



# 7TH BIENNIAL SYMPOSIUM

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## Host Committee

University of Alberta Palaeontological Society

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# Abstracts

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## Snails on acid: Effects of ocean acidification and fear on gastropod shell defenses

Kristina M. Barclay<sup>1</sup>, Brian Gaylord<sup>2</sup>, Brittany M. Jellison<sup>2</sup>, Priya Shukla<sup>2</sup>, Eric Sanford<sup>2</sup>, Lindsey R. Leighton<sup>1</sup>

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

<sup>2</sup>UC Davis, Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA, USA, 94923-0247; bpgaylord@ucdavis.edu; bmjellison@ucdavis.edu; prishukla.sci@gmail.com; edsanford@ucdavis.edu

Ocean acidification (OA), caused by human-induced carbon dioxide emissions, has negative consequences for many organisms, yet it is unclear how biotic interactions or ecosystems may be affected by OA. For example, many organisms use calcified hard skeletons to provide protection from shell-crushing predators such as crabs, yet OA can hamper calcification. Here we test the effects of both OA and predation cues on shell growth and strength in two common intertidal snails from the northeastern Pacific, *Tegula funebris* (the black turban snail) and *Nucella ostrina* (the striped dogwhelk). Both gastropods live in the same habitat and are consumed by the same predators, including crabs, yet have different trophic roles (herbivore and predator, respectively), as well as distinct shell shapes and compositions. We grew 160 specimens of each gastropod species for 185 days under one of 4 water treatments: 1) ambient pH, no predator cue; 2) ambient pH, cue present; 3) low pH, no predator cue; 4) low pH, cue present. Shell growth and strength were then measured as a proxy for vulnerability to crab predation. *Tegula funebris* shell growth was greatly affected by both OA and predation, with controls growing 786% more than those exposed to low pH and predator cues ( $p < 0.0001$ ). Shell strength of *T. funebris* was also compromised by OA, with shells grown under low pH failing at forces 50% less than controls ( $p < 0.0001$ ). In contrast, shell growth of *N. ostrina* was only affected by predation cue, with individuals exposed to cue growing 150% less than non-cue specimens ( $p < 0.0001$ ). However, shell strength of *N. ostrina* was 9% weaker under low pH conditions ( $p = 0.0175$ ), indicating OA may compromise shells, even if growth appears unaffected. Our results suggest that OA will negatively affect predator-prey relationships by decreasing growth and/or strength of shells. These results may then be used to interpret how the fossil ancestors of both gastropods have been affected by both human-induced, and deep time OA events. Such multidisciplinary studies can be used to provide immediate value for conservation efforts, and promote the usefulness of the fossil record to conservationists.

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# Patterns of extirpation prior to the Last Glacial Maximum in Alberta, Canada: Bayesian analysis of radiocarbon data of six genera of mammals and one genus of coniferous evergreen

Christina I. Barrón-Ortiz, Christopher N. Jass, and Matthew S. Bolton

Royal Alberta Museum, 9810 – 103A Ave., Edmonton, AB, Canada T5J 0G2; christina.barron-ortiz@gov.ab.ca; chris.jass@gov.ab.ca; matthew.bolton@gov.ab.ca

Throughout most of the Pleistocene, regions of western Canada acted as a passageway between Beringia and unglaciated areas of the North American mid-continent. Geological and paleontological evidence indicates that this passageway was closed during the Last Glacial Maximum (LGM; ca. 24,000 to 18,000 calendar-equivalent years before present [cal yrs BP]) as a result of the coalescence of the Laurentide and Cordilleran ice sheets over much of western Canada (e.g., Burns 1996; Dyke et al. 2003; Heintzman et al. 2016; Young et al. 1994). This geologic event resulted in the eradication of animal and plant populations over the glaciated area. Exactly how individual species and populations in this region responded to environmental changes leading up to the LGM is currently unclear. In this study, we used new and previously published radiocarbon data to provide insights into the timing of pre-LGM animal and plant extirpation in Alberta.

Using Bayesian modeling techniques implemented in the software OxCal 4.3, we estimated timing of pre-LGM extirpation using radiocarbon data for six mammalian taxa (*Equus* spp., *Bison* spp., *Mammuthus* spp., *Mammot americanum*, *Megalonyx jeffersonii*, and *Cynomys niobrarius churcherii*; n = 36) and one genus of coniferous evergreen (*Picea* spp.; n = 6). A combined analysis of all taxa and dates of specimens identified as Proboscidea indeterminate (n = 10) was also performed.

Although the sample size for some taxa is low, our results indicate that *Mammot americanum*, *Megalonyx jeffersonii*, and *Picea* spp. may have disappeared from Alberta by ca. 35,000 cal yrs BP, prior to the onset of the LGM. The apparent disappearance of *Mammot americanum* well before the LGM is comparable to patterns observed in Beringia (Zazula et al., 2014). These lines of evidence suggest that Alberta experienced an environmental shift to more open habitats prior to the coalescence of the ice sheets. The results for the remaining species suggest that they survived until ca. 25,000 cal yrs BP. An additional analysis combining the radiocarbon data of all seven taxa as well as data for ten specimens identified as Proboscidea indeterminate (n = 52) provides a more precise estimate for the timing of animal and plant extirpation prior to the LGM, yielding a median date of 25,438 cal yrs BP. After this time there is a hiatus in the fossil record of Alberta (Burns, 1996), which is interpreted to indicate either the presence of continental ice sheets or a landscape rendered uninhabitable due to the proximity of ice.

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## Riparian macrofossil record as a means to quantitatively reconstruct regional Holocene climate trends

Matthew S. Bolton, and Alwynne B. Beaudoin

Royal Alberta Museum, 9810 103a Ave NW, Edmonton, AB T5J 0G2; Matthew.Bolton@gov.ab.ca; Alwynne.Beaudoin@gov.ab.ca

Following the considerable flooding that occurred in southwestern Alberta in spring 2013, the Archaeological Survey of Alberta initiated a multidisciplinary project to assess, record, and study archaeological sites along the banks of impacted streams. As part of this project, consultants also recorded postglacial palaeontological and palaeoecological sites. This project achieved not only the assessment of erosion damage to previously-known historic resources but also the documentation and collection of new information from previously undocumented sites. Site documentation included recording their depth, stratigraphy, and lateral extent and collection of Quaternary palaeontological material, especially where loss from further erosion was impending. One major part of this effort was the collection of palaeoenvironmental samples from macrofossil-rich strata. These samples, ranging in age from the end of the Pleistocene, throughout the Holocene, to nearly the present, contained seeds and shells buried in alluvial sediments. Because the presences and abundances of certain taxa in the macrofossil record indicate specific environmental conditions from when the organisms lived, palaeoenvironmental researchers can use macrofossil assemblages to reconstruct environments of the past.

In total, consultants collected 36 macrofossil samples from 25 localities along the banks of the Highwood and Kananaskis rivers and Tongue and Jumpingpound creeks, all part of the Bow River watershed. Staff at the Royal Alberta Museum's Quaternary Environments laboratory processed the samples to extract the macrofossils. The samples were grouped into six age-classes, adding the temporal dimension to the analysis. Given the unique shared spatial and depositional contexts of the samples, a distinct palaeoclimatic pattern was discerned from the disparate samples whose biological composition, and thus the climate signal encoded therein, varied over time.

This study's full methods and results are described in Bolton and Beaudoin (2017), while this short note explains its conceptual framework and key findings. Specimens recovered during this study are now accessioned into the Royal Alberta Museum's collections, where they are available for further research. The Quaternary Environments collection includes a large assemblage of macrofossils, pollen, and other fossils from palaeoenvironmental studies across Alberta, supported by modern and fossil reference material (seeds, molluscs, and pollen). Reference material from the collection was used to confirm most taxonomic assignments in this study.

Particular to late Quaternary palaeoenvironmental and palaeontological studies is the ability to use the distribution of extant taxa to make inferences about those same taxa and the environments they lived in long ago. It is the application of this principal, using what we know about the present to inform us of the past, which allowed us to numerically reconstruct Holocene climatic conditions based on the macrofossil record. Using the present distribution of taxa in conjunction with climate data (e.g., temperature and precipitation), various models can be employed to model each taxon's capacity to succeed in response to environmental gradients. This type of model is known as a "species response curve" (SRC), and is often unimodal, approaching the Gaussian (normal) distribution (Ter Braak and Looman 1986; Horsák 2006). The relative importance of environmental factors in deter-

mining the realized niches (and the SRCs) of taxa can also be modelled. As a simple example, we can gauge what percentage of the ecological niche for a taxon is determined by temperature compared to precipitation (assuming those two variables wholly comprise the niche). For this study, global occurrence data of 15 taxa commonly found in the samples were used in conjunction with climate data to model the environmental niche (e.g., optimum conditions from SRCs and relative contribution of two factors: mean annual temperature and total cumulative precipitation) using a maximum entropy modelling structure (MAXENT, Phillips et al. 2006).

The results of the niche modelling were combined with the relative abundances of indicator taxa per age-class from the macrofossil assemblages using a dual-layered weighted calibration function. In essence, this method weighted each taxon's climatic optima with the relative macrofossil recovery of each taxon (a proxy for actual productivity) and the modelled contribution of each parameter to the realized niche (see Bolton and Beaudoin 2017 for details). The results were point estimates for site-specific annual temperature and precipitation for discrete postglacial time intervals.

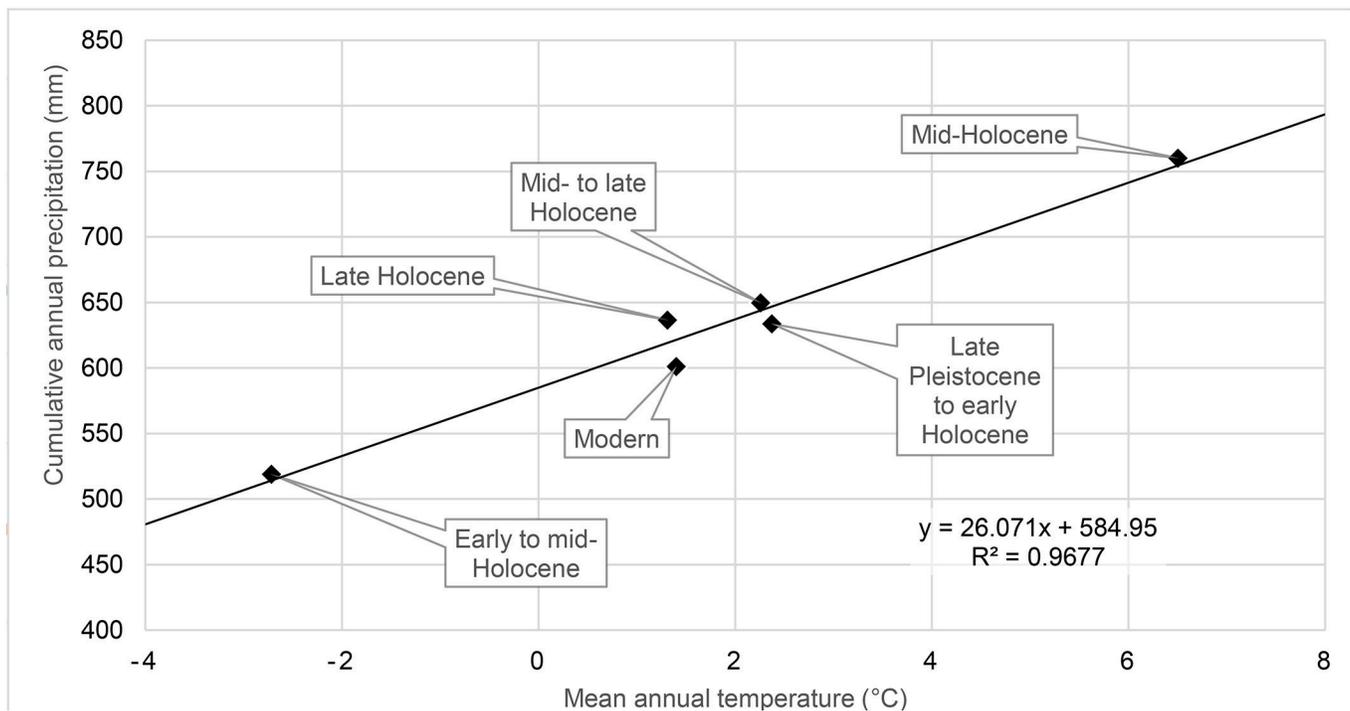


Figure 1. Reconstructed climate at riparian sites in southwestern Alberta for six intervals. Trendline plotted is equivalent to the trend from which divergence is measured in Figure 2.

The point estimates generally agree with other reconstructions from the area, such as MacDonald (1982), Beirle and Smith (1998), and Gajewski and Viau (2011). We stress that these earlier studies are not directly analogous to this study, as their contexts are different and they are primarily based on pollen, limnological, and sedimentological records (i.e., not riparian macrofossils). Our study's results show a very strong positive correlation between temperature and moisture conditions ( $R^2 = 0.9677$ ; Fig. 1). This relationship is probably amplified by the riparian context of the sites because fluvial discharge, driven by increased melting, acted as a partial environmental proxy for precipitation. Despite this correlation, our results indicate that from the early/mid-Holocene until the late Holocene conditions were wetter than would be expected based on temperature alone, especially in the late Holocene (Fig. 2). However, this trend is reversed in both the late Pleistocene/early Holocene and modern intervals, where the temperature is much higher than would be indicated by the moisture regime (Fig. 2). In general, indications of the coldest temperatures and driest conditions were from the early to mid-Holocene interval, followed by the Holocene maximum in both parameters during the mid-Holocene. Climate appears to have largely stabilized following this interval up to modern times, although a slight increase in temperature and decrease in moisture since the late Holocene can be discerned.

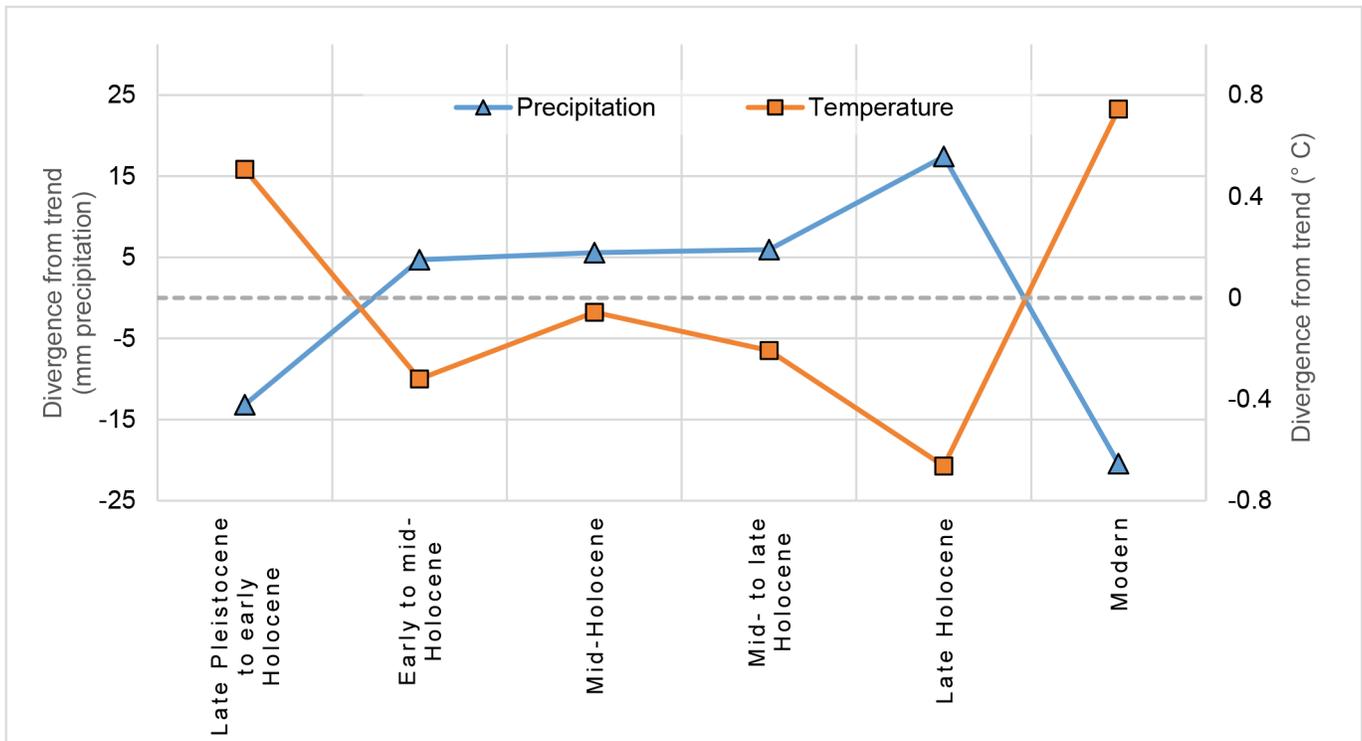


Figure 2. Divergence of predicted climatic values at riparian sites in southwestern Alberta from linear model (seen in Figure 1). Horizontal dashed line represents the trend (i.e., 0 divergence).

This study shows an intriguing new reconstruction of riparian environmental conditions for southwestern Alberta utilizing novel methods of analysis and modelling. Perhaps more importantly, it shows that successful and meaningful research findings can emerge from work undertaken as part of cultural resource management (CRM) initiatives.

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# Following your gut: A new Cenomanian-Turonian pontosaur (Squamata, Pythonomorpha) and the first described dolichosaur stomach contents provides strong evidence for a long-standing paleoecological theory

Michelle M. Campbell Mekarski, and Michael W. Caldwell

University of Alberta, Edmonton, Alberta T6G 2R3, Canada; mmc7@ualberta.ca; michael.caldwell@ualberta.ca

The Upper Cretaceous limestones from the Dalmatian Coast of Croatia and the Komen Plateau of eastern Italy and Slovenia have produced a large number of well preserved fossil aquatic marine ophidiomorphs with distinctively long, cylindrical bodies and small reduced limbs. These include *Acetosaurus tommasinii*, *Adriosaurus suessi*, *Adriosaurus skrbiniensis*, *Adriosaurus microbrachis*, *Mesoleptos zendrinii*, and *Pontosaurus lesinensis*. In the late 18th century, a fossil lizard was found in upper Cenomanian platy limestones on Hvar Island, Croatia. It was in the possession of a local collector until 1982 when it was donated to the Croatian Natural History Museum in Zagreb, Croatia. The 36 cm long fossil is well preserved and articulated, missing only the anterior tip of the skull and the greater part of the tail. The new taxon is described and diagnosed by the following features: elongate pontosaur-like skull; unique supraoccipital-parietal articulation, with supraoccipital resting on top of and forming v-shaped suture with parietal; elongate axial skeleton (12 cervical, 29 dorsal vertebrae); robust, semi-circular ribs; a reduction of the appendicular skeleton, flatter joints, and a broadening of the manus and pes; shorter forelimbs than hindlimbs; considerable dorso-ventral expansion of the caudal region. The new taxon was unequivocally at least partially aquatic: pachyostotic ribs, a laterally compressed tail, and reduced, flattened limbs indicate adaptations for undulatory locomotion. Local sedimentation and associated fauna provide evidence for a productive tropical rudist reef ecosystem on a shallow inner shelf. Preservation of teleost remains within the body cavity of the new specimen represents the first evidence of identifiable gastric contents described from a dolichosaur. At least three individual fish, representing at least two teleost families are identifiable. One is preserved complete, indicating that it was swallowed whole. Such findings provide strong evidence of a primarily piscivorous diet for these animals, that so far has only been presumed. Together, these lines of evidence support the interpretation of this animal as an ambush predator, able to hide in nooks and crannies, and agile enough to catch fish via tail propelled locomotion in a shallow marine environment.

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# Engaging the sand and gravel industry to help uncover Alberta's Ice Age Record

Katherine Bramble, Christopher N. Jass, Christina I. Barrón-Ortiz

Quaternary Palaeontology, Royal Alberta Museum, 9810 - 103A Avenue NW, Edmonton, AB T5J 0G2, Canada; Katherine.Bramble@gov.ab.ca; Chris.Jass@gov.ab.ca; Christina.Barron-Ortiz@gov.ab.ca

In Alberta, sand and gravel deposits are the most productive settings for recovery of Ice Age fossils. Fossils are common but thinly distributed amongst large volumes of gravel. As a result, fossils infrequently appear via normal erosive processes. The vast majority of Ice Age remains from sand and gravel deposits are recovered as the result of aggregate extraction by industry. The Quaternary Palaeontology Program at the Royal Alberta Museum has an active program focused on engaging these industry stakeholders to facilitate the recovery of Ice Age fossils across the province. On-site visits to gravel pits and in-house tours of the palaeontological collections have traditionally been the primary methods of engagement.

To further enhance efforts to recover Ice Age fossils and raise awareness of fossil resources across the sand and gravel industry, we are working to develop a booklet for distribution to industry stakeholders. The booklet will include a brief, broad introduction to Alberta's Ice Age, and will highlight the various Ice Age animals commonly recovered in gravel pits. Picture references of typical Ice Age fossils will be emphasized. We view a figure-heavy booklet as essential to communicate that Ice Age fossils are more similar in appearance to recent skeletal remains than to older fossil materials found in Alberta (i.e., dinosaurs). We will also include information on procedures that should be taken when a fossil is found, and discuss the implications of finding fossils for industry (i.e., we will address the "Will we be shut down?" question). With this booklet, we hope to raise the recognition of fossil resources among industry employees and increase the recovery of Ice Age fossils. At a minimum, the booklet should further enhance positive and proactive working relationship between the Quaternary Palaeontology program at the Royal Alberta Museum and the operators of gravel pits across Alberta.

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# A catalogue of type specimens of fossil fishes for the University of Alberta Laboratory for Vertebrate Palaeontology

John C. Bruner

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

This study provides the first list ever compiled of the fossil fish type specimens deposited in the collections of the University of Alberta Laboratory for Vertebrate Palaeontology (UALVP). This collection contains 88 fish holotypes, 966 fish paratypes, 55 casts of fish holotypes from other museums, and 18 casts of fish paratypes from other museums. The catalogue number, the latest classification, a short description of the material, the collector(s) of the holotype (if known), the type locality, the full citation including the pages on which it was described, and listings of any figures are provided for each type specimen. A list of unpublished "types" languishing in Ph.D. and M.Sc. theses is also included, as these specimens are listed in the collection as "types" on the museum labels and in the computer catalogue. There are 13 fish holotypes and 156 fish paratypes in this unpublished category. Additionally, there are two UALVP fish holotypes from a currently submitted publication.

# Reconstructing the paleoenvironments of Kalodirr and Moruorot, Kenya using stable carbon isotopes.

Catherine Butts<sup>1</sup>, Susanne Cote<sup>1</sup>, and John Kingston<sup>2</sup>

<sup>1</sup>Department of Anthropology and Archaeology, University of Calgary; catherine.butts@ucalgary.ca; scote@ucalgary.ca

<sup>2</sup>Department of Anthropology, University of Michigan; jkingst@umich.edu

The transition from the Paleogene into the Neogene (23 Ma) in Africa is marked by continued physiographic evolution that affected the landscape, climate and immigration of Eurasian fauna. Valley formation across East Africa in the early Miocene (23–16 Ma) created a large expanse of accommodation space for sediment accumulation and fossilization, providing fossil sites across Kenya and eastern Uganda that together represent the total extent of the early Miocene. This timeframe is of interest as it was a period of great taxonomic and morphological diversity among early fossil apes and monkeys (Primates: Catarrhini), which exceeded their living counterparts.

Traditionally, early Miocene environments of East Africa have been reconstructed as dense tropical forests composed of C<sub>3</sub> plants and likely would have been represented as a continuous stand of evergreen trees with closed, interlocking crowns (Verdcourt 1963; Andrews and Van Couvering 1975). These environments are believed to remain stable until the middle Miocene (16 – 11 Ma) when forested conditions gave way to mixed forest and grasslands. To date, fossil remains indicate that the earliest C<sub>3</sub> grasslands appear in Fort Ternan, Kenya around 14 Ma and C<sub>4</sub> grasses appeared in Kenya by 15.3 Ma but did not become a dominant feature in African environments until the late Pliocene and Pleistocene (Retallack 1992; Morgan et al. 1994; Cerling et al. 1997; Uno et al. 2011). However, emerging isotopic evidence from Ugandan fossil sites of Napak (20 Ma), Moroto (21 Ma) and Kenyan fossil sites of Rusinga Island (20–17 Ma) and Tinderet (20 Ma) indicate open canopy forests, forest mosaics and woodland environments (Kingston et al. 2009, 2011; Garrett et al. 2015; Arney et al. 2017).

This study builds on preliminary research by analyzing stable carbon isotopes of mammalian tooth enamel collected from Kalodirr and Moruorot, Kenya. Kalodirr and Moruorot are two fossil localities situated in northern Kenya representing the latest early Miocene (17.5–16.8 Ma) and host three taxonomically distinct hominoids that are restricted to the Turkana Basin (Leakey and Leakey 1986a, 1986b, 1987; Boschetto 1998; Boschetto et al. 1992). The goal of this project is to not only give environmental context to the fauna of these sites, but also investigate whether or not environments of East Africa began opening before the climate change of the middle Miocene, which is recorded in the  $\delta^{18}\text{O}$  values of deep-sea benthic foramina (Zachos et al. 2001). Due to the age of these sites, we expect the  $\delta^{13}\text{C}$  values to be more positive than those observed in the other early Miocene sites listed above, indicating a more open canopy.

We analyzed the stable carbon isotopes from 98 specimens belonging to 8 large bodied herbivorous mammal families: Deinotheriidae, Gomphotheriidae, Rhinocerotidae, Anthracotheriidae, Suidae/Sanitheriidae, Tragulidae, Giraffoidea/Pecora, and Titanohyracidae. These families were selected due to their availability from Kalodirr and Moruorot as well as across other early Miocene sites of East Africa. Specimens were bulk sampled and run through an isotope mass spectrometer at the University of Florida. Proxies from modern African environments were adjusted to accommodate the change in atmospheric carbon from the modern value of -8.2 ‰ to -5.27 ‰, based on preindustrial values collected from high-resolution benthic foramina (Tipple et al. 2010). Environmental proxies were taken from modern African environments according to data collected by Cerling and Harris (1999) and Cerling et al. (2003, 2004, 2011).

Preliminary analysis of the isotope signatures from Kalodirr and Moruorot suggest a mosaic of C<sub>3</sub> vegetation too irradiated to indicate a closed canopy forest environment and are more similar to that of open canopy forests or woodlands. This is contrary to previous environmental interpretations, indicating that early Miocene environments were opening earlier than previously described.

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# Morphology of an early jawless fish from the Late Silurian of Cornwallis Island, Canada

Mori Chida

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

Anaspids form one of the extinct lineages of early jawless vertebrates. They are characterized by a compressiform profile, extensive dermal skeleton, and the absence of endoskeletal mineralization. Much of the trunk skeleton is composed of elongate rod-shaped dermal scales, and the skull consists of a combination of dermal plates (Forey 1995; Janvier 1996). Other diagnostic characters include a hypocercal tail and a series of external branchial openings demarcated by small plates (Forey 1995). Anaspids are known from the Lower Silurian to Upper Devonian marine deposits in North America and Europe (Forey 1995; Janvier 1996; Blom et al. 2001). Here, I describe and illustrate a well-preserved anaspid specimen collected from the Late Silurian of Cornwallis Island in Canada.

The specimen GSC C-26661-005 shares some characters with birkeniid anaspids, the anaspid group possessing eight to six gill openings and hook-shaped dorsal scutes (Janvier 1996). The specimen is a whole-body exoskeleton, and some parts of the scales are pyritized. Dermal plates on the skull roof have a smooth texture, whereas other facial plates and scales in the lower lip have two to four rows of round tubercles that are nearly symmetrically distributed across the middle ridge. There are eight external branchial openings in a posteroventrally inclined row. The trunk scales are elongate dorsoventrally and organized in repeating columns of five scales toward the caudal fin. Paired ventral fins are compressed together along the ventral midline. The anal fin is demarcated by a plate with multiple spines. The single-peak scales along the dorsal midline are preserved as impressions. The caudal fin is not hypocercal, but is rather symmetrical and perhaps homocercal. On the basis of the overall morphology, GSC C-26661-005 has unique characters among birkeniid anaspids.

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# New information on the anatomy of *Saurornitholestes langstoni* (Dromaeosauridae, Dinosaur Provincial Park)

Philip J. Currie<sup>1</sup>, and David C. Evans<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, T5N 2E9, Canada; pcurrie@ualberta.ca

<sup>2</sup>Department of Palaeobiology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6, Canada; d.evans@utoronto.ca

In 1978, a University of Alberta MSc student (Hans-Dieter Sues) described the dromaeosaurid *Saurornitholestes langstoni* on the basis of a partial skeleton that is in the collections of the Royal Tyrrell Museum of Palaeontology. Over the years, four partial skeletons of this animal were collected in Alberta and Montana, although reasonably complete skeletons remained elusive. Nevertheless, isolated teeth and bones of this animal are relatively common, and are easily identified because of our more complete knowledge of related taxa; these include *Bambiraptor* and *Velociraptor*. Cranially, the skull was only known from an ectopterygoid, frontals, parietals, a toothless premaxilla, a maxilla with teeth, a quadrate, a quadratojugal, and a nearly complete mandible. The lack of truly diagnostic cranial material has restricted phylogenetic assessments, and the position of *Saurornitholestes* within Dromaeosauridae has been volatile. In 2014, a field party from the University of Alberta collected an almost complete skeleton, including the skull, from the Steeveville end of Dinosaur Provincial Park. It is as well preserved as some of the *Velociraptor* skulls from Mongolia, although the facial region of the skull is relatively deeper and wider. The snout is neither as deep nor as short as that of *Atrociraptor* from the Horseshoe Canyon Formation near Drumheller. Unusual, apparently autapomorphic characters include pneumatic nasals and a relatively low number of teeth. Reanalysis of its taxonomic position within Dromaeosauridae suggests a close relationship with *Atrociraptor* and *Bambiraptor*, and a more distant relationship with the Asian velociraptorines. Taphonomic evidence collected with the specimen suggests that *Saurornitholestes* was a predator capable of killing and consuming animals larger than itself.

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## Passive flows in 3D printed models of atrypide brachiopods

Rylan V. Dievert, Darrin J. Molinaro, Kristina M. Barclay, and Lindsey R. Leighton

Department of Earth and Atmospheric Sciences, University of Alberta, T6G 2E3, Edmonton, Alberta; dievert@ualberta.ca; molinaro@ualberta.ca; kbarclay@ualberta.ca; lindseyrleighton@gmail.com

Brachiopods of the order Atrypida, some of the most common and diverse Siluro-Devonian organisms, are known to have morphologies associated with environmental gradients. Globose, biconvex morphologies have been associated with higher-energy and cleaner carbonate systems, while more shield-shaped, plano-convex morphologies have been associated with low-energy, muddy systems. This study seeks to evaluate the effects of these two end-member atrypide shapes on passive water flow through the brachiopod to compare feeding performance between the two valve shapes. Brachiopods use tentacled lophophores to actively circulate water for feeding, but even active suspension-feeders typically pump in the same direction as passive flow to conserve energy. Thus, passive flow direction through models of fossil organisms may be used as a reliable indicator of flow through the once-living animal. This approach can also be used to evaluate life orientations and existing theories on feeding

currents in atrypides. The spirolophe lophophore of the extant order Rhynchonelida has been used as a functional analogue for the spirolophe of atrypides. However, the two spirolophes are morphologically distinct, and may induce different flow patterns through their mantle cavity.

Using 3D scanning and printing, we constructed two highly accurate gaping models of both end-member brachiopod shapes, which contained mantle tissue reconstructed with modelling clay and lophophores reconstructed with false eyelashes. A recirculating flume tank and dye streams were used to visualize passive flow through the models in multiple orientations relative to flow direction. All trials were conducted at a velocity of 0.2 m/s. The plano-convex shape outperformed the biconvex shape in all experimental orientations, demonstrating more efficient flow of dye across the lophophore, and a steady medial exhalent current above the model, similar to a chimney. These results suggest that the plano-convex morphology was more capable of using passive flow, while the biconvex morphology may have been forced to rely more on active pumping. This is consistent with observed morphological distributions along environmental gradients, where quiet water taxa such as plano-convex atrypides rely on body shapes that maximize passive flow/food capture.

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## Experimental compaction of gastropod shells: Implications for interpreting predation intensities in the fossil record

Aaron D. Dyer, Evan R. Ellis, Darrin J. Molinaro, and Lindsey R. Leighton

University of Alberta, 1-26 Earth Sciences Building, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3; adyer@ualberta.ca; eellis@ualberta.ca; molinaro@ualberta.ca; lindsey.leighton@ualberta.ca

Palaeoecologic interpretations drawn from the fossil record are at risk of being biased by taphonomic processes. Post-depositional compaction of gastropod shells may alter perceived predation intensities by fragmentation. For example, predatory drill holes may reduce shell strength (Roy et al. 1994; Zuschin and Stanton 2001), and be preferentially lost during compaction, thus observed drilling frequencies may be lower than their original frequencies (Klompaker 2009). To test this hypothesis, 280 *Olivella* biplicata shells (248 undrilled and 32 successfully drilled) were subjected to compaction at 4000 psi in a coarse-grained sand matrix. For each trial, multiple shells were tested simultaneously, but were spaced so that no shells were in contact. Erosional artifacts (e.g., removed apices) were observed on both drilled and undrilled shells prior to testing, and the effects of these on compactional strength had to be tested prior to comparing drilled and undrilled shells. Shells possessing erosional artifacts that significantly altered compactional strength would then be removed from statistical analyses comparing drilled and undrilled shells. Shell strength was tested at three increasingly severe thresholds (Fig. 1): damaged (fractured but intact), fragmented, and obliterated (< 50% intact). This equated to both conservative (any damage) and practical (potentially removed from the fossil record) testing of compactional strength. The difference in compactional strength between altered and unaltered shells (taphonomic artifact present versus absent; drill hole present versus undrilled) at each damage threshold was determined utilizing Fisher's exact tests with a sequential Bonferroni corrected p-value. Erosional artifacts did not significantly alter compactional strength, therefore, all 32 drilled shells were compared to all 248 undrilled shells. Drilled and undrilled shells did not significantly differ in compactional strength (drilled: 88% damaged, 44% fragmented, and 16% obliterated; undrilled: 75% damaged, 39% fragmented, and 5% obliterated). Therefore, drilled gastropod shells are inferred to not be selectively damaged by compaction, and studies utilizing drill hole data need not worry about bias from compaction.

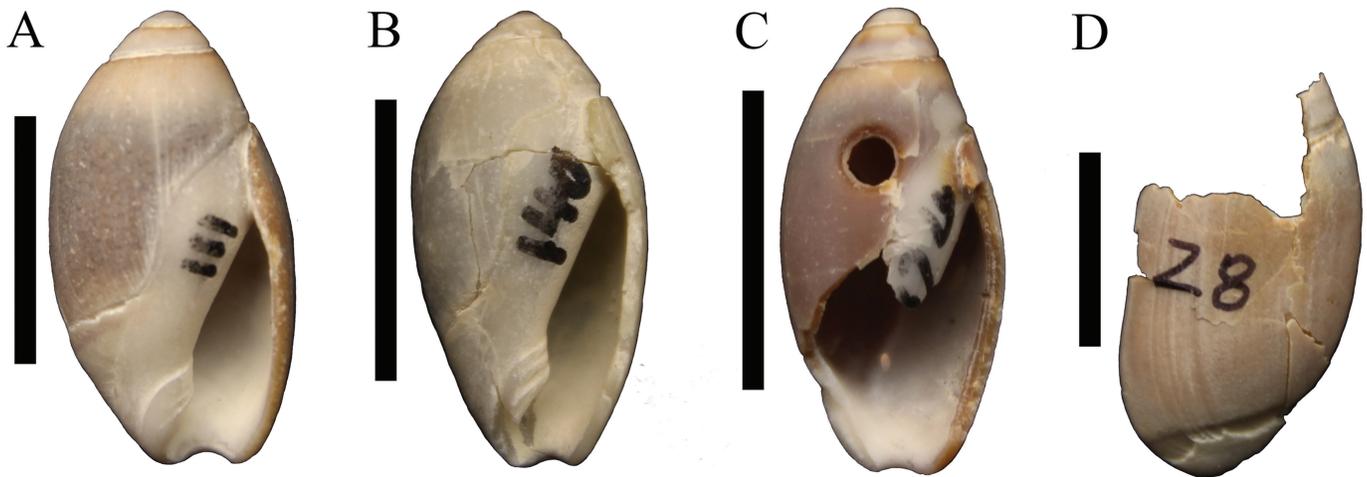


Figure 1. Examples of *Olivella biplicata* shells displaying compactional damage thresholds used to infer compactional strength. A) Undamaged. B) Fractured but intact. C) Fragmented. D) Obliterated (< 50% intact)

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## Variation in lesion origins: histologic support for intravital bone resorption and invertebrate bone boring in pachycephalosaur cranial domes

Aaron D. Dyer, Aaron R.H. LeBlanc, and Philip J. Currie

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

Numerous behaviours are likely to result in bone damage, making palaeopathology a useful tool in assessing the behaviours of fossil vertebrates. Osteomyelitic lesions (bone infections) have been diagnosed from external morphology and from CT scans of pachycephalosaurid frontoparietal domes. These lesions support the hypothesis that the domes of these dinosaurs were used in agonistic head-butting contests. However, histological features are key to eliminating alternative (i.e., taphonomic) explanations; therefore, further examination is needed to demonstrate pathologic origins. This study uses micro CT technology and thin-sections to test for histological evidence of bone resorption (a response to bone infection) in suspected pathologic frontoparietal domes. Pathologic lesions will be lined with Howship's lacunae (remnants of osteoclastic resorption) and secondary bone

deposition, neither of which result from taphonomic weathering.

Micro CT scans reveal no support for osteomyelitis. Histological features previously attributed to osteomyelitis (lower density surficial bone) were only observed in UALVP 5 (*Pachycephalosauridae* indet.). Scans of several domes reveal trace fossils from bone boring invertebrates. UALVP 5 and 8504 (cf. *Foraminacephale*) possess cylindrical branching galleries, which are reminiscent of the sponge boring trace *Entobia*. These are likely derived from the Lethbridge Coal Zone of the Dinosaur Park Formation, where some river channel and estuarine sediments show marine influence. Micro CT scans of UALVP 8503 (*Stegoceras* sp.) aid in identifying external ovoid pits as the insect pupal chamber trace *Cubiculum ornatum*, which is reported for the first time in the Cretaceous of Alberta. The appearance of *Cubiculum ornatum* demonstrates the expected presence of bone-boring insects in the Dinosaur Park ecosystem.

Thin-sections of UALVP 8504 revealed Howship's lacunae and secondary bone deposition along portions of the lesions, indicating a pathologic origin. Thus, *intra vitam* (during life) bone resorption is diagnosed as the lytic agent in UALVP 8504. Additionally, Howship's lacunae frequently line vascular canals in the exterior, non-pathologic region of the dome, suggesting an associated inflammatory response. Osteomyelitis cannot be diagnosed at this time, as localised sclerosis and periostitis (additional responses to infection) are absent. It is concluded that lytic lesions in pachycephalosaur domes have pathologic origins, while internal canals and ovoid pitting result from invertebrate bone-boring. Because the diagnosis of osteomyelitis is inconclusive, pathologic support for head-butting behaviours is questioned. However, further histological examination may reveal more precise origins for these pathologic lesions.

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## A new didactyl oviraptorid provides evidence of social behaviour in a non-avian theropod

Gregory F. Funston<sup>1</sup>, Philip J. Currie<sup>1</sup>, Chinzorig Tsogtbaatar<sup>2,3</sup>, Tsogtbaatar Khishigjav<sup>2</sup>, and Yoshitsugu Kobayashi<sup>3</sup>

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

<sup>2</sup>Institute of Palaeontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; chinzorig.tsogtbaatar@gmail.com; tsogtmondin@gmail.com

<sup>3</sup>Hokkaido University Museum, Hokkaido University, Sapporo, Japan; ykobayashi@museum.hokudai.ac.jp

Sociality, the phenomenon of non-reproductive aggregation, is widespread in extant animals (Alexander 1974). Social behaviours vary from predator aversion through aggregative foraging to forfeit of reproduction in eusocial colonies. These behaviours must have their origins in the fossil record, but testing the evolution of sociality in extinct animals is difficult because of the filter of taphonomy. Although social aggregations can be inferred through mass death assemblages, the factors leading to grouping can only be speculated upon. However, in exceptional circumstances, fossils can preserve animals engaging in behaviour, like the 'Fighting Dinosaurs' of Mongolia (Barsbold 2016), or an ichthyosaur in the act of giving birth (Motani et al. 2014).

Here, we describe one such exceptional fossil, capturing a group of oviraptorid theropods resting together. The specimens were poached from an unknown locality in the Nemegt Formation of Mongolia (Fanti et al. 2017), and were confiscated in 2006. One block preserves the remains of three juvenile animals. The individuals are crouched in a resting position, with their arms and head tucked towards the body. The skeletons are in close contact, which indicates that these animals were huddling together before death. In addition to representing a

new species of crested oviraptorid with an unusual didactyl manus, the specimens shed light on the ontogeny and behaviour of oviraptorid dinosaurs.

There is much evidence of gregarious behaviour in oviraptorosaurs (Funston et al. 2016) and other theropods (Varricchio et al. 2008), but this specimen is the first aggregation of individuals in life positions. This allows us to directly infer their behaviour before death as well as speculate on the life history traits that brought about this behaviour. Huddling is common in small extant endothermic homeotherms (Gilbert et al. 2009), where it is important for thermoregulation and maintenance of social relationships (Takahashi 1997). Its record in an oviraptorid therefore supports previous assertions of homeothermy and possibly endothermy in this group (Grady et al. 2014; Amiot et al. 2017). This record of huddling in a non-avian theropod also potentially informs us of the sociality of oviraptorids. Huddling is an intimate behaviour that is more likely to occur between kin or closely affiliated individuals (Wada and Ogawa 2009). The similar developmental stages of these oviraptorids may indicate that they are kin, and therefore that oviraptorids maintained kinship after fledging. Evidence from this and other assemblages suggests that oviraptorosaurs were more social than other maniraptoran theropods. This may be linked to herbivory (Smith 1992; Zanno and Makovicky 2011) and sexual signalling (Funston and Currie 2016), which are both correlated with increased social complexity in modern birds.

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# Why we need conservation paleobiology: Just ask Johnny Depp!

Patricia H. Kelley

Department of Earth and Ocean Sciences, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC, USA 28403-5944; kelleyp@uncw.edu

Human population growth, accompanied by habitat destruction, environmental degradation, and overharvesting of species, has led to biodiversity loss on a scale comparable to mass extinctions of the past. A new field, conservation paleobiology (CPB), offers hope for addressing the modern biodiversity crisis. CPB applies geo-historical data to the conservation and restoration of modern biodiversity and ecosystem services. Data from the geological record (e.g., fossils, sediments, ice cores) can be used to establish baselines and the natural range of variability of ecosystems and to understand the response of species and ecosystems to environmental change.

The following studies exemplify the CPB approach: 1) “Live-dead” analyses comparing time-averaged death assemblages and local living communities of molluscs have been used to detect recent anthropogenic change in coastal habitats; 2) archeological work on shell middens has tested hypotheses about overharvesting of shellfish by Native Americans; 3) studies of diversity, ecosystem structure, and ecological interactions in the fossil record have yielded information on natural baselines and variability and on ecosystem response to environmental change; and 4) species invasions in the fossil record can help predict modern ecosystem response to invasive species.

Nevertheless, the scientific results of CPB studies will only make an impact on management and policy when the training of students includes the human dimension of conservation issues. Thus CPB curricula must be truly cross disciplinary, extending beyond the natural sciences to courses in fields such as the social sciences, management sciences, planning, communication, and law. Training must be oriented towards problem solving and policy and provide students with hands-on, real-world experience working with stakeholders. PhD programs focused solely on research skills will not prepare students well for conservation jobs beyond academia. In cases where institutional constraints impede the development of formal cross-disciplinary CPB programs, students can still develop a skill set useful in the conservation world, given appropriate mentoring and student initiative. Ultimately, changes in the way students are trained will yield a new generation of conservation practitioners skilled in detecting anthropogenic change, predicting results of ongoing environmental change, planning ecosystem restoration, and influencing management policy.

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# A new species of rare, shell-crushing mosasaur (Squamata: Mosasauridae) from the Late Cretaceous of Morocco

Aaron R. LeBlanc, and Michael W. Caldwell

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9; arl@ualberta.ca; mikec@ualberta.ca

Mosasaurids were giant marine lizards that inhabited the world's oceans during the last 25 million years of the Late Cretaceous (90–65 MYA). Their large size (up to 15 meters in length) and formidable dentitions made them apex predators in marine ecosystems. Whereas most mosasaurids probably fed on fish, cephalopods, or other marine reptiles, one lineage specialized on hard-shelled invertebrates. The best known of the shell-crushing mosasaurids is *Globidens*, a genus characterized by a bulbous, crushing dentition and a broad, robust skull. Known mainly from North America, *Globidens* was until very recently known only from a handful of partial and crushed skulls, as well as isolated teeth. In recent years, the record of these rare and enigmatic mosasaurids has improved dramatically with new discoveries from the United States and northern Africa.

Here we describe a new species of *Globidens* from the Maastrichtian phosphate deposits of Morocco and highlight new anatomical details about these unique mosasaurids. This new species is distinguished from the closely related *Globidens phosphaticus* from Morocco and Angola by the presence of laterally compressed crushing teeth that lack cutting edges, grooves, or swellings, a shorter tooth row along a straight dentary, and a lack of accessory vertebral articulations (zygosphenes and zygantra) on the cervical vertebrae.

The relatively undistorted skull elements of this new species reveal that the skull of *Globidens*, unlike that of modern shell-crushing lizards, was akinetic, exhibiting no movement between the skull bones during feeding. This new species also had teeth that were attached to the jaws by a system of ligaments that would have dissipated the compressive forces of feeding, instead of being fused to the jaws as they are in most other lizards. In order to accommodate a shell-crushing bite, the skull of *Globidens* was also reinforced at the attachment sites for the jaw adductor musculature. This new species has the proportionally largest coronoid of any mosasaurine (the site of origination of many jaw adductor muscles) and a dorsally vaulted temporal arcade into which the jaw adductor musculature was inserted. Lastly, histological analysis of a cervical rib from this specimen revealed the first evidence of osteosclerotic-like bone compactness in a mosasaurid, which we interpret as buoyancy compensation for feeding on bottom-dwelling invertebrates.

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# An assemblage of flocking oviraptorids (Theropoda: Oviraptoridae) from the Late Cretaceous of southern Mongolia

Denise C.A. Maranga, Gregory F. Funston, and Philip J. Currie

Department of Biological Sciences, CW405 Biological Sciences Building, University of Alberta, Edmonton, AB, Canada, T6G 2E9; maranga@ualberta.ca; funston@ualberta.ca; pjcurrie@ualberta.ca

The Gobi Desert of Mongolia and China is home to a rich and diverse assortment of dinosaur fossils. Unfortunately, this wealth of fossil material has fallen victim to increased rates of poaching in the past decades. In recent years, there have been efforts to find and return poached fossils to their rightful place of origin. One such repatriated specimen is a slab of oviraptorids, a clade of small-bodied theropod dinosaurs, from the Upper Cretaceous beds of southern Mongolia. Although the precise locality from which the specimen was recovered is unknown, it is likely that it was collected from the Baruungoyot or Nemegt formations exposed in the Nemegt Basin. The specimen consists of five well-preserved individuals in death poses arranged close to each other. These specimens are unambiguously oviraptorids, but some unusual anatomical features, such as spatulate ischia, contrast with other oviraptorids and suggest that they represent a new taxon. The skeletons are all articulated, indicating that their proximity to each other is the result of congregation at the time of death rather than artificial aggregation through taphonomic activity. The specimen is thus evidence of a singular mass mortality event and contributes to a growing body of evidence of gregariousness throughout Oviraptorosauria. This slab shows the best and most distinct evidence of “flocking” behaviour in oviraptorosaurs to date. The similar size of the specimens and incomplete fusion of neural arches and sacra suggest that these individuals represent an age-segregated juvenile assemblage, as have been recorded in ornithomimids and other dinosaurs. While it is likely that this flock formed in response to heavy predation pressure by the tyrannosaur *Tarbosaurus* in the Nemegt Basin, the specimen also highlights a link between herbivory and increased gregariousness in theropods, as the majority of bonebed assemblages contain herbivorous taxa.

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# Juvenile naticid drill hole stereotypy within a predator–prey system of small bivalves from the St. Marys Formation of Maryland

Denise C.A. Maranga<sup>1</sup>, Ryan D. Wilkinson<sup>1</sup>, Matthew J. Pruden<sup>1</sup>, Nicolas A.B.J. Beausoleil<sup>1</sup>, Darrin J. Molinaro<sup>1</sup>, Patricia H. Kelley<sup>2</sup>, and Lindsey R. Leighton<sup>1</sup>

<sup>1</sup>Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB, Canada, T6G 2E3; maranga@ualberta.ca; rwilkins@ualberta.ca; mpruden1@ualberta.ca; beausole@ualberta.ca; molinaro@ualberta.ca; lleight@ualberta.ca

<sup>2</sup>Department of Earth and Ocean Sciences, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC, 28403-5944; kelleyp@uncw.edu

Naticid (Gastropoda: Naticidae) drilling predation is one of the most well-studied predator-prey interactions within palaeontology. Naticids are known to show a consistency in drill hole placement on their prey – a phenomenon known as stereotypy – which can provide useful information on ecological trends and behavioural patterns. Drill holes can provide information on predation frequency, success rate, and prey selection, as well as serve as a proxy for predator size. There have been numerous studies examining the interactions between naticids and their prey, such as bivalves; however, more information is needed on interactions in systems in which both the predator and prey are small, as these systems may exhibit different predator-prey dynamics. This study examines drilling predation by small, ontogenetically young *Euspira* naticids on small (< 15 mm) bivalves from the Little Cove Point Member of the St. Marys Formation (Miocene, Maryland). All the specimens examined bear small drill holes less than 2 mm in diameter; these holes are attributed to small, young naticids, as *Euspira* is the only species of naticid in the unit. *Spisula subcuneata* is the most abundant bivalve in this size range, as well as the most common prey item for the young naticids.

Geometric morphometrics (Bookstein Shape Coordinates) and a 9-sector grid system were used to analyze drill hole stereotypy. The results were compared to those of Kelley (1988) for large naticids preying on larger prey species from the same unit. Juvenile naticids demonstrated drill hole stereotypy like that of adult naticids. This was demonstrated by (1) the presence of strong prey-size selectivity, as drill hole diameter and prey size were significantly correlated, and (2) strong drill hole location stereotypy at the umbo of *S. subcuneata*. In both studies, drill hole location stereotypy varied with different prey species, indicating that drill hole location stereotypy is a function of prey handling and prey shape. Therefore, naticids show stereotyped behavior, even early in their ontogeny.

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# First dinosaur trackway from the Horseshoe Canyon Formation of Alberta, Canada

Mark Powers<sup>1</sup>, Steven Mendonca<sup>2</sup>, Matthew Rhodes<sup>1</sup>, Ryan Wilkinson<sup>1</sup>, Matthew Pruden<sup>2</sup>, Philip J. Currie<sup>1</sup>, and Gregory Funston<sup>1</sup>

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

<sup>2</sup>Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton AB, T6G 2E3; smendonc@ualberta.ca; mpruden1@ualberta.ca

Dinosaur footprints are trace fossils preserved under very specific conditions. They contain information about animals' behaviour, which can be used in tandem with osteological information to help build a more complete view of dinosaur paleobiology. The most common preservation of dinosaur tracks reported is concreted slabs of rock that retain foot impressions left by animals as they walked through the paleoenvironment. Trackways of this preservation can be massive – stretching for kilometers – and are resistant to weathering. Less commonly, trackways can be preserved via casts of the foot impressions, which are referred to as concretionary footprints. Here we report on the first dinosaur trackway from the Horseshoe Canyon Formation near Morrin, Alberta, commenting on the type of preservation and proposing possible track-makers. Concretionary footprints were exposed, revealing a series of similarly-sized tracks with overlapping morphological features: track length less than or equal to width, widely spaced toes with rounded terminal ends, and interdigital pad impressions. Several footprints demonstrate exceptional preservation of skin impressions on various digital pads and from a fleshy interdigital pad. Given the size and spacing of these footprints, the most likely track-maker is a large hadrosaurid dinosaur. Skeletal material for hadrosaurids from the same stratigraphic position suggests three possible trackmakers – *Edmontosaurus regalis*, *Hypacrosaurus altispinus*, or *Saurolophus osborni*.

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## Testing ecological niche modeling using paleoclimatic data: Implications for modern conservation

Matthew J. Pruden, Alberto V. Reyes, and Chris L. Schneider

Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB, Canada, T6G 2E3; mpruden1@ualberta.ca; areyes@ualberta.ca; clschnei@ualberta.ca

Global warming has had a profound effect on the distribution of modern species. Predicting how species will respond to the projected rise in global temperature has become an integral part of conservation. Ecological niche models (ENM) are the most common method for modeling a modern species' ecological niche based on occurrence data, and can be projected into the future to analyze how their ecological niche and subsequently its' distribution will shift due to climate change. However, the results of these models are predictions which can only be tested empirically with the passage of time. Yet, waiting to test the model puts at risk the very species that the predictions are trying to protect. The paleontological record allows us to test the accuracy of ENMs empirically over multiple time spans. Furthermore, recent advances in paleoclimatic reconstructions provide gridded paleoclimate data suitable for ENMs. This study tests the predictive capabilities of the ENM Maxent (Phillips et al. 2018) by modelling the ecological niche space for Caribbean coral and mollusc species using both modern and Pliocene (~3 Mya) climate data.

Modern Caribbean coral and mollusc species occurrences were compiled from the online Global Biodiversity

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Information Facility (gbif). Pliocene occurrences were taken from the Paleobiology Database (PBDB) and the Panama Paleontology Project (PPP). Modern sea surface temperature and bathymetry gridded climate data were obtained from the NOAA National Centers for Environmental Information, and the Pliocene climate data from the PRISM 4 Paleoenvironmental Reconstruction Project (Dowsett et al., 2016). To test Maxent's predictive capability and the accuracy of ENMs, ecological niches of extant species were modelled in Maxent using the modern climate and species occurrence data. The model was then applied to the gridded Pliocene climate data to predict their Pliocene niches. Modelled Pliocene niches were compared to known Pliocene faunal niches from occurrence data. Furthermore, to ensure the model worked in both directions, data from ecological niches of Pliocene species were also modelled in Maxent and projected onto the modern environment to be compared to present-day species distributions as an additional test of the accuracy of the ENM.

The modelled Pliocene ecological niches based on the modern Caribbean fauna predicted that the species' ecological niches would restrict their distributions, migrate out of the equatorial regions, moving southernly along the Pacific coast of South America. This is consistent with current hypotheses, which predict that equatorial species will migrate poleward during periods of global warming (e.g. Perry et al., 2005; Chen et al., 2011). When the modelled niches of the modern fauna were projected into the Pliocene, their predicted distributions were consistent with the Pliocene distributions. The same was true when the modelled niches of the Pliocene fauna were projected into the present day. The striking similarity between the modeled distributions and known occurrence data suggests that ENMs can accurately predict faunal movement in response to climate change. Furthermore, the results demonstrate the usefulness and applicability of the paleontological record in providing relevant information for modern conservation efforts.

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# The lateral process of the pubis of Microraptorinae (Theropoda: Dromaeosauridae) and its functional implications for respiration and locomotion

Matthew M. Rhodes, and Philip J. Currie

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

The Microraptorinae is a clade of dromaeosaurid dinosaurs closely related to birds, characterized by a prominent lateral tubercle or process on the midshaft of the pubis, among other features. Previously, this tubercle has been interpreted as a muscle attachment site with little evidence or functional reasoning. The holotype of the microraptorine *Hesperonychus elizabethae*, a partial pelvis discovered in Alberta, allows detailed examination for functional morphology. Comparison to its closest living relatives (i.e., crocodylians and birds) offers reasonable interpretation of soft tissue sites, providing a perspective not possible from strictly observing bones. Microraptorine pelvic soft tissue is reconstructed based on extant phylogenetic bracketing and direct observation of attachment sites.

Inspection of the lateral pubic process of *H. elizabethae* reveals a highly unusual texture for muscle attachment and it is therefore reinterpreted as an anchor for pubo-gastralial ligaments. In this location, well-preserved dromaeosaurids have gastralia, extant crocodylians possess a ligamentous sheet connecting to gastralia, and theropods ancestral to Dromaeosauridae have robust pubic boots for ligament attachment. This ancestral attachment surface was modified in Microraptorinae probably because of pubic retroversion and mediolateral compression of the pubic boot, resulting in development of the lateral tubercle to maintain a pubo-gastralial connection. Enlargement of the lateral process is concomitant with reduction of the pubic apron, from which locomotory muscles originate. This results in a secondary function as a pulley for the lateral process of the pubis. This unique morphology among microraptorines suggests that a pubo-gastralial connection remained important and that some pelvic locomotory muscles may have required unique organization for hindlimb manipulation, both possibly related to the acquisition of four-winged flight in this clade.

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## Preliminary report on the vertebrate diversity of a Late Cretaceous marine bonebed from the Bearpaw Formation

Hallie P. Street

Royal Saskatchewan Museum, T. rex Discovery Centre, PO Box 460, Eastend, SK, S0N 0T0; hallie.street@gov.sk.ca

While the presence of large marine reptiles from upper Campanian-lower Maastrichtian Bearpaw Sea deposits of southern Alberta and Saskatchewan has been well reported, the overall vertebrate diversity of the seaway is relatively poorly documented. A Bearpaw Formation bonebed discovered near the town of Herschel, SK has been heavily collected over several field seasons by Royal Saskatchewan Museum staff. These collecting efforts have yielded over 2,000 specimens; most specimens consist of isolated elements, but a few examples of associated fossils, such as the holotype of the plesiosaur *Dolichorhynchops herschelensis*, have been recovered. Elasmosaurid and mosasaurine fossils have also been identified among the collection. Interestingly, many of the marine reptile elements are relatively small, and there is also a high occurrence of disarticulated plesiosaur vertebrae, which is another indicator of indi-

vidual immaturity. In addition to the marine reptile fossils, numerous teeth and vertebrae of both bony and cartilaginous fish have been found. The teeth indicate the presence of actinopterygian groups such as Enchodontidae, Pachycormidae, and Ichthyodectidae. The majority of the chondrichthyan teeth represent Lamniformes, but specimens of Hybodontidae and Callorhynchidae are also present. At least six morphotypes of fish vertebrae have been identified, and investigation continues in order to more accurately account for the diversity of fishes from this locality. Based on the faunal composition of the Herschel bonebed, this region of the Bearpaw Sea appears to have been a productive, shallow system that served as a refuge for juvenile marine reptiles.

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## Flight before birds: Were ancestral pennaraptoran theropods capable of aerial locomotion?

Corwin Sullivan

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

Primitive birds such as *Archaeopteryx* and *Jeholornis* were undoubtedly capable of some form of flight (flapping and/or gliding). Among non-avian members of Pennaraptora, the clade of theropod dinosaurs that encompasses birds and their closest relatives, the distribution of volancy is complex and difficult to understand. The pennaraptoran clades Troodontidae and Dromaeosauridae – which together with birds make up the Paraves – both appear to include a mixture of volant and non-volant taxa, suggesting that flight may have been an ancestral paravian condition that was abandoned in most troodontids, most dromaeosaurids, and some birds. Still more problematic are the pennaraptoran clades Scansoriopterygidae and Oviraptorosauria. Scansoriopterygids lack the pennaceous, blade-like feathers that are otherwise pervasive in Pennaraptora, but at least one member of the group was evidently capable of gliding on unusual membranous wings. All known oviraptorosaurs were too bulky and short-armed to have been volant, but the well-known Early Cretaceous taxon *Caudipteryx* shows a number of features suggestive of recent descent from volant ancestors, including not only pennaceous feathers but also a short tail, a wrist capable of folding in a bird-like manner, a reduced third finger, and arguably a propatagial membrane extending between the wrist and shoulder. Furthermore, oviraptorosaurs resemble dromaeosaurids and most birds in exhibiting a high level of ribcage ossification compared to other theropods. The functional implications of this feature are uncertain, but a stiffened thorax may be better equipped to withstand the stresses associated with aerial locomotion and/or sustain the level of ventilation needed for volancy. Particularly given that the earliest stages of oviraptorosaur history are not represented in the known fossil record, the possibility that volancy was an ancestral pennaraptoran trait and that oviraptorosaurs are secondarily flightless should not be dismissed.

# Optimization of Bayesian inference framework for the analysis of morphological data by using empirical character state frequencies

Oksana V. Vernygora

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

Recent advances in computational phylogenetics have significantly facilitated evolutionary research by allowing time efficient processing of large data sets. However, utility of statistical model-based approaches (maximum likelihood and Bayesian inference) to phylogenetic reconstructions using morphological data has long been a controversial subject due to apparent unrealistic assumptions of the available models of evolution. The explicit time-reversible Markov model (Mk) of morphological data evolution specifies an oversimplified evolutionary scenario with a single rate of character state substitutions and equal character state frequencies – assumptions which are almost never corroborated by empirical data sets. Development and implementation of new models of evolution, which would provide a more accurate estimation of the morphological evolution, are hindered by both an infinitely complex nature of the morphological trait evolution and computational power constraints. Despite these limitations, optimization of the model-based approaches for the morphological data analysis is necessary for a more accurate estimation of evolutionary relationships. Here, I present a model of morphological trait evolution which implements empirical character state frequencies for each individual character in a data set. The model can be applied to binary as well as multistate characters. To test performance of the new model, I analyzed empirical as well as simulated morphological data sets under traditional Mk model and my newly proposed model. Results of the two models' estimations were compared using the model-fit tests (Akaike information criterion [AIC] and Bayes factor [BF]) as well as Robinson-Foulds (RF) distances to assess accuracy of the topology reconstructions. The major findings indicate that the new model has higher model-fit values under both AIC and BF as well as higher accuracy of tree topology reconstruction as shown by lower RF values compared to the Mk model for both empirical and simulated data sets.

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# A new and unusual microfossil assemblage from the Horseshoe Canyon Formation of southern Alberta, Canada

S. Amber Whitebone, Philip J. Currie, and Gregory F. Funston

University of Alberta, Department of Biological Sciences, CW-405 Biological Sciences Building, Edmonton AB, Canada T6G 2E9; swhitebo@ualberta.ca; pjcurrie@ualberta.ca; gfunston@ualberta.ca

Microfossil sites (more commonly called microsites) are localities where small fossil remains of vertebrates have been concentrated, usually due to low-energy fluvial environments. The majority of documented microsite material from southern Alberta has been collected from the Dinosaur Park Formation (DPF) with comparatively little from the Foremost and Oldman Formations, and, to an even lesser extent, the Horseshoe Canyon Formation (HCF) (Brinkman, 1990). This has led to difficulty in assessing the faunal turnover of vertebrates that are better represented through microfossil material throughout the late Cretaceous of North America.

Here we describe a new microsite from the HCF with an unusual faunal assemblage, characterized by an abundance of troodontid and anuran material, theropod and ornithomimid perinates, and the first fossil eggshell from



Figure 1. Fossil material from the Morrin microsite locality. a. – c. *Troodon* teeth. d. & e. *Troodon* eggshell. f. Dromaeosaur tooth. g. perinate hadrosaur dentary (scale = 5mm). h. perinate hadrosaur vertebra (scale = 5mm). i. premaxillary tyrannosaur tooth (scale = 5mm). j. *Pediomys* tooth. k. perinate ornithomimid claw (scale = 5mm) l. ankylosaur tooth. m. pachycephalosaur tooth. n. Holostean A scale. o. anuran maxilla. p. anuran ilium. Unless otherwise specified, scale bars = 1mm.

the HCF. As in most Alberta assemblages, ornithopods are the most common fossils at the site. In contrast, rare taxa like troodontids, anurans, tyrannosaurs, and holosteans (Brinkman, 1990) are unusually abundant. The site is similar to another troodontid-dominated site described by Ryan et al. (1998) but is unique in the abundance of anurans and eggshell.

Microsites are usually found at the bases of channel lag deposits, where material has been concentrated by transport. However, at this locality we find both large fossils and microfossils in close association, suggesting less taphonomic bias than other microsites. The sedimentology is typical of a low-energy overbank deposit, incapable of transporting material long distances. Together, these features suggest that the accretion of small vertebrate material here may represent a true biological association. The presence of amphibians is an indication of a healthy environment (Hilty and Merenlender, 2000; Carignan and Villard, 2002) and suggests that the depositional environment at this locality is a body of standing fresh water (such as a pond). This is supported by the preservation of eggshell material, which was likely only possible in the absence of soil acidity (Ryan et al., 1998).

Examination of the eggshell suggests it belongs to a troodontid nester, probably *Albertavenator*. The fossil assemblage at this locality therefore suggests that a nesting site for troodontids was nearby. This suggests a non-random association between troodontids and perinate material from other dinosaurs. Although we find no direct evidence of predation, it is likely that the altricial hadrosaur perinate (Horner et al. 2001) found here were a food source for the precocial fledgling *Troodon*. Similarly, the presence of anurans and other perinates, like ceratopsians and theropods, may be the result of targeted predation by *Albertavenator*.

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# Ontogenetic variation in the bone histology of caenagnathid mandibular symphyses

Ryan D. Wilkinson, Gregory F. Funston, and Philip J. Currie

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

Caenagnathidae is a clade of middle to Late Cretaceous theropod dinosaurs found in Asia and North America. Caenagnathid growth, development, and variation is difficult to study as most caenagnathid specimens are preserved as isolated elements. This study examines the histological characteristics of four caenagnathid mandibles from the Dinosaur Park Formation suspected to represent an ontogenetic series to identify trends or patterns in the cell- and tissue-level features of these dinosaurs. Thin sections of the mandibular symphysis were examined with light microscopy and their histological features were observed and described. The larger specimens were characterized by a reduction in the rate of growth, an increase in lamellar bone, and an accumulation of secondary remodelling structures such as Haversian canals throughout ontogeny, which we interpreted as ontogenetic trends. Lines of arrested growth indicated an increased developmental age in two of the specimens. Additionally, developmental and growth patterns including the rapid fusion and obliteration of the mandibular symphysis and the widening of the mandible at the symphysis were identified in later ontogenetic stages. The concentration of Haversian canals along the occlusal margin and lingual ridges suggests remodelling as a histological response to high levels of repeated stress. These descriptions add to our knowledge of the growth and development of caenagnathids and the identification of an ontogenetic series may aid in the taxonomic classification of partial or incomplete caenagnathid skeletons.

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# Microwear and finite element analyses of theropod denticles highlight shared feeding strategies among theropods and divergent prey selection between dromaeosaurs and troodontids

Ryan D. Wilkinson<sup>1</sup>, Angelica Torices<sup>2</sup>, Victoria M. Arbour<sup>3,4</sup>, Jose Ignacio Ruiz-Omeñaca<sup>5</sup>, and Philip J. Currie<sup>1</sup>

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

<sup>2</sup>Departamento de Ciencias Humanas, Universidad de La Rioja, 26004, Logroño, La Rioja, Spain

<sup>3</sup>Royal Ontario Museum. Department of Natural History, 100 Queens' Park, Toronto, Ontario, M5S 2C6, CANADA

<sup>4</sup>University of Toronto. Department of Ecology and Evolutionary Biology. 25 Willcocks St, Toronto, Ontario

<sup>5</sup>Grupo Aragosaurus-IUCA, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, Spain

The teeth of putatively carnivorous dinosaurs are often blade-shaped with well-defined serrated cutting edges. These serrated teeth are often easily differentiated based on the morphology and density of the denticles. A tearing function has been proposed for theropod denticles in general, but the functional significance of denticle morphological variation has received less attention. In particular, the unusually large and hooked denticles found in troodontids suggest a different feeding strategy or diet compared to other small theropods. We used a two-pronged approach to investigate the function of denticle shape variation across theropods with both similar body shapes and sizes (e.g., dromaeosaurids vs. troodontids) and highly disparate body shapes and sizes (e.g., troodontids vs. tyrannosaurids), using microwear and finite element analyses. We found that many toothed coelurosaurs employed a puncture-and-pull feeding movement generating two main families of microwear scratches; scratches parallel to the long axis of the tooth that form while biting down into prey and scratches oblique to the long axis of the tooth that form as the head is pulled backwards with the jaws closed. In the finite element analyses, a 90 N bite force was applied to three theropod tooth models representing different denticle morphologies – *Dromaeosaurus* with rounded denticles, *Saurornitholestes* with angled denticles, and a troodontid with large hooked denticles – at a variety of angles to test if they perform optimally when the bite angle is aligned with their oblique microwear scratches and how denticle morphology effects stress distributions within the tooth. All three theropod teeth showed the lowest von Mises stress when the bite force was aligned with the oblique family of microwear scratches, demonstrating denticle morphology is adapted to minimize stress during the pulling portion of the bite. The three tooth models showed similar values of von Mises stress at their optimal bite angles; however, the troodontid model showed the highest von Mises stress at its not-optimal bite angle compared to the other models, suggesting the large hooked denticles of troodontids are more likely to fail when the applied bite force deviates from the optimal bite angle. A predator has little control over the violent, struggling motion of its prey and therefore the applied forces will deviate from its optimal bite angle. The large hooked troodontid denticles are particularly vulnerable to these forces suggesting troodontids may have favoured softer, smaller, or immobile prey. The *Dromaeosaurus* and tooth models are less vulnerable to these forces, suggesting they are capable of pursuing larger prey.

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