determining clade survival and success across the successive climate crises of the P–T transition.

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# A reassessment of early Eocene equid species distribution from South Pass, Wyoming

Mikenna A. Smith and John-Paul Zonneveld

Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB, T6G 2E2, Canada; mikenna1@ualberta.ca; zonnevel@ualberta.ca

The Green River Basin area in South Pass, Wyoming, is home to a rich assemblage of taxa, including some of the earliest forms of Equidae. However, evolutionary transitions and taxonomy of these early Eocene equids remain uncertain, and the interplay between possible driving factors for these changes remains unresolved. This is in large part due to the complex nature of the bedrock, and unclear faunal transitions across the late Wasatchian (Lostcabinian [Wa7]) to earliest Bridgerian (Gardnerbuttean [Br1a]), which previous work has failed to ascertain. In order to clarify this longstanding uncertainty, species distribution across the Green River Basin must be analyzed in relation to basin-margin dynamics. Using isolated and in situ tooth specimens from the South Pass area, we assessed faunal overlap using dental morphology, and placed taxa at the lowest possible taxonomic level. Stratigraphic analysis has pinpointed a notable anachrony involving hypothesized ancestor-descent taxa, driven by the transgression and regression cycles at the basin margin. We have also determined a higher degree of species richness in ancient basin margin regions than further lowland. These results are harmonious with other taxonomic groups of the region, anachrony is being reported in other animals. Our results provide new insights into the predominant driving factors for rapid speciation at the time, and offer a framework for understanding speciation in response to environmental and geological change.

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# Taxonomic diversity and development of Late Carboniferous amphibamiforms from the Mazon Creek Lagerstätte

Cal So<sup>1</sup>, Miranda E. Montgomery<sup>1</sup>, Naiomi I. Cookson<sup>1</sup>, Jason D. Pardo<sup>1</sup>, Hillary C. Maddin<sup>2</sup>, Hans-Dieter Sues<sup>3</sup>, and Arjan Mann<sup>1</sup>

<sup>1</sup>Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL, USA

<sup>2</sup>Department of Earth Sciences, Carleton University, Ottawa, ON, K1S 5B6, Canada

<sup>3</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, USA

Living lissamphibians are diverse in their ecology and life history. The earliest anatomically modern representatives of frogs, salamanders, and caecilians all occur in the Triassic; however, there is a significant gap in our understanding of how and when these lineages diversified. Historical narratives suggest a stepwise acquisition of lissamphibian features and a protracted evolution of modern ecology from plesiomorphic Permo–Carboniferous amphibamiform relatives (i.e., temnospondyl hypothesis). Recent research instead suggests that the radiation of lissamphibian morphology and ecology occurred more rapidly and earlier than previously proposed.

*Amphibamus grandiceps* from the Mazon Creek Lagerstätte is both the oldest occurring and one of the most morphologically derived amphibamiforms. New amphibamiform specimens (at least 10), including adults and juveniles with soft tissue preservation have been assigned to *Amphibamus*, but lack of comprehensive systematic and anatomical revision of this taxon has hindered our assessment of this material. Here, we revise the anatomy of all known Mazon Creek amphibamiform specimens using comparative anatomical and phylogenetic methods,  $\mu$ CT, 3D segmentation, and SEM. We rediagnose *Amphibamus grandiceps* by the following combination of characters including bicuspid and pedicellate teeth, 20 presacral vertebrae, and a blunt snout, among other characters. Furthermore, we recognize a diverse assemblage of at least four additional taxa. Notably, this includes a new long-bodied taxon (FMNH PR 5055) with a unique count of 30 presacrals, a worm-like body, and proportionately longer limbs than *Amphibamus*; a *Platyrhinops*-like taxon (YPM 795) with 26 presacrals; and the first definitive branchiosaur from North America, *Micrerpeton caudatum* (FMNH UR 38). The numerous larval specimens allow us to identify discrete ossification patterns in *Amphibamus* life history that establishes a staging table for *Amphibamus*. Phylogenetic analysis under maximum parsimony and Bayesian inference recovered specimens in derived positions, including FMNH PR 5055 as the immediate sister taxon to Lissamphibia. This study highlights the need to revisit other Permo-Carboniferous amphibamiform assemblages as they may record further evolutionary and ecological context significant to lissamphibian origins.

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## Fossil resource management and palaeontological research permits in Canada

Daniel N. Spivak<sup>1</sup>, Scott Rufolo<sup>2</sup>, Patrick Brunette<sup>3</sup>, Kim Cloutier<sup>4</sup>, Pascale Daoust<sup>5</sup>, Tim J. Fedak<sup>6</sup>, Todd Keith<sup>7</sup>, Glen MacKay<sup>8</sup>, Leanne J. Pyle<sup>9</sup>, and Grant Zazula<sup>10</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; dan.spivak@gov.ab.ca

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

<sup>3</sup>Department of Canadian Heritage, Movable Cultural Heritage Program, Gatineau, QC, J8X 4B5, Canada; bcm-mcp@pch.gc.ca

<sup>4</sup>Heritage Conservation Branch, Ministry of Parks, Culture and Sport, Regina, SK, S4S 5W6, Canada; kim.cloutier@gov.sk.ca

<sup>5</sup>Société du patrimoine mondial Anticosti, Port-Menier, QC, G0G 2Y0, Canada; pascale.daoust@mail.mcgill.ca

<sup>6</sup>Nova Scotia Museum, Halifax, NS, BH3 3A6, Canada; tim.fedak@novascotia.ca

<sup>7</sup>Yoho National Park, Field, BC, V0A 1G0, Canada; todd.keith@pc.gc.ca

<sup>8</sup>Prince of Wales Northern Heritage Centre, Yellowknife, NT, X1A 2L9, Canada; Glen\_MacKay@gov.nt.ca

<sup>9</sup>B.C. Fossil Management Office, Heritage Branch, Victoria, BC, V8T 5J9, Canada; leanne.pyle@gov.bc.ca

<sup>10</sup>Yukon Government, Palaeontology Program, Whitehorse, YT, Y1A 2C6, Canada; grant.zazula@yukon.ca

As a large country with a diverse geology, Canada enjoys a rich fossil heritage with a long history of palaeontological discovery and research. It is therefore not surprising that the nation hosts a comparatively robust heritage management system focused on palaeontological resources. By combining legal protection, land-use planning, scientific evaluation, and intergovernmental collaboration, the country seeks to ensure that fossil resources are preserved for research, public education, and long-term stewardship. This integrated approach supports both conservation and responsible access, highlighting Canada's commitment to safeguarding its extensive fossil record for future generations. Although advanced, Canada's system for protecting fossil heritage is not highly centralized and occurs within a regulatory framework involving federal, provincial, territorial, and Indigenous authorities. The complexities can provide challenges for heritage officials, museum staff, and researchers to navigate.

Founded in 2019, The Canadian Fossil Resource Management Committee (CFRMC) was established to strengthen existing fossil-related regulation and promote greater collaboration between and integration of palaeontological resource management in the country. Consisting of fossil resource managers from jurisdictions across Canada, the CFRMC is able to work with palaeontologists and heritage officials to facilitate the approval of palaeontological field projects by connecting them with the appropriate contacts and helping to ensure that the permit application and reporting processes are completed correctly and in a timely manner.

In most jurisdictions across Canada, fossils are legally protected, with ownership most commonly defaulting to the Crown or, on Indigenous-governed land, to the respective community. This means collection of fossils typically requires permits and regulated oversight. Provincial and territorial governments administer most fossil management, with Alberta and British Columbia maintaining particularly developed systems due to their rich fossil deposits. Some modern self-government treaties, such as those in the Yukon, have given significant responsibility to Indigenous governments in the regulation of fossil research and resource management in Canada's North. At the federal level, the Department of Canadian Heritage, in conjunction with the Canadian Border Services Agency, regulates the export of controlled fossils from Canada, and Parks Canada manages fossil resources within all national parks.

To facilitate palaeontological research in Canada, we have compiled all contacts necessary for properly initiating palaeontological fieldwork across Canada and summarized steps necessary for the legal export of fossil material for study outside of the country.

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## Relocating historic dinosaur quarries in the Horseshoe Canyon Formation (Late Cretaceous, Alberta) to refine and preserve biostratigraphic data

Jordan C. Stock<sup>1</sup>, Jordan C. Mallon<sup>2</sup>, Caleb M. Brown<sup>1,3</sup>, François Therrien<sup>3</sup>, Mark J. Powers<sup>1</sup>, Colton C. Coppock<sup>1</sup>, and Philip J. Currie<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; jstock@ualberta.ca; Powers1@ualberta.ca; ccoppock@ualberta.ca; pjcurrie@ualberta.ca

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

<sup>3</sup>Royal Tyrrell Museum of Paleontology, Drumheller, AB, T0J 0Y0, Canada; Caleb.brown@gov.ab.ca; francois.therrien@gov.ab.ca

The Horseshoe Canyon Formation (HCFm) of Alberta, Canada, is famous for its extensive exposures along the Red Deer River where palaeontologists have been collecting dinosaurs for over a century. This formation preserves a long and relatively continuous terrestrial record from the late Campanian to middle Maastrichtian, an interval of limited terrestrial sampling in North America. Beginning in the late 1800s, the formation produced some of the first dinosaur discoveries in Canada, a trend that has continued to the present day. The HCFm has produced more than 100 vertebrate skulls and skeletons now housed in museums across North America. As the number of specimens grew, biostratigraphic patterns emerged, leading to the recognition of major faunal and environmental transitions through time in the HCFm. However, the exact location and stratigraphic positions of many historic dinosaur quarries have been lost over the decades, owing to imprecise field notation. Here, we present a specimen based database compiling precise (GPS) locality, collection, and stratigraphic data for associated vertebrate skeletons from the HCFm. We use original field notes, photographs, and maps, combined with in situ evidence, to relocate missing quarries and recover geographic and stratigraphic data. This database can be shared with accredit-

ed researchers actively collecting fossils from, or doing research on, the formation, ensuring that stratigraphic and locality data remain accessible and continuously updated. Together, quarry relocation and data consolidation will continue to refine current understandings of vertebrate biostratigraphy in the formation and strengthen ongoing studies of vertebrate taxonomy and palaeoecology.

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# The developmental origin of the ornithischian predentary and its derived morphology

Giles D. Suddert and Philip J. Currie

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; [suddert@ualberta.ca](mailto:suddert@ualberta.ca); [pjcurrie@ualberta.ca](mailto:pjcurrie@ualberta.ca)

One of the key diagnostic features of Ornithischia is an unpaired, anterior element of the lower jaw known as the predentary. Overlying it was a gnathotheca, the keratinous sheath of the lower beak. As an adaptation for food acquisition, the lower beak and its supporting predentary coincided with the ornithischians' herbivorous ecology. The predentary is traditionally considered a neomorphic element without a precursor observed in the fossil record. Nevertheless, recent studies have tangentially inquired as to the origin of the element, through both ontogeny and evolutionary time. Only two other lineages of vertebrates, teleost fish and early avians, possess a predentary, and variably so. The ornithischian predentary is not homologous to that of either the fish or avian taxa which bear the element, though either of these might share a similar pattern of development with the ornithischian predentary. During embryonic development, multiple tissues would have converged near the location of the predentary, including the overlying epithelium, symphyseal ligament, mentomeckelian cartilage, and dentary bone. Here, we formulate origin hypotheses that reflect each of these potential precursors.

This study analyses the ornithischian predentary through thin-section histology, alongside micro- and nano-CT scanning. The sampled predentaries, of distinct ontogenetic stages ranging from embryonic to fully mature, are compared with originally-produced sections of other osseous tissues in the ornithischian skeleton. The lack of intrinsic fibres dismisses our hypotheses of metaplastic origin within the symphyseal ligament or epithelium. Our observations through histology and CT scanning instead indicate an intramembranous origin of the predentary. The implications of this origin hypothesis support the direct comparison of the denticles of hadrosaur predentaries with those lining the jaws of pelagornithid birds. While these denticles are not homologous with pelagornithid pseudo-teeth, the growth-form hypotheses applied to pelagornithid pseudo-teeth are apt for consideration in hadrosaurs as well. Our analysis of the microstructure of hadrosaur denticles furthermore integrates our interpretations of histology with the functional morphology of that particular clade.

While the exact origin of the predentary in evolutionary time still requires further resolution, histology and microstructure analysis reveal unique details regarding the predentary's genesis in the early stages of ontogeny. Through a development-centred approach to the predentary, the unique ornithischian feeding apparatus can be further understood in a manner congruent with their paleoecology and evolutionary radiation.

# Theropod feeding traces provide insight into the taphonomy of the Danek Bonebed

Victor T. Sumka, Colton C. Coppock, Mikenna A. Smith, and Philip J. Currie

University of Alberta, Biological Sciences, Edmonton, AB, T6G 2E9, Canada; vsumka@ualberta.ca; ccoppock@ualberta.ca; mikenna1@ualberta.ca; pjcurrie@ualberta.ca

Non-avian dinosaur tooth traces provide valuable insight into both inter and intraspecific interactions, allowing for interpretations regarding the palaeobiology and palaeoecology of the presumed trace makers. In general, the homogeneity of tooth traces makes it difficult to definitively assign a tooth trace to a specific taxon without having the tooth embedded in the specimen. Bone utilization, such as gnawing, is typically associated with mammals, and is considered to be rare or potentially absent in non-avian dinosaurs. A 250 mm section of ornithischian rib, cf. *Edmontosaurus*, discovered at the Danek Bonebed in Edmonton, Alberta, preserves at least 53 identified theropod tooth traces. These tooth traces depict two trace morphologies in cross section: V-shaped and U-shaped. The distinct morphologies accompanied by a difference in trace width indicate that there were likely two distinct trace makers. An analysis of the trace morphologies along with the shed theropod teeth collected in close proximity to the specimen, determined the trace makers were likely a tyrannosaurid and a dromaeosaurid. 13 of the traces depict a wide U-shaped cross section and are presumably created by a tyrannosaurid, the other 40 traces depict the narrow V-shaped cross section, likely representing the traces left by the dromaeosaurid. The concentration of numerous tooth traces bearing similar morphologies and orientations within a relatively constrained region suggest gnawing-like behavior for the dromaeosaurid. This specimen serves to expand our understanding of scavenging behavior in Theropoda and provides insight into the palaeobiology of Dromaeosauridae and the taphonomy of the Danek Bonebed.

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# *Cryptoryctes* is a micropternodontid, but not a synonym of *Micropternodus*: new lipotyphlans from John Day Fossil Beds, Oregon

Jessica M. Theodor<sup>1</sup>, Jonathan J-M. Caledo<sup>2</sup>, Craig Scott<sup>3</sup>, and Joshua X. Samuels<sup>4</sup>

<sup>1</sup>University of Calgary, Department of Biological Sciences, Calgary, AB, T2N 1N4, Canada; jtheodor@ucalgary.ca

<sup>2</sup>University of Oregon, Department of Earth Sciences, Eugene, OR, 97403, USA; jcaledo@uoregon.edu

<sup>3</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; craig.scott@gov.ab.ca

<sup>4</sup>East Tennessee State University, Center of Excellence in Paleontology, Department of Geosciences, Johnson City, TN 37614, USA; SAMUELSJX@mail.etsu.edu

The genera *Cryptoryctes* and *Micropternodus* are lipotyphlans known from the late Eocene through the Oligocene and earliest Miocene respectively. *Cryptoryctes* has been known exclusively from isolated humeri, while *Micropternodus* is known only from cranial material, leading to the suggestion in the literature that the humeri of *Cryptoryctes* belong to *Micropternodus*, rendering it a junior synonym.

New material from the Arikareean (late Oligocene) Turtle Cove Member of the John Day Formation, Oregon, consisting of a partial associated skull and humerus of *Cryptoryctes* n. sp. (JODA 6793), and a partial skull of *Micropternodus* cf. *M. morgani* (JODA 6211), convincingly demonstrates that these taxa are indeed separate with distinct cranial and dental morphologies.

JODA 6793 (*Cryptoryctes*) displays characteristics of Micropternodontidae: a short, wide, and deep rostrum as in *M. morgani* or *M. strophensis*, a short and large infraorbital foramen, the absence of a lacrimal tubercle, and in the dentition the presence of three upper incisors, a greatly enlarged I1, the absence of a P1, a nearly triangular P3 with a reduced protocone, a submolariform P4, a p3 much larger than p2, M1-2 that are much larger than p2, and cheek teeth with strongly linguallly-slanted ectolophs. It differs from JODA 6211 (*Micropternodus*) which, like other members of Micropternodontidae, bears dilambdodont molars. JODA 6211 also differs from JODA 6793 (and other micropternodontids) in the absence of both p2 and its alveolus.

Both specimens retain partial basicrania including partial auditory bullae, bony labyrinths, and malleus and incus. The malleolar head of JODA 6211 is more inflated than JODA 6793, and both bear a very deep round fossa on the body distal to the incudal articulation, differing from the morphology of extant talpoids.

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## Dinosaur running abilities and predator-prey relationships in iconic Late Cretaceous tyrannosaur-dominated ecosystems of North America and Asia

François Therrien<sup>1,2</sup>, Jared Voris<sup>2</sup>, Kohei Tanaka<sup>3</sup>, and Darla K. Zelenitsky<sup>2</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; francois.therrien@gov.ab.ca

<sup>2</sup>Department of Earth, Energy, and Environment, University of Calgary, Calgary, AB, T2N 1N4, Canada; jared.voris@ucalgary.ca; dkzeleni@ucalgary.ca

<sup>3</sup>Faculty of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan; koheitanaka@geol.tsukuba.ac.jp

Paleontologists commonly use the proportions of hindlimb segments (i.e., tibia/femur and [metatarsus + tibia]/femur length ratios) to estimate the relative running abilities of dinosaur species. However, such proxies are rarely considered in an ecological context in combination with running speed estimates to evaluate potential predator-prey relationships within ecosystems. Here, ratios of hindlimb segments and maximum running speed estimates based on limb length and body mass were calculated for bipedal (i.e., theropods, thescelosaurids, pachycephalosaurids), facultatively bipedal (i.e., hadrosaurids), and quadrupedal (i.e., ankylosaurs, ceratopsians, and sauropods) dinosaurs from three iconic Late Cretaceous ecosystems: the late Campanian Dinosaur Park ecosystem (Alberta, Canada), the late Maastrichtian Hell Creek/Scollard ecosystem (U.S.A. and Canada), and the Maastrichtian Nemegt ecosystem (Mongolia). Comparison between these tyrannosaur-dominated ecosystems can potentially reveal similarities related to ecological niches, faunal composition, and paleoenvironmental conditions.

Dinosaurs from these formations consistently fall within four locomotor categories, based on [metatarsus + tibia]/femur length ratios: 1) alvarezsaurids, small oviraptorosaurs and hatchling tyrannosaurids are hypercursorial, 2) medium-sized oviraptorosaurs, dromaeosaurids, ornithomimids, troodontids, and immature tyrannosaurids are cursorial, 3) leptoceratopsids, pachycephalosaurs and adult tyrannosaurids are hypocursorial, and 4) ankylosaurs, ceratopsids, hadrosaurids, sauropods, therizinosaurids, and the giant ornithomimosaur *Deinocheirus* are non-cursorial. Interestingly, tyrannosaurids underwent a major decline in locomotor abilities through onto-

geny, from hypercursorial as hatchlings to subcursorial as adults, whereas those of herbivorous dinosaurs did not change through ontogeny.

Evaluating hindlimb ratios and locomotor categories against estimated maximum running speeds shows that they cannot be used as direct indicators of dinosaur running capabilities. Indeed, non-cursorial ceratopsids and hadrosaurids were as fast as hypocursorial adult tyrannosaurids, cursorial immature tyrannosaurids ran faster than hypercursorial small oviraptorosaurs, and the latter had the same running speed as cursorial dromaeosaurids and hypocursorial pachycephalosaurs. Instead, limb segment proportions are more likely indicators of the initial acceleration capacity of species, whether to initiate prey pursuit or predator evasion, rather than of their running capabilities. Ontogenetic changes in limb segment proportions and running speed in tyrannosaurids suggest adaptations to capture different prey species at different growth stages, small and rapid prey as juveniles and large and slower prey as adults, supporting the existence of an ontogenetic niche shift in these apex predators.

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## Femoral morphology and muscle moment arm estimates suggest an unusual hindlimb posture in ceratopsid dinosaurs

Brandon Theurer

Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; btheurer@ualberta.ca

Dinosaurs are generally considered to have an upright limb posture, as opposed to the sprawling posture commonly employed by extant salamanders and lizards. However, in ceratopsid dinosaurs the distal end of the femur is asymmetrical, with the lateral condyle extending farther distally than the medial condyle. Given that the proximal end of the ceratopsid tibia is essentially flat, the asymmetry of the femoral condyles seems incongruous with a vertically held limb. By contrast, the femoral condyles are more symmetrical in extant elephants and rhinoceroses, where an upright posture can be directly observed.

To explore possible articular configurations of the ceratopsid hindlimb, digital models of the hindlimb and pelvic elements of *Centrosaurus* were generated using photogrammetry. The models were scaled based on comparisons with an articulated *Centrosaurus* specimen (UALVP 55261) to minimize error from using bones from multiple individuals and were positioned using Autodesk Maya. Both an upright and a semi-sprawling posture were modeled. In the upright posture, the asymmetry of the femoral condyles created a large gap on the medial side of the knee. However, abducting the femur  $\sim 23$  degrees into a semi-sprawling posture, while leaving the crus vertical, eliminated the gap. As an additional line of evidence regarding limb posture, muscles around the hip joint were reconstructed to allow estimation of their moment arms. The reconstruction was based on preserved muscle scars and comparisons with previous reconstructions of ornithischian musculature. Moment arms for adduction are larger overall in a semi-sprawling posture. For example, the adductor moment arms for adductor 1, adductor 2, and caudofemoralis longus are 0.080, 0.109, and 0.118 respectively in the semi-sprawling posture, but only 0.040, 0.063, and 0.064 respectively in an upright posture. However, some muscles have larger retractor moment arms in an upright posture. For example, the two adductors and caudofemoralis longus have retractor moment arms of 0.270, 0.260, and 0.276 respectively in the semi-sprawling posture, but 0.275, 0.271, and 0.296 respectively in the upright posture. The differences in moment arms between the postures suggest that the muscles may have been slightly more efficient for propulsion in an upright posture, whereas in a semi-sprawling posture the muscles would be more efficient at resisting gravity. The full implications of the moment arm differences for ceratopsid posture are still being evaluated.

Evidence for a semi-sprawling posture in the ceratopsid hindlimb is particularly intriguing as a semi-sprawling posture has been repeatedly proposed for the ceratopsid forelimb and suggests that ceratopsid posture may have been even more unusual than previously thought.

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# Re-evaluation of megaherbivore faunal turnover in the Dinosaur Park Formation, Alberta using a newly resolved biostratigraphic framework

Mira Thompson<sup>1</sup>, Kirstin Brink<sup>1</sup>, Caleb Brown<sup>1,2</sup>, and Paul Durkin<sup>1</sup>

<sup>1</sup>Department of Earth Sciences, University of Manitoba Clayton H. Riddell Faculty of Environment Earth and Resources, Winnipeg, MB, Canada

<sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada

Biostratigraphic research in the Campanian Dinosaur Park Formation (DPF) in Dinosaur Provincial Park (DPP), Alberta has focused on megaherbivore dinosaur fossil assemblages, which appear to differ between lower and higher strata. This biostratigraphic shift indicates a faunal turnover occurred in megaherbivore communities in the DPF environment through time. However, despite over a century of work in DPP, the exact timing and cause of this faunal turnover remains unclear. This uncertainty is produced by the highly variable nature of DPF strata, which are composed of fluvial sandstones and floodplain mudstones with uneven thickness and horizontal extent due to erosion, lateral accretion, and localized deposition. Thus, a stratigraphic framework based on marker beds with known ages and detailed fluvial stratigraphic observations is necessary to resolve issues regarding dinosaur biostratigraphy in the DPF.

Recent geochronological and geochemical research on DPF bentonites has allowed for aging and initial correlation of the Plateau Tuff bentonite (PT;  $75.639 \pm 0.025$  Ma) in DPP. Using field observations, geochemical fingerprinting, orthomosaic aerial photography, elevation data, and structure-from-motion drone photogrammetry, we further correlate the PT across DPP, allowing for its use as a radiometrically dated marker bed. To test the utility of the PT as a marker bed, we focus on several megaherbivorous dinosaur fossil sites preserved in channel-belt sandstone deposits located near outcrops of the PT. We employed detailed stratigraphic sections taken in the field and digital stratigraphic sections from drone-based outcrop models to determine the boundaries of individual channel-belt deposits and stratigraphic position of fossil quarries. Comparison of the traditional method of elevation relative to the Oldman Formation contact to the methods done in this study demonstrate that many dinosaur fossil sites are considerably different age than that suggested by use of strict elevation-based measurement. We produce a biostratigraphic succession that is a significant departure from previous DPF biostratigraphic studies. Our results demonstrate that several species of megaherbivorous dinosaur that were previously thought to live at different times coexisted for at least a part of their evolutionary history. This has substantial implications regarding evolutionary hypotheses, such as anagenesis or cladogenesis, in dinosaur lineages. Additionally, we observe a significant decline in megaherbivore species in strata younger than the PT compared to strata older than the PT. Our work ultimately demonstrates that age constraints and careful, detailed analysis and understanding of fluvial stratigraphic architecture are necessary to place fossils preserved in fluvial deposits into an accurate stratigraphic context.

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# New perspectives on the origins and evolution of Eutyranosauria (Theropoda: Tyrannosauroidae)

Jared T. Voris

Department of Earth, Energy, and Environment, University of Calgary, Calgary, AB, T2N 1N4, Canada; Jared.voris@ucalgary.ca

During the last 20 million years of the Cretaceous, tyrannosauroids occupied the terrestrial apex predator niche in North America and Asia, through the radiation of the clade Eutyranosauria. After more than a century of fossil discoveries and hundreds of specimens recovered, eutyranosaurians have become one of the best-sampled groups of non-avian theropod dinosaurs, which has allowed a thorough assessment of their phylogenetic interrelationships. Although several hypotheses of eutyranosaurian interrelationships have been previously proposed, the character datasets use numerous non-independent cranial and postcranial characters linked to allometry (gracile vs. robust) and do not sufficiently sample clade-specific synapomorphies, which resulted in an abundance of homoplasy that artificially “pull” distantly related taxa close together. This problem is exemplified by the recovery of juvenile specimens of late diverging taxa into early diverging positions as well as in the recovery of gracile but clearly eutyranosaurian taxa (e.g., Alioramini) closer to gracile basal non-eutyranosaurian tyrannosauroids.

To resolve such issues, a new phylogenetic dataset was constructed for Tyrannosauroidae based on extensive first-hand examination of nearly all eutyranosaurian taxa and of a new early Late Cretaceous tyrannosauroid from Mongolia, *Khankhuuluu mongoliensis*. Phylogenetic analysis of the new dataset recovers *Khankhuuluu* as the sister taxon to Eutyranosauria and novelly recovers a strongly supported sister taxon relationship between the giant, hyper-robust Tyrannosaurini (*Tyrannosaurus*, *Tarbosaurus*, and *Zuchentyrannus*) and the small, gracile Alioramini (*Alioramus* and *Qianzhousaurus*) as late diverging tyrannosaurine tyrannosauroids. Divergence time and biogeographic ancestral state estimations, taking into consideration both stratigraphic and phylogenetic uncertainties, support a novel evolutionary scenario for tyrannosauroids. The clade Eutyranosauria originated after the dispersal of mid-sized tyrannosauroids, like *Khankhuuluu*, from Asia into North America at ~86 Ma and remained an exclusively North American clade early in its evolutionary history. Early eutyranosaurian evolution was heavily influenced by peramorphic heterochrony. At ~79 Ma, a late-diverging eutyranosaurian lineage dispersed from North America back to Asia, where it gave rise to the clades Alioramini and Tyrannosaurini through divergent heterochronic processes: Alioramini retained several juvenile eutyranosaurian features into adulthood (e.g., small size, shallow skulls, narrow teeth) via paedomorphosis, whereas Tyrannosaurini developed exaggerated morphologies (e.g., giant size, hyper-inflated paranasal sinuses, conical teeth) via peramorphosis. Finally, the dispersal of a tyrannosaurin in the latest Cretaceous (around 73-67 Ma) from Asia to North America resulted in the establishment of *Tyrannosaurus rex* in North America. Our results resolve issues with previous eutyranosaurian phylogenetic analyses and present a cohesive, statistically well-supported scenario for the evolutionary history of Eutyranosauria.

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# The Morrin Bridge fossil flora: vegetation and palaeoclimate of the Upper Cretaceous Horseshoe Canyon Formation, Alberta

Christopher K. West<sup>1</sup>, Katharina Halbwidl<sup>2</sup>, Leyla J. Seyfullah<sup>2</sup>, Tammo Reichgelt<sup>3</sup>, and David R. Greenwood<sup>4</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; Christopher.West@gov.ab.ca

<sup>2</sup>Department of Palaeontology, University of Vienna, 1090 Vienna, Austria

<sup>3</sup>Department of Earth Sciences, University of Connecticut, Storrs, CT, 06269, USA

<sup>4</sup>Biology Department, Brandon University, Brandon, MB, R7A 6A9, Canada

The Horseshoe Canyon Formation of southern Alberta preserves abundant plant fossils from the upper Campanian to lower Maastrichtian, but its macroflora is taxonomically outdated and underutilized for palaeoclimatic reconstruction. Fifty-eight plant taxa are documented from the Morrin Bridge locality in the lower Maastrichtian Horsethief Member. The assemblage comprises diverse gymnosperms, particularly Cupressaceae, alongside cycadophytes and ginkgophytes, rare ferns, and diverse angiosperms, including Platanaceae, Cercidiphyllaceae, Trochodendraceae, Betulaceae, multiple indeterminate dicots, and two monocots. Leaf physiognomic palaeoclimate analyses and closest climatic analogue comparison reveal a temperate oceanic to warm-summer humid continental climate situated near marine influences. Net primary productivity estimates are consistent with a temperate seasonal forest or woodland/shrubland biome. Collectively, these results indicate a warm-temperate, humid climate characterized by moderate thermal seasonality and limited precipitation seasonality, consistent with conifer-dominated temperate floodplain forests with a diverse angiosperm component. The climatic reconstructions align with palaeosol and sedimentological evidence for saturated floodplain environments transitioning toward thicker and more frequent palaeochannels, reflecting enhanced fluvial activity and an intensified hydrological regime. This assemblage provides an important baseline for refining regional palaeoecological reconstructions of Late Cretaceous vegetation in Alberta in the lead-up to the K–Pg extinction and offers environmental context for interpreting dinosaur palaeoecology within the Horseshoe Canyon ecosystem.

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## New insights into the early evolution of parvipelvian ichthyosaurs based on undescribed material from the Pardonet Formation (Upper Triassic) of British Columbia

Andrzej S. Wolniewicz<sup>1</sup> and Ilaria Paparella<sup>2</sup>

<sup>1</sup>Institute of Paleobiology, Polish Academy of Sciences, 00-818 Warsaw, Poland; wolniewicz@twarda.pan.pl

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

Ichthyosaurs were a successful clade of Mesozoic marine reptiles that likely originated in the aftermath of the Permian–Triassic Mass Extinction Event (ca. 252 Ma). A major evolutionary transition in ichthyosaurs occurred in the Norian (Late Triassic, ca. 225 Ma) with the emergence of Parvipelvina, a clade characterized by a stream-

lined, ‘fish-shaped’ body plan adapted for efficient thunniform locomotion. Parvipelvians were the only group of ichthyosaurs to survive the Triassic–Jurassic Mass Extinction Event (ca. 201 Ma) and are thought to have undergone adaptive radiation in the Early Jurassic. However, it remains unclear whether this apparent diversification reflects a true evolutionary event or is merely an artefact arising from incomplete sampling of the Norian–Rhaetian (latest Triassic) marine fossil record. Despite their abundance in the Early Jurassic, ichthyosaurs from the Norian–Rhaetian are known from only a few localities worldwide and are represented largely by incomplete material, hindering our knowledge of their anatomy, taxonomy, and ecology. The Pardonet Formation of British Columbia, Canada, preserves the only Norian ichthyosaur fauna in the world represented by relatively complete specimens and is therefore crucial for understanding early parvipelvic evolution during the Triassic. Here, we present preliminary results from an investigation of an undescribed collection of ichthyosaur specimens housed at the Royal Tyrrell Museum of Palaeontology in Drumheller, Alberta, collected from Pardonet Formation outcrops in British Columbia between 1983 and 2003 by teams led by Betsy Nicholls. This material includes several parvipelvic ichthyosaur specimens and has the potential to significantly enhance our understanding of ichthyosaur evolution in the Norian.

## Cretaceous leftovers: behavioural implications of theropod tooth marks on hadrosaurid cranial elements from the Late Cretaceous of western North America

Taia C.A. Wyenberg-Henzler<sup>1</sup>, Jack Milligan<sup>1</sup>, Michael Willis<sup>2</sup>, Caleb Brown<sup>1,3,4</sup>, Darren H. Tanke<sup>3</sup>, Phil R. Bell<sup>5</sup>, Nicolás E. Campione<sup>5</sup>, Emily Bamforth<sup>1,6</sup>, Jackson Sweder<sup>6</sup>, and Corwin Sullivan<sup>1,6</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada; wyenberg@ualberta.ca; jmillig1@ualberta.ca; corwin1@ualberta.ca

<sup>2</sup>Western Australian Organic and Isotope Geochemistry Centre, School of Earth and Planetary Sciences, Curtin University, Bentley, WA 6102, Australia; 23816248@student.curtin.edu.au

<sup>3</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, AB, T0J 0Y0, Canada; caleb.brown@gov.ab.ca; Darren.Tanke@gov.ab.ca

<sup>4</sup>Department of Earth Science, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada

<sup>5</sup>Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia; ncampion@une.edu.au; pbell@une.edu.au

<sup>6</sup>Philip J. Currie Dinosaur Museum, Wembley, AB, T0H 0C0, Canada; curator@dinomuseum.ca; jsweder@dinomuseum.ca

Although tooth marks on fossil bones have been studied for decades, the specific behaviours involved in the formation of these features are still poorly understood. Tooth marks resulting from feeding should logically be concentrated on high-economy elements, defined as those associated with the most amount of edible soft tissue. However, a standardized methodology for assessing this pattern currently does not exist in the literature. Here, we conduct the first large-scale composite mapping survey of tooth marks left by carnivores on the skulls of hadrosaurid dinosaurs and associate these behaviours with potential tracemakers. To demonstrate the utility of this workflow, we apply it to a survey of 265 tooth marks across 58 hadrosaurid cranial elements representing 46 individuals recovered from Late Cretaceous formations across western North America. For each specimen, we created simple line drawings (‘mark maps’) visualizing the approximate locations of the tooth marks on each element.

Individual mark maps were then isometrically scaled and overlain onto line drawings of articulated hadrosaurid skulls to produce composite mark maps. We added polygons to the maps approximating the major jaw adductor muscles which likely accounted for most of the edible soft tissue of the head.

As expected, many of the tooth marks were concentrated in regions associated with the musculature, particularly the lateral surfaces of jugals and dentaries. However, tooth marks also occurred in locations farther from the adductor muscles, including the lateral surface of the snout, the anterior part of the maxilla, and the ventromedial and ventrolateral margins of the mandible. The positions and orientations of these more distant marks suggest that they were inflicted during the consumption of other soft tissues, such as the tongue, or during attempts to manipulate the skull while feeding. Numerous skulls remained at least partially intact even when tooth marks were present and/or many elements on one side of the face were missing. Many of these relatively intact skulls presumably had not been fully consumed by carnivores, and some may have had skin in place on one side of the head at the time of burial.

Carcass utilization sequences of modern carnivores often begin with the most easily accessed, high-economy regions of the body such as the internal abdominal organs, and progress towards regions that are harder to access and/or offer lower yields such as the skull. When the skulls in our dataset are considered in decreasing order of completeness, the distribution of tooth marks generally follows this expected trend, with the more complete and presumably less heavily utilized skulls tend to show marks only in high-economy regions. Furthermore, many of the tooth-marked skulls lack associated postcrania, possibly indicating that the tracemakers usually fed on cranial tissues only after the postcranium had been largely dismantled. Comparatively wide spacing among marks that appear to have been inflicted by adjacent teeth during single bites suggests tyrannosaurids were predominantly responsible for producing the tooth marks in our dataset, because other, smaller theropods present in Campanian–Maastrichtian Laramidia had much more closely spaced teeth than the spacing data indicate. Two specimens bear tooth marks that could have been inflicted by dromaeosaurids, but in these cases the mark spacing also overlaps with that expected for smaller tyrannosaurids (tooth row length  $\leq 240$  mm). These results suggest that mark spacing is only useful for broadly approximating the size of the tracemaker and the use of mark spacing for tracemaker identification should be done with caution. Even with limited ability to discern tracemaker size, tooth spacing suggests that tyrannosaurids with tooth row lengths greater than 240 mm were responsible for most of the tooth marks observed on hadrosaurid skulls and likely exhibited similar carcass utilization patterns to modern carnivores.

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## Tale of the tail: tooth marked caudal vertebrae suggest tyrannosaurs systematically processed hadrosaur tails

Taia Wyenberg-Henzler<sup>1</sup> and Darren H. Tanke<sup>2</sup>

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

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

The recognition of large-scale patterns in dinosaur behavior has been limited due to issues pertaining to specimen collection and/or a general lack of large-scale surveys involving multiple specimens. This is true for many fossiliferous formations, even the Dinosaur Park Formation in Dinosaur Provincial Park, Alberta. Although multiple areas of research have been hindered by this relatively limited line of inquiry, tooth mark research is one area that has perhaps suffered the most. Despite early recognition in 1913, expeditions have only begun specifically collecting tooth marked specimens for the last 40 years and tooth marked specimens have only started to receive the interest of researchers since the middle 1990s even though tooth marks are one of the few fields of vertebrate

paleontology where researchers are able to amass relatively large datasets. Within the Royal Tyrrell Museum of Palaeontology (TMP) collections alone, over 1000 dinosaur specimens are registered as having tooth marks. Yet, there is relatively little literature that makes use of many of these specimens. To begin filling this gap, we present a survey of 37 tooth marked sub-adult and adult hadrosaurid vertebral elements from the Late Cretaceous of Alberta. Of these, 26 elements are from the Dinosaur Park Formation in Dinosaur Provincial Park. Tooth marks are relatively restricted to the lateral surfaces of neural spines and centra and are generally oriented at an angle to the long axis of the vertebral column. Across the tail, the average number of tooth marks per element exhibit a parabolic increase and decrease antero-posteriorly and appear to correspond to changes in the relative amount of flesh surrounding the vertebrae. Together, these results suggest Cretaceous carnivores may have been systematically targeting the musculature surrounding the vertebrae while avoiding the complex latticework of ossified tendons present in hadrosaurids in the lateral to the neural spines on the proximal half of the tail. Because these results are amassed across numerous hadrosaurid specimens and presumably many individuals through time, this points to a more generalized pattern of feeding behavior than is typically documented in the literature and highlights the need for future large-scale studies.

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## Stable isotopes from tooth enamel provide novel implications for Late Cretaceous tyrannosaurid ecology

Gianni Zambonin<sup>1</sup>, Thomas Cullen<sup>1,2</sup>, Jordan Mallon<sup>1,3</sup>, and Hillary Maddin<sup>1</sup>

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

<sup>2</sup>Auburn University Department of Geosciences, Auburn, AL, 36849, USA; tmc0093@auburn.edu

<sup>3</sup>Beaty Centre for Species Discovery and Palaeobiology Section, Canadian Museum of Nature; Ottawa, ON, K1P 6P4, Canada; JMallon@nature.ca

Tyrannosaurids are one of the most popular and extensively researched taxa within paleontology. However, their home ranges (the geographical spaces individuals occupy within their lifetimes) are still unknown. The fossil record leaves gaps in our knowledge of dinosaur home ranges because individual body fossils are static and do not singly reflect spatiotemporal patterns. Despite this limitation, stable isotopes preserved in tooth enamel can provide unique insight into dinosaur life history.  $^{87}\text{Sr}/^{86}\text{Sr}$  from bioapatite can be used to reconstruct an individual's geographical movements, providing some insight into the individual's home range.  $\delta^{18}\text{O}$  intra-tooth variation can offer further ecological understanding, potentially linking geographical movement to seasonal changes. Based on standard allometric relationships, we hypothesize that large tyrannosaurids inhabited large home ranges. From this, we predict to see varying  $^{87}\text{Sr}/^{86}\text{Sr}$  values from geographically distinct areas both within and between teeth. To test this, we serially sampled the enamel from five adult Late Cretaceous tyrannosaurid teeth from Dinosaur Provincial Park (DPP), Alberta, for  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{18}\text{O}$ . Four teeth were vertically sampled at five sites, and one at seven, representing around a year of tooth formation for each tooth, assuming an enamel growth rate of 5 cm/year. The strontium data produced diverse  $^{87}\text{Sr}/^{86}\text{Sr}$  ranges; whereas some individuals showed minimal variation (0.706508-0.706532), others varied widely (0.706557-0.707172). In multiple instances, individuals exhibit  $^{87}\text{Sr}/^{86}\text{Sr}$  values consistent with those of contemporaneous localities up to ~200 km away from DPP. Interestingly, most individuals show fairly stable  $^{87}\text{Sr}/^{86}\text{Sr}$  values throughout tooth formation, which may indicate that movement between localities was sporadic rather than within one year of tooth growth. Across all samples,  $^{87}\text{Sr}/^{86}\text{Sr}$  data are consistent with, but also exceed, data reported for hadrosaurs known to be moving at least 80 km away

from DPP. Together, these results support our hypothesis that tyrannosaurids inhabited large geographic areas, suggesting intermittent movement of up to ~200 km between neighbouring localities and DPP. Resulting  $\delta^{18}\text{O}$  values are congruent with previously collected  $\delta^{18}\text{O}$  values from Late Cretaceous tyrannosaurid teeth. However, our  $\delta^{18}\text{O}$  data do not show consistent changes associated with  $^{87}\text{Sr}/^{86}\text{Sr}$  data, suggesting that movement is independent of seasonal changes. Overall,  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{18}\text{O}$  data support that tyrannosaurids occupied large home ranges, but attribute movement between localities to sporadic behaviour rather than association with seasonality. Therefore, this results in a deeper understanding of tyrannosaurid ecology and effectively helps to decrease a knowledge gap in the field of paleontology.

## Tooth-like dermal structures in osteostracans and implications for the origin of vertebrate teeth

Jad Zouein and Bradley Scott

Department of Biology, Concordia University of Edmonton, Edmonton, AB, Canada; jzouein@student.concordia.ab.ca, bradley.scott@concordia.ab.ca.

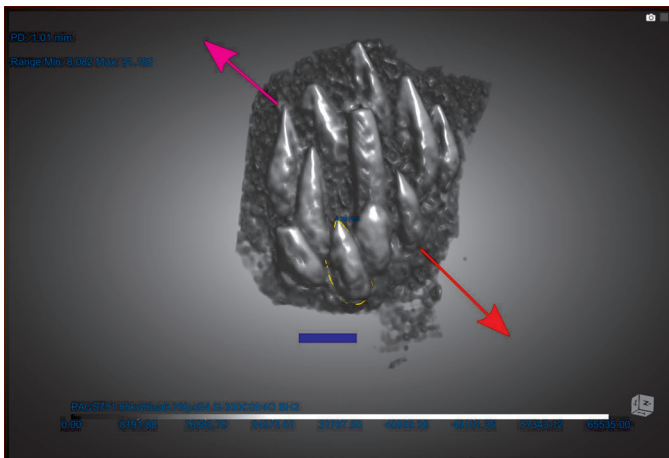
The evolutionary origin of vertebrate teeth has been a subject of long-standing debate among paleontologists, with two main hypotheses being debated. The traditional outside-in theory suggests that teeth evolved from external dermal denticles, which initially formed on the body surface and were later incorporated into the oral cavity, whereas the inside-out theory suggests that teeth originated internally within endodermal pharyngeal tissues and, over time, spread to the jaws (Rücklin and Donoghue 2016, 2019). Osteostracans are extinct jawless vertebrates from the Silurian and Devonian periods that are ideal for testing hypotheses of the origins of vertebrate teeth because they are the jawless vertebrates most closely related to jawed vertebrates (Sansom 2009; Scott and Wilson 2015).

Some specimens from the Man On The Hill (MOTH) locality, Northwest Territories, have tooth-like structures on their dermoskeleton (e.g., Fig. 1), but the histology of these osteostracans has not been well studied (Scott and Wilson 2015). The tooth-like dermal structures of osteostracans exhibit morphological features comparable to early gnathostome odontodes (Sire et al. 2009). We explored whether these tooth-like projections exhibit morphological similarities to teeth in jawed vertebrates. A detailed histological analysis of their tooth-like structures provides critical insight into whether these features represent homologous precursors to true teeth or independently evolved dermal specializations.

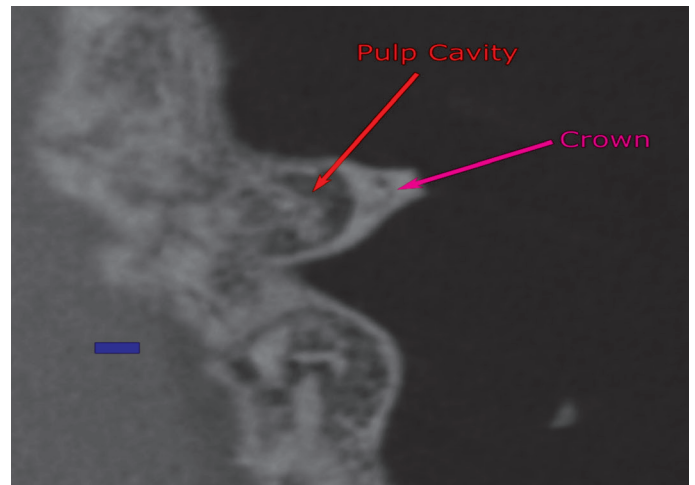
The main objective of this study is to document the histological features (tooth-like projections) of osteostracan scales using CT scans, thereby addressing a key knowledge gap by determining whether osteostracan denticles provide evidence linking dermal denticles to true teeth.

Osteostracan specimens were selected primarily based on preservation quality, with a priority given to dermal scales that exhibit tooth-like structure. Specimens are from MOTH and are housed at the University of Alberta Laboratory of Vertebrate Palaeontology (UALVP 32408, 43640, and UALVP 43641). High-resolution CT scanning was conducted at the Permafrost Archives Science Laboratory, providing 3D visualization of internal tissue architecture without damaging the fossils. CT data was analyzed at Concordia University Edmonton, using Dragonfly 3D to identify features found in the structures scanned.

Tissues of toothlike projections, such as those of *Dentapelta* (Fig. 2), are compared with other published histologies from other osteostracans, placoderms, and other early gnathostomes, especially focusing on the possible presence of pulp cavities, a key feature of odontodes.



**Figure 1.** Three-dimensional image of an osteostracan dermal tooth-like projection digitally isolated from surrounding dermal bone using Dragonfly imaging software (UALVP 43641).



**Figure 2.** Virtual cross-section through a tooth-like projection in a *Dentapelta* osteostracan specimen, revealing internal anatomy and morphology (UALVP 32408).

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