

Meeting Logo Design: Many thanks to Maria Hussain for creating our 2024 CSVP logo! The logo features the skull of the predatory fish *Xiphactinus* whose fossil remains have been found from Cretaceous rocks of the Western Interior Seaway in Manitoba.



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# Abstracts

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# Preservation of a nearly complete trematopid skull in a dense accumulation of partially articulated and disarticulated skeletal elements from Richards Spur, Oklahoma

# Adrian F. Osterling Arias<sup>1</sup>, Ethan D. Mooney<sup>1</sup>, Joseph J. Bevitt<sup>2</sup>, and Robert R. Reisz<sup>1</sup>

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Modern-day terrestrial amphibians pale in comparison to their monstrous ancient relatives, the Late Carboniferous and early Permian trematopid temnospondyls. With a skeleton that clearly indicated a terrestrial mode of life and armed with an impressive set of large, recurved marginal dentition and very large palatal fangs for holding their prey, this group of terrestrial temnospondyls roamed the Early Permian (~298 million years ago (Ma)) of North America and Central Germany as a top predator. Lack of substantial informative fossil material has previously limited our understanding of trematopid diversity and ontogeny. Fortunately, this has been changing in the last few decades with the help of exceptional localities like the early Permian locality Richards Spur, which has already produced an exceptional collection of cranial and postcranial material. Interestingly, while multiple species of dissorophid temnospondyls have been described from Richards Spur, only one trematopid species has been confidently recognized: Acheloma dunni. Here we report on the presence of a new, large, relatively mature trematopid skull from this famous locality, which has been found encased within a limestone rich block containing a very high density of various articulated and disarticulated skeletal remains from several other taxa. With the help of neutron computed tomography (nCT), a non-invasive method of analyzing internal and external morphologies, this specimen has revealed several features consistent with the genus, Acheloma, but distinct from Acheloma cumminsi (Cope 1882), and Acehloma dunni (Polley & Reisz 2011). These distinct features include: a lateral exposure of the ectopterygoid (l.e.e.) larger than the orbit, a unique oval-like cranial ornamentation texture, an exclusion of the lacrimal-jugal contact from the maxillary element produced by a contact between the l.e.e. and quadratojugal, and the maximum skull width occurring at the same level as the pineal foramen. The identification of these new features, in addition to the characters it shares with other Acheloma species, not only constitute it as a new species of this genus, but also challenges the notion of having synonymized Acheloma dunni with Acheloma cumminsi. In this study, new data has been collected for the purpose of elucidating the taxonomic diversity of trematopids at Richards Spur, while simultaneously supporting the reinterpretation, redescription and diagnosis for the genus Acheloma. As a result of not being hindered by ontogenetic disparities, these new characters and descriptions could potentially be used to resolve some of the complexities involving the evolutionary history and phylogenetic relationships of this fascinating group of Paleozoic terrestrial predators.

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## Horncore size as an ecometric indicator? Considerations from the examination of North American *Bison*

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Historically, American bison (*Bison bison*) were found across North America (i.e., northern Mexico to northern Canada) and in a variety of climatic conditions, which may have influenced their morphology. Bison horncores may be particularly susceptible to climatic influence because they are highly vascularized and thus might represent sites of considerable heat loss. Larger horncores may, for example, possess a larger surface through which body heat can be lost. In warmer climates, shedding excess heat may be beneficial; in colder climates, retaining body heat is critical. The purpose of our research is to evaluate the relationship between bison horncore size and climate. Cranial material for 131 North American *Bison bison* specimens across the latitudes of  $35^\circ$ – $65^\circ$ N were measured for horncore length, circumference, and body size proxies. Horncore basal circumference and body size show strong support (Pr(>|t|) = 1.4e-10) and unexpectedly, ANOVA supports a positive correlation between basal horncore circumference and latitude for bison (Pr(>|t|) = 0.008). Though the trend is overall positive, Tukey HSD indicates this significance is driven by a few highly significant pairs. These preliminary results may be due to additional factors (e.g., Sexual dimorphism, subspecies variation and/or other physiological constraints) which may obscure the variation in horncore size driven purely by latitude and climate, by not accounting for these factors, latitude bins may not be comparable. Work is ongoing and the results reported here are preliminary.

# 'Mini bosses'; new specimens help to elucidate the ontogeny of the *Pachyrhinosaurus* (Centrosaurinae, Ceratopsidae) boss

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Late Cretaceous ceratopsian dinosaurs are renowned for their elaborate head ornamentation, including orbital horns, nasal horns, and embellishments of the parietal frill. While these features are well represented in adult animals, and indeed often define species, the ontogeny of the structures is not well understood in most ceratopsian taxa. The centrosaurine *Pachyrhinosaurus* is notable among ceratopsians for having a massive bony boss in place of

the nasal horn, as well as bony bosses over the orbits. Currie et al. (2008) speculated that the nasal boss developed as two ridged 'demihorns' from the paired nasal bones, which fused together and accreted bone laterally in sub-adulthood. In some, though not all cases, the nasal bosses become deeply invaginated as the animal matured. The paucity of cranial material from the youngest juvenile animals has hindered further research regarding the nasal boss development. The development of the orbital bosses has hitherto remained undescribed. Herein, we present four new specimens of *Pachyrhinosaurus lakustai* which may aid in the establishment of an ontogenetic pathway for boss development.

The Pipestone Creek Pachyrinosaurus Bonebed outside Wembley, Alberta is a monodominant allochthonous bonebed preserving hundreds of *P. lakustai* individuals. Thought to represent a large herd of animals killed in a catastrophic event, the bonebed contains a range of ontogenetic stages. While no complete juvenile skulls have yet been recovered, fragments of juvenile cranial material are present in the bonebed. The specimen that sparked interest in this study is PCB 2017.312, collected from Pipestone Creek in 2017 and prepared in 2024. Originally misidentified as a jugal fragment, PCB 2017.312 is a juvenile orbit with a distinctive blade-like ridge where the orbital boss is situated in an adult animal. A second specimen, UALVP 60396.1, was identified from an older collection, also originally misidentified. UALVP 60396.1 is also an orbital bone from a very young animal, displaying a similar blade-like ridge over the eye. These two specimens suggest that, like the nasal boss, the orbital boss began as a bladed 'demi-horn'. During development, these ridge-like demihorns, may have begun to laterally accrete bone mass to produce the orbital boss. A third specimen, PCB 2022.092, the partial skull of a subadult P. lakustai collected from Pipestone Creek, provided another intriguing clue into orbital boss development. The area immediately below the orbital boss in PCB 2022.291 is represented by a hollow cranial cavity. CT scans attained in 2023 of a complete adult P. lakustai skull, TMP.2002.29.1, suggest this cavity beneath the orbital boss is present in mature animals as well. As resorption of bone material occurs in the nasal bosses *P. lakustai*, it may be suggested that resorption also occurs beneath the orbital bosses as the animal ages, creating the orbital boss cavity. The biological purpose for this orbital boss cavity remains unclear; more specimens and more research will be needed to fill in the ontogenetic gaps in the orbital boss sequence. However, these four specimens provide an important insight into the development of these highly unique cranial characters.

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# Enigmatic new specimens broaden the marine paleodiversity of the Late Cretaceous Western Interior Seaway, Manitoba

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The marine vertebrate diversity of the Late Cretaceous Western Interior Seaway (WIS) of North America is mainly represented by large marine reptiles, birds, bony fish, and sharks. Although the great majority of previous descriptions have been based on macrovertebrate specimens, recent analyses of microvertebrate fossils (<2 cm) have revealed new occurrences of taxa previously unknown from Manitoba, suggesting the faunal assemblage of the WIS was richer and more diverse than thought before. In this work, we analyse microfossils collected from sites typically associated with large macrofossils to reconstruct niche occupancy and mid-level trophic structure of the WIS in Manitoba. Samples were mechanically prepared out of sediment from field jackets collected from

the Millwood Member of the Campanian-aged Pierre Shale. Initial results suggest that the specimens represent new species of bony fish and embryonic marine reptiles. Two small specimens, preserved in nodules, have unusual rows of tooth-like ornamentations. Scanning Electron Microscopy images and Computed Tomography scans, segmented using Amira software, suggest they are teeth belonging to Pycnodontidae indet., and have an unusual tooth replacement pattern. The identification of these two enigmatic specimens will add further insights to our knowledge of the marine diversity of the Western Interior Seaway during the Late Cretaceous of Manitoba.

## Functional diversity and structure of Late Cretaceous microsite palaeocommunities of the Belly River Group (Campanian; Alberta)

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Latitudinal and altitudinal differences in faunal composition in the Cretaceous of North America have become important for the study of faunal turnover in greenhouse climate systems. The composition and diversity of many taxa recovered in this region are strongly tied to their altitudinal distance and to long-term transgression-regression cycles. Understanding the functional ecology of such systems may be relevant to predicting biological responses to modern climate-mediated sea level changes and biogeographic range shifts. Here we use a high-resolution record (60 sites, >75,000 specimens) of vertebrate microfossil bonebeds to examine functional diversity among vertebrate communities in a coastal plain ecosystem experiencing climatic change and sea level fluctuations. We find that functional richness is highest during more marine-influenced intervals of higher sea level and lower during more terrestrial communities associated with lower sea level. Conversely, we see functional disparity, evenness, and divergence highest during periods of greater terrestrial exposure. This suggests that while palaeocommunities under higher sea level may have a larger total number of ecologies represented, the relative distributions of taxa may indicate that the more terrestrial communities were as functionally complex, with more even distributions of differing ecologies and energy among taxa. Results thus far suggest that vertebrate communities in nearshore epeiric marine systems in this Cretaceous greenhouse climate were comparatively simple when compared to the greater niche-partitioning present among adjacent terrestrial palaeocommunities.

# Were tyrannosaurs 'lions' or 'dragons'? Investigating the ecological role of *Gorgosaurus libratus* in the Dinosaur Provincial Park biota using trophic networks

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The body size, feeding morphology, energy requirements, and ontogenetic history of a predator at the top of its community's food chains have long been known to affect its prey selection as well as the shape of its community's trophic pyramid through biomass distributions. Together, these traits offer strong baselines to assess an ecosystem's stability. On land, only two extreme suites of traits seem to persist in apex predators in the present: a combination of high metabolic requirements through endothermy (thus low biomass densities) and consistent prey selection through ontogeny, as seen in large carnivoran mammals; and inversely one of low metabolic requirements through ectothermy (thus high biomass densities) and clear ontogenetic dietary shifts, as seen in the Komodo dragon, *Varanus komodoensis*. Where, then, would large extinct theropod dinosaurs such as tyrannosaurs land between these extremes considering combined evidence for endothermy (or mesothermy) and ontogenetic dietary shifts inferred from fossil specimens at different life stages? In other words, was the ecological role of tyrannosaurs more akin to 'lions' or 'dragons'? Based on current palaeontological evidence, we hypothesize that it was not analogous to either of these predator types, instead lying in an intermediate position along the spectrum they delineate. If this hypothesis is true, it could suggest an alternate stable community structure in Late Cretaceous Asiamerica that no longer exists.

We test this hypothesis by comparing the tyrannosaurid *Gorgosaurus libratus*, with the African lion *Panthera leo* and *V. komodoensis* using biomass distributions and trophic network properties. *G. libratus* is the ideal tyrannosaurid species for this study because its fossil record has a relatively complete ontogenetic series and it was the most abundant apex predator of the Late Cretaceous (Campanian) Dinosaur Provincial Park (DPP) biota. This is one of the few Mesozoic non-marine localities to have a sufficiently complete fossil record to infer trophic interactions, body size, and relative taxon abundances, which together form an ecological network that lays a foundation for the present study. The role of *G. libratus* in its food web was compared to that of *P. leo* and *V. komodoensis* by aggregating two published food webs of the Serengeti community and by designing the first food web for Komodo Island.

Estimates of the predator-prey biomass density relationship of DPP revealed that this community had a systematically higher predator-prey ratio than African savanna communities of similar prey biomass and landed instead within the range of biomass densities obtained for Komodo. Secondly, the DPP trophic network reveals that traits such as prey-averaged and chain-averaged trophic level vary in *G. libratus* through ontogeny in a similar way to the variation observed in the Komodo dragon, which reflects their inferred ontogenetic dietary shifts. However, these traits become more comparable to the lion when the possibility of cooperative hunting in tyrannosaurs of different age classes is accounted for. Together, these results appear to confirm the hypothesis that *G. libratus* had a unique suite of apex predator traits compared with approximate extant trophic analogues.

# Examination of a novel ichnofossil assemblage near Tumbler Ridge, BC., provides insights into the Cenomanian palaeoecology and palaeoenvironment of northern British Columbia

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The fossil record of the Cretaceous of western Canada is dominated by the diverse fossil assemblages of southern Alberta, which allow for detailed regional palaeoecological and palaeoenvironmental reconstructions. However, these reconstructions represent a limited geographical and temporal section, which limits the understanding of the overall palaeoecology of Cretaceous North America. Creating palaeoecological reconstructions of other geographical areas and time periods is thus important for understanding, for example, how the Cretaceous palaeoecology of Canada changed over time. In this study, we examine the Babcock Creek tracksite, a Cenomanian ichnofossil site, from the basal Kaskapau Formation of northwestern British Columbia, southeast of the community of Tumbler Ridge. The site comprises multiple interbedded layers of rippled mudstone and fine-grained to medium-grained sandstone beds, and exhibits a diverse assemblage of ichnofossils, including various invertebrate traces, small and large vertebrate traces, and trackways. This abundance of ichnofossils can provide insights into the Cenomanian paleoenvironment and palaeoecology of what is now northwestern Canada.

Invertebrate traces include *Lockeia*, *Thallassinoides*, *Rhizocoallium*, *Teredolites* in wood-rich beds, and possible lobster burrows in the lower mudstone beds. These traces, along with the associated sedimentological features, suggest a shallow, coastal, deltaic environment with shallow water displaying multiple current directions due to ladder ripples, and a change between deltaic channel and coastal marine deposition. Fossilized bivalves, consistent with a known bivalve bed in the basal Kaskapau Formation, further support the coastal, deltaic environment hypothesis. Large vertebrate traces include *Tetrapodosaurus* manus and pes prints that are attributed to an ankylosaurid, and tridactyl pes prints, which can likely be attributed to a large ornithopod, due to the size and shape of the print. Individual traces include possible crocodilian tail traces, both a small and large *Magnoavipes* print, and a small, irregularly shaped track resembling the manus of *Pteraichnus*. Finally, a trackway that resembles *Haenamichnus*, and is tentatively attributed to a large pterosaur, includes two left and right manus-pes pairs, with pes prints ~36 cm in length and a stride length of ~160 cm, indicating a large trackmaker.

The Babcock Creek ichnofossil assemblage provides insights into the regional Cenomanian palaeoecology. Ankylosaurid and ornithopod tracks are consistent with other studies of Cenomanian dinosaur diversity. While the identity of the large *Magnoavipes* trackmaker is still debated, the size of Babcock Creek specimens suggests a medium-sized theropod trackmaker, possibly a large maniraptoriform. Finally, the resemblance of the purported pterosaur trackway to *Haenamichnus* suggests that the trackmaker was similar to an azhdarchid pterosaur, although there is no reported Cenomanian North American azhdarchid body fossil material. Overall, the Babcock Creek tracksite contains a diverse assemblage of ichnofossils and provides insights into the palaeoecology of the Cenomanian of what is now northwestern Canada.

# Ecological implications of feeding mechanics in a contemporaneous lambeosaurine and hadrosaurine (Ornithopoda: Hadrosauridae) from the Dinosaur Park Formation, Alberta, Canada

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Lambeosaurines, a lineage of duck-billed herbivorous dinosaurs, exhibit extreme modifications to the facial skeleton, where the premaxillae, nasals, and prefrontals are modified to form prominent supracranial crests that developed early in ontogeny. The crests are hypothesized to have facilitated intraspecific communication via sound production and sociosexual visual display. Oddly, these crests are extensions of the premaxillae and nasals onto the skull roof, where stress from feeding is usually dissipated in amniotes. Their sister group, the hadrosaurines, exhibits the plesiomorphic condition, lacking hollow crests and having proportionately longer skulls. It has been suggested that these differences in skull shape may have forced lambeosaurines to feed on softer vegetation than hadrosaurines, but it is unknown exactly how these differences in skull shape affected feeding mechanics through ontogeny and between crested and non-crested forms. To test for differences in feeding mechanics, we used finite element analysis (FEA) to describe the distribution of stress in the skull of the hadrosaurine Gryposaurus notabilis and an ontogenetic series of the contemporaneous lambeosaurine Corythosaurus casuarius during simulated feeding. A subadult Gryposaurus, and four Corythosaurus (two juvenile, one subadult, and one adult) were CT scanned and segmented to generate 3D models of the skull and lower jaws for manipulation. The models were then retrodeformed to repair missing or damaged areas. Jaw muscles were reconstructed to calculate maximum muscle input forces, and restraints were placed to simulate biting and chewing vegetation at four points: the tip of the premaxilla, the anterior end of dental battery, the middle of the dental battery, and the posterior end of the dental battery. The reconstructed models were then subjected to FEA to map the distribution of stress throughout the skulls at each position, with the bone and dental batteries modeled as separate materials. Mechanical efficiency (ME) was calculated at each bite point to determine what proportion of muscle force was converted into bite force. We found Gryposaurus generated greater muscle forces than similarly sized Corythosaurus due to relatively larger temporal chambers, and Gryposaurus also exerted greater force at each bite point. Interestingly, the skull of Gryposaurus also had greater ME than Corythosaurus across all bite points, meaning a greater proportion of muscle force was transferred to the bite point. Gryposaurus exhibits concentrated stress in the snout and braincase, as is typical for amniotes more broadly. Crestless juvenile Corythosaurus concentrated stress primarily through the lateral processes of the premaxillae, whereas the crested subadult and adult dissipate less stress through the premaxillae, instead concentrating it in the facial skeleton and temporal region. The greater bite force and ME in *Gryposaurus* suggests that this taxon may be better able to process tough foods, and Corythosaurus may therefore have had a more limited diet breadth. Additionally, the ontogenetic changes observed in Corythosaurus suggest that the expansion of the premaxillae and nasals to form the crest altered the distribution of stress in the skull during feeding. This work suggests the potential for an evolutionary trade-off between feeding efficiency and the development of bizarre cranial structures in lambeosaurine evolution.

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# Histological analysis of linear enamel hypoplasia in recent and fossil crocodilians

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Dental tissues are ideal to study records of disease and physiological stress. In particular, enamel formation can be disrupted during episodes of systemic metabolic stress, which present in the form of linear enamel hypoplasia (LEH). As enamel formation progresses apical-cervically (towards the root), systemic stress events permanently damage ameloblasts in their secretory phase. When the systemic stress resolves, enamel formation returns to normal. This results in a transverse groove in the surface of the enamel, which can be identified upon gross visual inspection. Counts and frequencies of LEH are commonly reported in archaeological and biological anthropology studies, where they are used to compare the general health between individuals or populations. Comparatively few palaeontological studies have utilized linear enamel hypoplasias to infer on the responses of prehistoric animal communities to environmental change.

Our knowledge and understanding of LEH are formed exclusively from research on mammalian teeth. LEH have yet to be reported in reptilian teeth. Thus, a huge gap exists in our knowledge of reptilian tooth development; is reptilian enamel susceptible to LEH formation? Features grossly similar to LEH have been briefly studied or mentioned in ichthyosaurs, pliosaurs, rauisuchians, thalattosuchians, and non-avian theropods. These are mainly discussed in terms of taxonomic utility or biomechanics with suggestions about them being a result of growth.

Given that apical-cervically directed enamel formation is ubiquitous across toothed amniotes, we suspect that many of these instances represent LEH. A survey of the recent skeletal remains and fossils of crocodilians is ongoing at the Royal Ontario Museum. Recent and fossil specimens which possess putative LEH were studied with micro-CT imaging, SEM imaging, and ground thin sections. These include captive raised and wild *Alligator mississippiensis* and *Caiman crocodilus, A. mississippiensis* from the Pleistocene of Florida, USA, *Brachychampsa* sp. from the Upper Maastrichtian Hell Creek Formation of South Dakota, USA, and isolated indeterminate eusuchian teeth from the Campanian Belly River Group of Alberta, Canada. Micro-CT images and ground thin sections demonstrate that the linear groove features are the result of abnormally thin enamel. Furthermore, incremental bands of enamel identified in ground thin sections conform to the morphology of the defect, demonstrating that the grooves are the result of abnormal growth as opposed to wear/damage. The identification of LEH in recent and fossil crocodilians to environmental and biotic change, and encourages the search for LEH in other reptilians.

## Utilizing fossilized tree resin geochemistry to understand anomalous Cretaceous dinosaur diets

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During consumption, biomineralized tissues such as enamel, dentine and collagen become enriched in 13C relative to the consumer's diet; the degree of enrichment is regarded as the trophic enrichment factor. Cretaceous vertebrate bioapatite is anomalously enriched when compared to expected values from a C3 plant dominated ecosystem. Cretaceous primary consumers exhibit an ~18‰  $\delta$ 13C increase in comparison to their diet; one of the highest non-diagenetically altered trophic enrichment factors ever observed. The cause of this enrichment is poorly understood but current consensus points towards environmental phenomena affecting vertebrate dietary systems. Here we suggest an alternative hypothesis that C3 plant δ13C values are enriched in comparison to modern plants and this enrichment is not being reflected in commonly used plant proxies. Such proxies are used to estimate primary consumer trophic enrichment factors but are often highly susceptible to diagenetic alteration or tissue-specific isotope values. Instead, the use of diagenetically stable fossil resins as a C3 plant proxy is favourable as they retain their  $\delta 13C$  values for millions of years. Cretaceous resins already display enriched  $\delta 13C$ in comparison to modern resins, suggesting similar  $\delta 13C$  enrichment in C3 plants. By comparing stratigraphically similar resins and vertebrate enamel, we hope to demonstrate that current trophic enrichment factors for Cretaceous vertebrates are closer to what would be expected based on modern organisms. Our results will hopefully allow for a better understanding of the diets of primary consumers during the Cretaceous carbon isotope anomaly and improved scrutiny of extinct food-webs. This will then hopefully allow for more accurate trophic enrichment factors for Cretaceous vertebrates to be made. If our study is conclusive, we hope that amber becomes a wider utilized proxy record able to be applied to multiple disciplines and element systems.

# Ordination methods for using vertebrate microsite fossils in palaeoecological analyses

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Vertebrate microfossil localities, also known as 'microsites,' are assemblages of disassociated and disarticulated vertebrate remains on the scale of millimetres to centimetres. Microsites tend to preserve durable elements that

are present in many different vertebrate taxa, such as fish scales and teeth, thus insulating microsites against size biases and making them useful for palaeoecological studies. However, these palaeoecologial studies have largely been descriptive in nature, and ordination techniques, which are commonly used in modern ecology and invertebrate palaeoecology, have rarely been applied to vertebrate microsite material. We are using microsite data collected throughout the 1990s and early 2000s to test whether ordination methods could be used to differentiate disparate palaeocommunities between the Oldman, Dinosaur Park, and Horseshoe Canyon formations of Alberta, Canada. Because these formations are temporally distinct and show different environmental signals, there should be differences in the structure of vertebrate communities in different formations. Using this assumption as a baseline for what an accurate ordination would look like, we tested different ordination methods and distance measures using both abundance and occurrence (presence/absence) data. We found that a two-dimensional non-metric dimensional scaling (NMDS) ordination using a Bray-Curtis distance measure on abundance data successfully differentiated vertebrate communities at the formation level. A few taxa, including *Lepisosteus* and the fish morphotype 'Holostean A,' were found to be driving the differences observed in the ordination. These results corroborate previous ecological studies that suggest that the aridity of the environment plays a large role in determining community structure.

## Mesozoic mammal teeth preserve daily records of growth

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Drastic differences in reproductive traits and maternal investment of extant mammals have spurred debate about whether life history played a role in the disparate survival and proliferation of mammals after the Cretaceous-Paleogene (K-Pg) extinction. Specifically, eutherian mammals (placental ancestors) reached greater abundance, diversity, and body sizes immediately after the K-Pg extinction, which has been argued to be related to their longer gestation periods than other mammals like metatherians (marsupial ancestors) and multituberculates (extinct). Testing this idea, however, has proved difficult, as until recently, proxies for life history and reproduction in extinct mammals were poorly constrained. Recent work has shown that palaeohistological data from teeth might be able to elucidate precise chronologies of early life in some ancient mammals. However, the applicability of these techniques to Mesozoic mammals has not been demonstrated—to date, there has never been a study on daily dental growth lines in a Mesozoic mammal. Here we present preliminary results from the first investigation into the incremental growth of Mesozoic mammal teeth, including eutherians, metatherians, and multituberculates. We find exquisite preservation of daily growth marks in these diminutive mammals, enabling us to establish detailed chronologies of tooth development. Whereas therian mammals exhibit incremental lines in both the enamel and the dentine, the unusual gigantoprismatic enamel of multituberculates prevents clear delineation of enamel laminations. However, the dentine of multituberculates does preserve excellent lines of von Ebner that allow measurement of crown formation times. Comparative growth metrics reveal substantial variation in dental growth rates between metatherians, multituberculates, and eutherians, but also within these groups. These results suggest that some of the major differences in life history between these groups were likely to have existed prior to the K-Pg extinction, but also that members of these clades did not necessarily adhere to singular, stereotypical life histories.

# Osteohistology of troodontid metatarsals from the Dinosaur Park Formation: implications for growth, stress, and understanding of pathology

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The Dinosaur Park Formation (DPF) in southeastern Alberta Canada is a rock unit of Campanian age deposited ~76–74 million years ago with a rich dinosaur fauna including multiple theropod families. Among the theropods, members of Troodontidae are some of the most enigmatic, as they are known from largely isolated material. This has created confusion when referencing specimens of various sizes as we currently lack ontogenetic or taxonomic precision for the clade within the DPF. Additionally, troodontids have a combination of features that make them unique among theropods within the DPF fauna. One example is their unique foot morphology, which shows an arctometatarsus condition with a specialized raptorial claw, like dromaeosaurids. While the biomechanics of the arctometatarsus have been studied broadly, the combination of this feature with a specialized raised medial ungual and the resulting stresses are poorly understood. Here we analyze the growth patterns, stress, remodeling, and pathologies observed in DPF troodontids over ontogeny using histology. Eleven specimens [three metatarsal IIs (MTII), three metatarsal IIIs (MTIII), and five metatarsal IV (MTIV)] across a broad range in absolute dimensions (length and circumference) from the Royal Tyrrell Museum of Palaeontology (RTMP) were selected to account for ontogenetic changes. Bone deposition patterns are consistent with biomechanical stress models of the arctometatarsalian condition, wherein secondary remodeling is concentrated posteriorly and along the contact surface of MTIII in MTII and MTIV. Growth curves were generated using circumference measurements of annuli and the cumulative areas within them. Most of the metatarsals analyzed show consistent growth rates very similar to those of birds, with rapid initial growth and subsequent plateau, with some conforming to the annuli of larger non-associated elements. This close growth relationship between specimens suggests that one species, or closely related troodontid species, are represented in the sample. The outliers that had slowed-down growth were the pathologic elements, which also occasionally demonstrated dual lines of arrested growth (LAGs) and accumulation of regionalized LAGs suggesting stressors accumulated throughout life. One notable specimen was an MTIV (associated with an MTII) that shows additional bone deposition forming a callus outside the normal margin of the shaft and a heavily deformed distal end, unlike anything observed in previous pathology surveys. In order to get a better picture of the pathology, computed tomography (CT) scanning was also employed to visualize the pathologies in 3D. Multi-LAGs towards the outer bone, finished external fundamental systems over the calluses in specific regions, and fractures contained within the cortical bone under the calluses suggest this animal succumbed to multiple pathologies that may or may not be associated throughout its life.

# Microvertebrate fossils in the Late Cretaceous Favel Formation of Manitoba, Canada: insights into paleoecology and trophic dynamics

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The Late Cretaceous Favel Formation (late Cenomanian to mid-Turonian) in Manitoba, Canada, offers a glimpse into ancient ecosystems. Recent analyses of microvertebrate fossils from the formation have revealed previously unknown diversity, including 14 species of fish, sharks, and birds identified for the first time in Manitoba. This increase brings the total known apparent diversity of Favel Formation microvertebrate taxa from 26 to 40 species and the combined total of macro- and microvertebrate taxa from 42 to 56 species. Through the analysis of microvertebrate fossils from the Favel Formation, our research aims to reconstruct the trophic dynamics of this ancient ecosystem, offering insights into the paleoecology of the Western Interior Seaway.

Microvertebrate assemblages were sampled from three fossiliferous stratigraphic horizons within the Favel Formation (lower, middle, and upper) containing four sites. Bulk rock samples of 63 to 110 kg were collected from 10-30 cm thick intervals of these horizons, and acid digestion was employed to extract microvertebrate fossils. We conducted trophic studies based on present-day analogues, particularly focusing on the Gulf of Mexico ecosystem, to compare the abundances of primary and secondary consumers and apex predators. Present-day studies indicate a balanced ecosystem in the Gulf of Mexico, with a higher biomass of primary and secondary consumers supporting apex predators. Similarly, analysis of microvertebrate data from the Favel Formation reveals a higher abundance of primary and secondary fish species, suggesting a trophic structure similar to typical marine habitats. These results contribute to broader discussions on ancient ecosystem dynamics and highlight the importance of microvertebrate fossils in reconstructing past environments. Overall, our study underscores the significance of microvertebrate fossils in unraveling the complexities of Late Cretaceous ecosystems.

# Tooth development and resorption in squamates—A comparison of living Teiidae and fossil Mosasauridae

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Teeth have defining characteristics that can be used to construct evolutionary relationships. Despite the diagnostic power of dentition, it is trivial within squamate phylogeny as squamates have a wide variety of tooth attachment types. Most notably, hard tissue histology and computerized tomographic (CT) scans have revealed that fossil marine lizards within Mosasauridae differ from their primitive ancestors by having a deep, socketed geometry of attachment instead of a shallow, asymmetrical one. Considering this morphological variation, internal investigation through soft tissue histology is necessary to determine relatedness between living and extinct squamates. This reasoning has been used to show that extant lizards, particularly *Tupinambis* (Teiidae), share a socketed mode of tooth attachment, symmetrical root structure, and three-layered attachment tissue system with mosasaurs. Because of these similarities, further comparative investigation is necessary to fully understand the geometry and mechanisms underlying tooth structure and resorption by osteoclasts (bone resorbing cells) within Mosasauridae. Thin-sectioning and histological staining of tooth tissues in extant *Tupinambis* will reveal the complex and unique attachment and resorption of teeth in teiid lizards, that will in turn help us understand the dynamics of mosasaur soft tissues at different stages of tooth development. Based on recent research findings, an analysis of tooth tissue development will be conducted at both the University of Alberta and King's College London with various historical stains—Tartrate-Resistant Acid Phosphatase (TRAP) staining (a marker for osteoclast activity) and Masson's Trichrome (a marker for collagen and other connective tissues)— in extant *Tupinambis* (Teiidae). The data produced will ultimately lead to various research outputs: a description of teiid tooth resorption, a comparison of mosasaur and teiid attachment geometry and tissues, as well as a description of mosasaur teeth that encompasses both tissue analysis and tooth reabsorption mechanisms.

## Why the long face? – a placoderm with extreme underbite reflects high disparity and modularity in early vertebrate evolution

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Jaws are a key structure that arose early in the vertebrate tree of life. Placoderms are stem gnathostomes and their study contributes to the understanding of diversification of feeding strategies, diets, and modularity early in our evolution. In these fossils, such variations in function are mainly expressed through jaw disparity. Modularity in the jaws can be expressed through disproportional lengths of the upper and lower jaws, as seen in marlins. *Alienacanthus malkowskii* is an arthrodire from the Famennian (Late Devonian) of Morocco and Poland, with lower jaws twice as long as the skull. All of its gnathal plates possess sharp, posteriorly recurved teeth that extend in the inferognathal past the occlusion with the upper jaw elements. A phylogenetic analysis places *Alienacanthus* as a selenosteid, and comparative study of the teeth with that of modern fish groups suggest the animal was piscivorous and used its sharp recurved teeth to catch and trap live prey. This armoured 'fish' expands the morphological and ecological diversity during one of the first radiations of jawed vertebrates with a combination of features so far unrecorded in arthrodires. This combination highlights a jaw mechanism that is different from any other placoderm, and further research is planned to shed more light on the function and articulation of the gnathal plates with the skull and themselves.

# Fishy tales from beneath prairie bales: a review of bony fish caudal fin morphologies from the Late Cretaceous Western Interior Seaway for taxonomic identification in the absence of skull material

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Fossilized bony fish skeletons are commonly preserved in halves, either as the anterior half containing the skull or the posterior half containing the caudal fin. Fish fossil specimens that include skull material are more scientifically valuable for the plethora of diagnostic features they contain, which makes taxonomic identification to a lower level possible. Since written and illustrated postcranial anatomical descriptions of Late Cretaceous bony fishes from North America are lacking for most known species, most taxonomic assignments of specimens that do not include skull material are either questionable or only identified to a high taxonomic level. This study examines well-preserved, articulated and semi-articulated bony fish specimens that contain caudal fins to identify important diagnostic features of penultimate and ultimate vertebrae, and caudal fin rays. Specimens containing both skull material and caudal fins are also reviewed in order to assign taxonomic identities to the caudal fin morphological categories identified in this study. Common Late Cretaceous bony fish genera of varying sizes are reviewed including *Apsopelix, Cimolichthys, Gillicus, Ichthyodectes, Pachyrhizodus, Pentanogmius, Protosphyraena,* and *Xiphactinus*. The aim of this study is two-fold: (1) to increase the scientific importance and usefulness of bony fish fossil specimens containing caudal fins but no skull material for phylogenetic, biogeographic, and biostratigraphic studies, and (2) to address a research bias against postcranial elements of Late Cretaceous marine bony fishes from North America.

# Cheek tooth morphology is not a reliable taxonomic indicator for Beringian *Equus*

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Throughout the Pleistocene, horses were among the most abundant land mammals in North America and are some of the best-represented animals in the fossil record. Despite the ample fossil material available and numerous studies, there are still no widely accepted conclusions regarding how many horse species may have co-existed on the continent or their taxonomic nomenclature and relationships. This lack of consensus is particularly problematic in Beringia, due to both fewer studies having been conducted in this region and the possibility of bidirectional dispersal across the Beringian Land Bridge. This potential for gene flow between northern North America and Eurasia has further confounded any taxonomic resolution to date. Up to seven different horse species have been proposed to have co-existed in Beringia during the Pleistocene, the validity of which has been debated. Recent research has demonstrated that species of *Equus* from the Pleistocene of North America exhibit complex occlusal enamel patterns that may be taxonomically informative, but this has not yet been rigorously tested in Beringian horses. Here, we use 2D geometric morphometric analysis to determine whether species of horses from eastern Beringia significantly differ in the shape of the occlusal enamel pattern for upper and lower 3rd and 4th premolars, and whether they form distinct taxonomic groups that are consistent with those that have been previously erected. We photographed a total of 149 teeth; 96 teeth had been previously attributed to three species of Equus (Equus caballus Linnaeus, 1758, Equus lambei Hay, 1917, and Equus verae Sher, 1971), while the remaining 53 teeth were only identified to the genus level. The latter were treated as an indeterminate group (i.e., Equus sp.). All teeth were radiocarbon-dated to establish temporal context. For the upper teeth, we digitized 24 landmarks spanning across the entire surface of the tooth and, for the lower teeth, we digitized 50 evenly spaced landmarks to outline the "double knot" feature on each tooth. We then performed Generalized Procrustes Analyses of Points, Principal Component Analyses, and Linear Discriminant Analyses to test whether morphology was correlated with a priori identifications and how the indeterminate specimens fit into the multivariate space. We show that only the morphology of the upper teeth from Beringian horses provides taxonomically useful information, while the lower teeth are morphologically indistinguishable among species. While the upper teeth with a priori species identities are successfully recovered, many taxonomically indeterminate specimens do not group with any of the three species. Further, there is no visible clustering related to either age or fossil locality, indicating that there is no spatiotemporal component that could explain the observed variation of the data. We suggest that, although we can identify upper teeth with distinct morphological characters to the species level, the teeth of *Equus* species exhibit considerable variation that limits their utility as taxonomic indicators using morphology alone. We suggest that future research aimed at resolving taxonomic uncertainties of Equus should not use dental characters in isolation, but should combine them with other methods of species identification such as osteological characters or DNA analysis.

# The first highly resolved ecological network for successive palaeocommunities of the Late Cretaceous (Campanian) Belly River Group of Dinosaur Provincial Park, Alberta

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Over the last three decades, network theory has been increasingly applied to ecological research, partly because of the possibility it raises to account for species' interactions in biodiversity measurements. So far, its application to palaeoecology has largely been limited to reconstructing food webs of Palaeozoic and Cenozoic communities with exceptional soft-bodied fossil preservation and/or the impact of species loss from mass extinction events at variable degrees of taxonomic resolution. What, then, does a highly resolved site-specific trophic network reveal about the structure of a more temporally stable Mesozoic community dominated by non-avian dinosaurs at a key stage in the evolution of terrestrial ecosystems?

The temporal biotic succession of the late Campanian Belly River Group preserved in Alberta's Dinosaur Provincial Park (DPP) constitutes one of the world's most complete non-marine fossil records for the Mesozoic era. Over a century of exploration has revealed a particularly high abundance of large dinosaur skeletons and bonebeds, a strong representation of small theropods, fishes, amphibians, turtles, crocodilians, and mammals across terrestrial and aquatic realms, as well as occasional fossil plant and invertebrate localities. Furthermore, individual vertebrate quarries within DPP are distributed at a very high spatial density across a temporal interval constrained to ~2.5 million years by the latest radiometric dates, and the variation in sedimentary facies over that period is known to reflect a transition from alluvial to coastal depositional environments. Altogether, this makes the DPP biota an ideal palaeoecological system to study with a network approach.

The DPP network was assembled from nodes (i.e., taxa) and links (i.e., feasible trophic interactions) based on different lines of evidence from the literature that varied with each node's preservation quality. This resulted in a consumer-resource matrix from which food webs were generated by selecting different node combinations according to habitat, stratigraphic interval, and ontogenetic niche shifts. The most inclusive version of the DPP food web thus contained all species known from each of the Belly River Group's locally exposed stratigraphic units, combining terrestrial, semiaquatic, and fully aquatic taxa, and including distinct nodes for each juvenile hadrosaur, ceratopsid and tyrannosaur species. The network was completed by an estimate of the land vertebrate biomass density at each trophic level in its most intensely sampled time interval (the lowermost Dinosaur Park Formation), obtained from an updated database of its fossil quarries combined with published body mass estimates.

Food webs for extant non-marine communities are often designed to be constrained to the terrestrial or aquatic realm, while ignoring the energy that frequently flows between them, and systematically recover higher trophic levels for aquatic apex predators than for terrestrial ones. The DPP network now offers a unique opportunity to test this pattern within a single locality where energy clearly flowed between terrestrial and aquatic communities due to its high diversity of semiaquatic tetrapod consumers.

# Preliminary evidence for a latitudinal size gradient in *Triceratops* (Dinosauria, Ceratopsia)

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The ceratopsian dinosaur *Triceratops* is one of the most widespread and abundant dinosaurs from the Upper Cretaceous of North America. Fossils of this genus are currently known from upper Maastrichtian strata as far north as the Scollard and Frenchman formations in Canada to as far south as the Denver Formation in Colorado, USA. Extant animals with similarly large geographical ranges frequently exhibit a trend of increasing body size with latitude. This trend, known as Bergmann's rule, is well-documented in extant animals, but no clear example has been reported in dinosaurs. The combination of their geographical range and abundance make *Triceratops* an ideal taxon to assess this trend in dinosaurs. It has been suggested that larger specimens of *Triceratops* tend

to occur in northern latitudes, but only a single study has sought to test this hypothesis, using occipital condyle dimensions as a proxy for skull size. The study found that the average size of *Triceratops* skulls increases moving northward from the Lance Formation of Wyoming into the Hell Creek Formation of Montana, whereas size decreases moving further northward into the Frenchman Formation of Saskatchewan. However, the study included only two skulls from Saskatchewan, one of which was a subadult, and the other of which is, in fact, from Wyoming. Thus, an updated test of the hypothesis, including a larger sample of Canadian skulls and some specimens from the southernmost range of *Triceratops*—the Denver Formation in Colorado—is warranted.

In this preliminary study, we expand the sample size to over 60 adult and subadult *Triceratops* skulls of variable completeness. We measure basal skull length and six other cranial dimensions known to correlate with basal skull length, where available. Our linear regressions show a significant positive correlation of both basal skull length and occipital condyle width with latitude. Most other measurements also exhibit a positive trend, but are, however, statistically insignificant at this time. Only the squamosal length shows a negative trend, which is also insignificant; this may reflect interspecific differences between *T. horridus* and *T. prorsus*, rather than an ecologically informative signal. Data collection is ongoing, but these preliminary results may represent the first documented case of a latitudinal size gradient in a dinosaur. This, in turn, would have interesting implications regarding the strength of the latitudinal climatic gradient in the late Maastrichtian of North America.

## Counting crocodiles: using vertebrate microsites to explore the paleoecology and preservational patterns in crocodyliform communities from the Frenchman Formation (latest Maastrichtian) of southern Saskatchewan

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Microvertebrate sites are extremely useful for studying and reconstructing paleocommunities. The Frenchman Formation (latest Maastrichtian) of Saskatchewan is well known for these sites, being the subject of several studies (e.g., Bamforth 2013; Redman et al. 2015; Milligan 2021).

Most crocodyliform material in the province comes from these microsites, represented by hundreds of elements including isolated osteoderms and teeth of diverse shapes and sizes. In the absence of more complete specimens, microsite elements can be informative of the composition, ecology, and taphonomic overprints preserving this crocodyliform community. A previous study of a bulk sampled Hell Creek Formation microsite indicates the overall population structure is likely preserved as well (Bennett 2012).

Crocodyliform fossils from four well sampled Frenchman Fm microsites ("B.I.N.G.O.", "Hairpin", "Tie Me Kangaroo Down Sport" (KADO) and "Garscale") were examined to identify patterns in element distribution, size, and composition. Shed teeth were sorted into size classes based upon Bennett (2012) to examine size distribution. Classification of teeth and osteoderms into two categories was based on characteristics of known contemporary crocodyliform genera from the region and time period; "*Borealosuchus*-like" (including a rare large unnamed gavialoid) and "Alligatoroidea-like" (*Brachychampsa* and *Stangerochampsa*).

The most common elements are osteoderms and teeth, followed by skeletal (crania/postcrania) fragments (Fig. 1). An individual crocodyliform has hundreds of osteoderms. A single animal also has dozens of teeth which are





Figure 1. Top: Proportions of crocodyliform elements from B.I.N.G.O, Hairpin, Kangaroo Down, and Garscale microsites. Bottom: Proportions of taxonomically identifiable osteoderms and teeth from these microsites.



Figure 2. Size-frequency distribution of shed teeth from B.I.N.G.O, Hairpin, Kangaroo Down. Distribution of Hell Creek Fm shed crocodyliform teeth (Bennett, 2012) and all isolated teeth collected from the Frenchman Fm (regardless if they possessed roots or not) are included for comparison.

continuously replaced, potentially shedding thousands over its lifetime. This likely contributes to an elevated number of these elements in the fossil record. The disproportionate number of Alligatoroidea-like osteoderms compared to *Borealosuchus*-like ones (Fig. 1) probably

stems from identification challenges based on osteoderm completeness, rather than an ecological cause. Most indeterminate teeth and osteoderms likely belong to one of the known taxa, but this is currently difficult to assess.

B.I.N.G.O and Hairpin show a visually similar, though not statistically significant, distribution of shed tooth sizes as the Bennett's (2012) Hell Creek data (Fig. 2). Both microsites have been bulk sampled and extensively surface collected, the latter likely contributing to skewing towards slightly larger teeth. Between 70-80 percent of teeth fall still into the two smallest size classes (under 6 mm height). When considering every tooth collected from this formation, most (71%) are less than size class 3 (under 9 mm height). This demonstrates an abundance of small individuals shedding teeth at a greater rate, similar to what is seen in the Hell Creek Fm and in modern crocodyliform communities.

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## Changing forest ecology heading into the end-Cretaceous extinction event

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Insects are near the base of many terrestrial food webs, and they play integral roles in recycling nutrients and pollinating plants. Most of the insect groups that dominate modern terrestrial ecosystems rose to positions of ecological prominence during the Cretaceous. Amber deposits provide an opportunity to study this transition in detail by preserving evidence of changing faunas, forest types, and ecological conditions. Amber preserves direct evidence of insects and plants in the form of inclusions, while its chemistry can be compared to modern resins to identify source plants, and its stable isotopic composition provides clues about ancient atmospheric conditions and precipitation patterns. Recent work on amber deposits from the Late Cretaceous strata of western Canada and the USA provides data from many vertebrate bonebeds or microsites, as well as the wider context of surrounding rock layers. Together, these deposits provide glimpses of conditions in the forests around the Western Interior Seaway. Similar groups of cupressaceous trees seem to have produced many of the amber deposits in this region; however, conditions and inhabitants in the forests changed dramatically. Recent work has shown that insect faunas underwent major changes—many of the wasp and fly taxa that were widespread and common in the earlier parts of the Cretaceous disappeared toward the end of the Cretaceous. New amber deposits from Saskatchewan and North Carolina constrain these changes to somewhere between 77 and 67 Ma, and this pattern appears in both North America and Asia. This would suggest that the transition from conifer-dominated forests to forests where angiosperms played a larger role had a strong impact on insect faunas, which may in turn have changed the food webs that many vertebrates relied upon. The insect faunal turnover also included ecological engineers like ants, which may have had profound effects on forest floor and arboreal communities. Heading toward the end of the Cretaceous, large changes were taking place in forest ecosystems, but we may not be able to spot them based on plant fossils alone. If we want to understand what these changes meant for vertebrate evolution or diversity, studying amber deposits provides a good starting point.

# Paleoenvironmental reconstruction based on carbon and hydrogen isotopes from amber associated with dinosaur remains in Western Canada

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Amber has been praised for its ability to preserve the remains of biological inclusions. Some world-famous sites include the Dominican Republic, Baltic region, and Myanmar, but research on many of these gem-grade ambers comes with significant ethical concerns. In more recent years, amber has been investigated from a geochemical standpoint, providing insights that inclusions such as arthropods, botanicals, and fungi alone cannot give. Western Canada offers an exceptional region to perform these geochemical studies on amber associated with dinosaurs and other Mesozoic life, particularly within the latter half of the Cretaceous period. By studying the carbon and hydrogen stable isotopic compositions, as well as using Fourier Transform Infrared (FTIR) spectros-copy, and incorporating geological and paleontological data, a higher-resolution picture of paleoenvironments can be built. Hydrogen isotopes give information on the continentality of the sites, providing insights into precipitation patterns and the transgression and regression of the Western Interior Seaway. Carbon isotopes give insight into atmospheric composition, as well as the climate, and whether the plants in the ecosystem were under any stress—possibly from insect infestation, drought, or fires. FTIR is a valuable tool for determining the botanical source of the amber, improving the characterization of ancient habitats.

Looking at sites in Alberta and Saskatchewan, a view of the last 10 million years of the Cretaceous period culminating in the K-Pg extinction event can be constructed. Isotope and FTIR analyses performed at the University of Alberta have given preliminary results that there was possibly increased plant stress close to the K-Pg extinction event and the Western Interior Seaway was actively transgressing and regressing throughout this time. These studies are essential because they allow a better understanding of how environments and the climate changed through time. They also allow a better picture of the types of environments that some of the most charismatic animals that ever lived occupied.

# Using trace fossils on *Triceratops* bones to reveal hidden invertebrate diversity in the Frenchman Formation of Saskatchewan

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Trace fossils on vertebrate material offer insight into the paleoecology of ancient ecosystems and the taphonomy of vertebrate remains. Using standard ichnologic methods, including pertinent ichnotaxobases for bioerosion trace fossils on bones is crucial to understanding the taphonomy of vertebrate body fossils and to reveal clues as to the identity and diversity of potential tracemakers. Herein, we present several trace fossil morphologies recorded on Triceratops cf. T. prorsus material collected from muddy and silty paleosols from the latest Cretaceous Frenchman Formation in southwestern Saskatchewan. The trace fossils described herein share superficial and morphological similarities with previously studied Mesozoic and Cenozoic material from around the world and have been historically attributed to beetles and other indeterminate insects. The trace fossils found on the Triceratops material include large tunnels with bioglyphs along their walls, active bone-chip-infilled and passively-infilled tubes, and various pupation chamber morphologies, both with and without bioglyphs. Trace fossils were classified using pertinent ichnotaxobases. As a result of this study, several behaviours were inferred from the trace fossils, including the construction of pupation chambers (Pupichnia), necrophagous and possible osteophagous feeding (Fodinichnia), and possible dwelling (Domichnia). By comparing the activity of insects on recent to modern bones through taphonomic experiments and assessing similarities with modern insect traces, many of these trace fossils can be attributed to beetles with similar behaviours and ecologies to modern carrion beetles and possibly tiger beetles. Using available sedimentological data, these trace fossils can be interpreted along a taphonomic pathway. The trace fossils on Triceratops bones were likely produced just before and during burial of the bones within the sediment. These observations demonstrate that multiple lines of evidence, including sedimentologic and ichnologic, are critical to reconstructing the taphonomic history of vertebrate specimens. Studies of this nature also reinforce the need for rigorous vetting of skeletal elements and facies analysis in taphonomic studies, and awareness of in situ structures around vertebrate remains, both in the field and during preparation. This approach will allow for enhanced discussion on the vertebrate body fossil record and the hidden diversity of invertebrate decomposers within ecosystems where paleoenvironmental conditions do not preclude the preservation of invertebrate body fossils.

## Cranial anatomy of the enigmatic middle Permian diapsid *Lanthanolania ivakhnenkoi* revealed by neutron CT

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The initial stages of diapsid evolution are poorly represented in the fossil record. During the late Carboniferous and early Permian, diapsid reptiles make their appearance with Petrolacosaurus, Spinoaequalis, Araeoscelis, and Kadaliosaurus, all members of the basal clade Araeoscelidia. The slightly more derived neodiapsids appear in the early Permian, exemplified by the fragmentary remains of Orovenator and Maiothisavros, but only in the latest Permian do we see the appearance of archosauromorph and potential lepidosauromorph taxa. Bridging this gap is the enigmatic Lanthanolania ivakhnenkoi, a middle Permian neodiapsid belonging to the Mezen faunal assemblage of Eastern Europe. The holotype and only known specimen is represented by a partial skull, including parts of the right side of the snout, a right jugal and postorbital, parts of the parasphenoid and epipterygoid, as well as a few fragmentary elements of the palate and the lower jaw. Despite the fragmentary nature of the holotype, the available evidence indicates that Lanthanolania was the oldest diapsid from the Russian platform and the original interpretation posited that it may have been the oldest known saurian. However, among current phylogenetic analyses, *Lanthanolania* consistently plots as an early neodiapsid and there is little consensus as to its precise position due to the lack of informative skeletal morphology. Here, we present a new, articulated skeleton of this enigmatic diapsid reptile, which includes a nearly complete skull in articulation with the postcranium. This discovery of a nearly complete articulated skeleton of Lanthanolania has allowed us to undertake a meticulous description using neutron and synchrotron CT imaging, with the potential to make it among the best known Paleozoic diapsids. A thorough reassessment of its phylogenetic relationships is now being undertaken. Notable features of the temporal region of this small diapsid include the presence of large supratemporal fenestrae, apparent absence of the quadratojugal and that of the subtemporal bar, and narrow elongate squamosals. Some other intriguing features are the lateral pronunciation of the prefrontals, reduced lateral exposure of the lacrimals that are excluded from the orbits, widely separated basicranial tubera, large footplate of the stapes, dramatically curved semi-covered tube-like morphology of the quadrate ramus of the pterygoids, and rather large, elongate suborbital fenestrae, and pleurodont dentition. The initial impression of a very large orbit in the holotype is reinforced by the new specimen and the presence of numerous, unusually large sclerotic ring elements. This may suggest a nocturnal habit, a possible strategy for early neodiapsids in the shadow of the synapsids and parareptiles of the late Paleozoic.

# Acanthomorph fishes from Upper Cretaceous Deposits of Madagascar

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Late Cretaceous (Maastrichtian) acanthomorph fishes are represented by many isolated elements from freshwater deposits in the Maevarano Formation, Mahajanga Basin, northwestern Madagascar. These are identified as belonging to several different acanthomorph fishes. Elements include vertebrae, fin spines, basioccipitals, dentaries, premaxillae and other bones. The different morphologies of these elements are interpreted as representing three or more species. However, the morphologies of the elements, although distinctive, bear close similarities to one another, and we interpret this to be a reflection of their shared ancestry. We therefore believe that the multiple species may represent a single lineage. It is likely that the material documents a single invasion of Madagascan fresh waters by a marine lineage, which then diversified into several taxa within the freshwater environment. An alternate explanation is that the lineage may have diversified first in marine waters followed by independent invasions of freshwaters by each species. This is the first documentation of acanthomorphs in freshwater Cretaceous deposits of Madagascar; a previous report of sciaenids, the first from Gondwana, from the same rock unit (Maevarano Formation) is incorrect. The Madagascan acanthomorphs include individuals that are fairly large compared to those reported elsewhere in the Late Cretaceous, and document that acanthomorph fishes had evolved relatively large body forms by the Maastrichtian, at least in East Gondwana.

### Enchodus specimens from the Albertan Bearpaw Formation

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*Enchodus* is an extinct genus of teleost fish from the order Aulopiformes. The genus lived in Cretaceous marine formations from around the globe, and it contains approximately 24 species that exhibit a significant range of morphologies. All members of the genus possess large fangs on the dentary and dermopalatine bones, and short, deep skulls. Many species were named from incomplete material, such as isolated palatal fangs, which has resulted in historical taxonomic conflict. That, combined with a lack of strong diagnostic characters, has confounded phylogenetic analyses of the genus. Contrasting phylogenies have been proposed for members within the family Enchodontidae, and while some larger clades have been consistently recovered, no reliable synapomorphies are agreed upon for *Enchodus*. My research is focused on describing specimens of *Enchodus* from Southern Alberta. Approximately fifteen specimens attributable to the genus were collected from the Enchanted Designs mine, South of Lethbridge. These specimens represent the first articulated *Enchodus* material from the Bearpaw Formation, which was deposited along the Western coast of the Campanian Western Interior Seaway (WIS). Many *Enchodus* species were described

elsewhere from the Cretaceous of the North American WIS, but they were synonymized into only five species by Goody in 1976. The Bearpaw specimens have articulated cranial and postcranial material, in addition to a variety of less complete and disarticulated specimens, including multiple isolated braincases. Several WIS *Enchodus* species lived contemporaneously with the Alberta specimens and are diagnosed primarily by characters of the tooth-bearing cranial elements. Traits of the neurocranium have not traditionally been used to diagnose North American *Enchodus* species but may be taxonomically informative. We will be comparing the Albertan braincases to those from Eastern specimens. Many of the more complete specimens are attributable to *Enchodus petrosus*, a taxon well-known from Late Cretaceous deposits in eastern North America, such as the Niobrara chalk and the Pierre Shale. The well-preserved Albertan specimens provide an opportunity to compare with those in eastern North America and expand our knowledge of the biogeography of the genus.

## The Fossil Backbone method: testing sister relationships within Serpentes using a novel dataset and method based on fossil taxa and their morphology

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Snakes (Serpentes) are a diverse group of lizards with a modern diversity of over 3500 species, approximately one third of all lizard species. Due to their fragile cranium and high vertebral count per individual, fossils are often partial and/or isolated, when preserved. Due to this, many taxa have been erected by isolated elements or assortments thereof, predominantly vertebrae. A handful of taxa containing skulls and vertebrae have been described (e.g., Dinilysia, Najash, Pachyrachis, or Wonambi) providing key information into the character suites present in fossils across the Cretaceous-Cenozoic boundary. The high abundance and diversity of modern derived snake taxa compared to known fossil snakes creates issues in exploring sister relationships between fossil and modern taxa. Generally, the oversampling of modern character-taxon datasets creates a barrier for fossil taxa in which they are placed stem-ward, rarely nesting within any existing sub-clade. While it is possible that all modern snakes are united by a small suite of derived characteristics to the exclusion of most, if not all fossil snakes, it does not complement the data provided by fossil taxa distributions in the Cretaceous. Problematic modern snake distributions of sister clades (e.g., New and Old-World boas and pythons) warrant re-examination of these relationships as no clear dispersal path can be ascertained. To test the possibility of alternative sister relationships within Serpentes, a novel dataset of primarily fossil taxa is being constructed with only characters expressed by these taxa being codified. Once an initial topology is recovered, it will act as the backbone to subsequent iterations. Modern taxa basal within their larger clades will be added in incrementally to explore alternative nesting hypotheses of modern snakes within the fossil assemblage. This methodological pipeline is here called the Fossil Backbone. As the dataset continues to develop, the aim will be to explore character evolution using snapshots through time. The logic is derived from the reality that any sampled species diversity we have through the fossil record or today, only represents a single point along evolutionary lineages, and cannot answer questions of character acquisition through time. By taking a bottom-up approach to examining evolutionary patterns, we gain the advantage of following the linear flow of time and limiting the characters of interest only to those maintained through time. This method will provide a means to produce alternative hypotheses of sister group relationships within clades with modern representatives, as well as tailoring inclusion of primary homolog statements (i.e., morphological character statements).

# An unusually complete *Cynodictis lacustris* from the Quercy Phosphorites and historical specimens of the Natural History Museum Denmark

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*Cynodictis* Bravard and Pomel, 1850 is one of the earliest amphicyonids known from Europe, occurring in the late Eocene, and continuing until the early Oligocene. The genus has had a long and complex taxonomic history, with up to 20 species recognised in the past, however today only seven are considered valid. The species are traditionally identified only by characters in the mandible and cranial material has rarely been described in detail and is not often found associated with mandible remains. Specimens where the mandible is preserved therefore provide an important holistic view of cranial anatomy and improved characterisation of complete skulls can lead to better identification of partial cranial remains. Here we describe two unusually complete skulls from the historical Quercy Phosphorites collection of the Natural History Museum of Denmark. Though collected in the early 19th century they have remained understudied. The first specimen (NHMD 196096) consists of a skull with associated mandible. Here we both carry out standard taxonomic measurements and description, and image the specimen in three dimensions (surface and CT scanning and photogrammetry). CT scanning and reconstruction using Dragonfly software allowed for measurement of characters obscured by matrix. Tooth measurements were plotted against identified tooth/jaw fragments from NHMD collections and those within the study of Bonis (2020). The specimen was identified as *Cynodictis lacustris* Gervais, 1852.

The second specimen (NHMD 196092) was originally identified as *Cynodictis lacustris*, however, due to differences such as the low snout, deep midline of the frontal and nasal, and the differences in temporal- and sagittal crest morphology, we could not affirm this taxonomic identity. Work on this specimen is ongoing but we tenta-tively identify this as a new but related taxon.

This study underlines the value of reassessing historical collections at scientific institutions, as the full description of the cranium is an important reference for the identification of additional specimens. Additionally, the identification of a new taxon increases our understanding of the evolution and distribution of early caniforms.

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## Redescription of a Miocene colubrid snake from West-Central Nevada using micro-CT

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Colubridae is the largest snake clade, with a fossil record beginning in the early Miocene. Despite large scale molecular analyses with robust taxon sampling, the phylogenetics of this clade remains uncertain. While incorporation of paleontological evidence can resolve clades deemed controversial with molecular data alone, the majority of studies do not attempt to resolve discrepancies using transitional fossils (Hsiang et al., 2015). This is in large part related to a paucity of fossil specimens with intact cranial elements. In particular, fossil colubrids from western North America are rare and poorly described. A partially articulated fossil snake from the middle member of the Truckee Formation in west-central Nevada (UNMSM 0001) was first described by Ruben (1971), but not named. UNMSM 001 was incorrectly thought to be from the early-mid Pliocene but a radiometric date of 9.8 Mya (Miocene) is now well-supported for the middle member of the formation. The specimen is preserved in nearly pure diatomite, and is dorsoventrally compressed with a partly articulated cranium and 76 anterior vertebrae. Most of the ribs/impressions are present and associated with their corresponding vertebrae. The cranium exhibits significant breakage and lateral displacement of bony elements. Micro Computed Tomography (µCT) scanning identified maxillary, dentary, pterygoid, ectopterygoid, palatine, and compound bone elements that are relatively well-preserved and close to anatomical position. Components of the frontal, nasal, braincase and anteriormost cervical vertebrae are identifiable but fragmented. The remains of three ray-finned fish are present within the body cavity. The first fish, cf. Gasterosteus doryssus, caused occlusion at either the esophagus or pylorus based on spatial analysis of organ position in extant snakes (Anderson and Secor 2015). Consuming larger vertebrates likely resulted in its demise from an inability to properly ingest or regurgitate the fish and also suggests that the specimen lived near a significant body of water. UNMSM 0001 shares many morphological traits associated with Coluber sp. and other closely related genera. Maximum parsimony using a modified morphological character matrix from Garberoglio et al. (2019) supports this specimen within the superfamily Colubroidea. Maximum parsimony and Bayesian inference using the matrix by Zaher and Smith (2020) reconstructs UNMSM 0001 as a well-supported sister clade to the extant species Coluber constrictor Linnaeus, 1758. However, known phylogeography of Coluber constrictor based on mtDNA evidence (Burbrink et al., 2008) demonstrates that this specimen predates the early Pleistocene radiation of Coluber sp. into western North America. An absence of an existing morphological character matrix for the family Colubridae makes exact genus distinction difficult, but it is likely that UNMSM 0001 is a new species of Coluber sp. or closely related genus and represents an early radiation of Colubridae into western North America.

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# Hindlimb morphology and kinematics of the varanopid *Mesenosaurus efremovi*

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The Richards Spur locality at the Dolese Brothers Limestone Quarry is renowned for its rich and diverse assemblage of terrestrial tetrapods, including a wide variety of early amniotes dating to 289–286 million years ago. Of the tetrapod taxa present within this site, the most commonly found include the stem lissamphibian Doleserpeton, the eureptile Captorhinus and the varanopid Mesenosaurus efremovi (Maho et al., 2019). Quarrying operations at this site in this century have yielded numerous varanopid skeletal remains that have been attributed to M. efremovi. Known materials include several near-complete skulls as well as numerous partially articulated and fragmentary cranial and postcranial remains. Of particular interest is the appendicular material of the pelvic girdle and hindlimb which provide a great deal of information on the anatomy and functional locomotory capabilities of this synapsid. Perhaps the most interesting aspect of the *M. efremovi* material preserved at this locality is its ankle morphology. The specimen that we use in this study consists of a partial tibia and fibula in articulation with a superbly preserved hindfoot, excluding only two phalanges from the fourth digit. Using a combination of Computed Tomography (CT) data and the software Avizo and Blender, we were able to resolve several important features of the specimen. The high quality of the materials available to use in the 3D software allowed us to explore the anatomy of the various surfaces of articulation and study possible ranges of motion. Notable and likely unique features of the ankle include: nearly rigid articulations between the astragalus-calcaneum complex and the tibia and fibula; a highly robust astragalus with a massive transverse flange and a large medially oriented surface of articulation with the tibia; an extension of the astragalo-calcaneal foramen into the astragalus; a pronounced lateral tuberosity of the calcaneum; and a complex, enlarged fourth tarsal. Available evidence indicates that the fourth and fifth metatarsals were capable of modest mediolateral rotation along their corresponding tarsals. Given these observations, in conjunction with the overall agile and predatory nature of *M. efremovi*, we hypothesize that all of these features are specializations for cursorial movement. To support this claim, we used the content creation software Blender to fully rearticulate the specimen and animate a walk cycle. With the morphological constraints, we find that the step cycle features a rigid ankle and tibia-fibula complex with flexion only occurring at the digits. These findings indicate the potential for high-speed movement in *M. efremovi*, which may have made this mid-sized predator particularly successful across its spatiotemporal range across northern Pangaea through the early and middle Permian.

# Preliminary analysis of the Upper Cretaceous Herschel Marine Bonebed: exploring palaeoecological dynamics and polycotylid plesiosaur ontogeny

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The Dinosaur Park Formation (upper Campanian, Upper Cretaceous) near Herschel, Saskatchewan hosts the Herschel Marine Bonebed (HMB), a diverse multi-taxic marine fossil locality rich in micro- and macro-vertebrate fossils, trace fossils, and carbonized plant material with some amber. Dominated by polycotylid plesiosaur specimens from various developmental stages, the HMB is interpreted to have been deposited within a shallow lagoon that was part of a barrier island system at the margin of the Western Interior Seaway. The relatively high prevalence of subadult specimens found within a protected, shallow environment could indicate that the HMB served as a plesiosaur nursery or calving ground. This project aims to investigate polycotylid plesiosaur ontogeny within the palaeoecological context of the HMB's protected shallow marine setting.

Morphological and histological analyses of propodial elements from juvenile, subadult and adult plesiosaur specimens aim to provide insight into the ontogeny of polycotylid plesiosaurs and to create a growth sequence for this taxon. Ontogenetic studies of these plesiosaurs will be supplemented by concurrent microvertebrate palaeoecological analyses to better understand the faunal composition, taxonomic diversity, and taphonomic effects on the HMB's faunal assemblage. This information will allow us to explore the nursery hypothesis in more depth and expand our knowledge of general plesiosaur palaeoecology, in areas such as their growth and development, life cycles, behaviour, and role in the ecosystem. Overall, this project strives to advance our understanding of the palaeoecology of polycotylid plesiosaurs and this poorly known Upper Cretaceous fossil site in western Saskatchewan.

## Compiling trends in published mosasaur combat pathologies for new insights into the social lives of Cretaceous marine lizards

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Mosasaurids, marine reptiles that inhabited Late Cretaceous oceans, are thought to have engaged in intraspecific combat due to the presence of healed bite marks on their skulls. Evidence for combat has been reported sporadically in the literature, however, no study has summarized the frequency of occurrences, trends, or types of evidence preserved in the fossil record. Therefore, it is difficult to determine the causes of these bite marks, particularly whether they are due to intraspecific aggression during mating (sexual selection), or interspecific aggression due to other types of competition. To address this, we performed a survey of the literature to compile all documented instances of facial bite marks in mosasaurs. The dataset of 18 published specimens contains information on species occurrences, size (age) of specimens, stratigraphic occurrence, location(s) of bite marks, and the degree of healing. Results show that, taxonomically, attacks on the face are most common in the subfamily Mosasaurinae, and that there is a strong bias in favor of bites on the anterior bones of the skull, as well as dorsally on the frontal and premaxilla. The bite marks are oriented sagittally on the maxillae, surangulars, prefrontals, and dentaries, and transversely on the frontal and premaxilla. The pattern of distribution and orientation of observed markings by other mosasaurs suggests a preference for attack from the anterior and lateral sides of the head. Bite marks that do not show any healing are interpreted as feeding traces that formed post-mortem during scavenging. This study shows that trends in mosasaur pathologies are quantifiable and interpretable, and that some published interpretations of mosasaur-on-mosasaur violence may need further justification and reassessment.

# A "South Pole" mosasaur in the Belgian Chalks challenges notions of mosasaurine biogeography and body form

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The phosphatic chalks of Mons, Belgium, were mined throughout much of the 19th century, producing a significant number of skeletons originally referred to the Late Cretaceous mosasaur species *Mosasaurus lemonnieri* Dollo 1889. This assemblage, comprising one of the largest known mosasaur samples referred to one species, has received extremely little attention in the 130 years since its initial description. Recent study of these specimens has recovered a revised hypodigm of *M. lemonnieri*, outside of which one individual confidently falls. This specimen is a nearly-complete skull and associated skeleton that can be reliably differentiated from *M. lemon-*

*nieri* by several characters of the skull and postcranial skeleton. Phylogenetic analysis recovers this taxon within Mosasaurini as sister to the taxon *Moanasaurus mangahouangae* Wiffen, 1980, from which it is differentiated only by the morphology of the maxilla-palatine contact and the ventral frontal surface. The genus *Moanasaurus* has been previously proposed to be endemic to the South Polar regions, a hypothesis unsupported by the phylogenetic position of this Belgian specimen. Phylogenetic trees of Mosasaurini mapped onto a prehistoric globe provide a complete lack of evidence for any kind of cladic endemism, as no two closest-related taxa have been found on the same continent. Previously-proposed endemism in south Pacific mosasaurines is completely unsupported; claims of endemism in marine reptiles are problematic as they rely on negative evidence of a taxon in certain areas, which is impossible to prove in the marine reptile fossil record. The articulated ribcage of this specimen is exceptionally preserved, and shows proximodistally short thoracic ribs angled posteriorly at ~45 degrees from vertical. Well-constrained 3D reconstruction yields a compact ribcage and a thin, cylindrical body, contrasting with the dorsoventrally deep fusiform shape commonly accepted for mosasaurs.

# Cranial osteology of *Ectenosaurus clidastoides* and a new specimen from the Santonian of Kansas, USA

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*Ectenosaurus clidastoides* is a unique plioplatecarpine mosasaur found in the Smoky Hills Chalk of the Niobrara formation, Kansas, USA. Important characters that differentiate it from all other plioplatecarpine mosasaurs are an elongated snout with high tooth counts, fused stapedial processes of the quadrate, and dorsal wing of the maxilla contacting the frontal and excluding the prefrontal from the narial margin. The holotype, formerly known as *Platecarpus clidastoides*, was destroyed in the Second World War, leaving a single referrable specimen, FHSM VP-401, as the neotype and the basis for genus *Ectenosaurus*. Recently, three additional species of *Ectenosaurus* have been constructed based on incomplete specimens. Here we describe a second existing specimen of the type species, TMP.2008.13.1 which displays all cranial features associated with *E. clidastoides*. It consists of a complete skull, the right side of which preserves all elements in articulation and the left side is mostly disarticulated. Many cranial elements that are not visible in the neotype are present in TMP.2008.13.1. This specimen provides novel insights into the osteology of *Ectenosaurus clidastoides* and grants us a near complete understanding of the skull of this rare and unusual mosasaur.

# Resolving stratigraphic and biostratigraphic uncertainty in the Dinosaur Park Formation, Alberta via geochemical fingerprinting of bentonite beds

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Outcrops of the Campanian aged Dinosaur Park Formation (DPF) are best studied Dinosaur Provincial Park (DPP), Alberta, a UNESCO World Heritage site that produces some of the highest quality and quantity of dinosaur fossils in the world. These abundant and diverse fossil assemblages, alongside the easily accessible outcrop that contains them, have made the DPF a prime subject for paleontologists to test hypotheses regarding dinosaur ecology and evolutionary trends. It has been noted that dinosaur assemblages in the DPF in DPP contain differing taxa between lower and higher strata, suggesting faunal turnover events occurred through the represented time interval. However, the exact timing and causes of these faunal turnovers remains unclear primarily because the DPF is composed of fluvial sandstones and floodplain mudstones with considerable variation in thickness and lateral extent. This variability has prevented the use of stratigraphic marker beds, resulting in a relatively poorly resolved stratigraphic framework for the DPF in DPP, and therefore uncertainty regarding the stratigraphic placement of dinosaur fossil sites and the boundaries of proposed dinosaur biozones.

To address this issue, we stratigraphically and geochemically analyzed seven bentonite beds in the DPF within DPP, five of which have well resolved absolute dates that temporally constrain ~2 million years. Bentonites are ideal chronostratigraphic markers because they represent rapid deposition during a single volcanic event over a large lateral extent and contain phenocrysts that can be geochemically analysed and dated, allowing for each to be assigned its own unique geochemical "fingerprint". Each sample was stratigraphically contextualized through a measured section, and elevation for each sampled bentonite bed was recorded to 2 cm vertical resolution. Geochemical fingerprinting utilized Electron Probe Micro-Analyzer analysis of mineral phenocrysts including biotite, feldspars, and other accessory minerals. To refine the geochemical fingerprint, phenocryst ratios were estimated visually and combined with geochemical data. Our results show that bentonites in DPP have previously unidentified unique geochemical and visual traits that can be differentiated, specifically using the percentages of Al, Fe, and Mg oxides within analyzed biotite crystals. The geochemical fingerprints reported herein for these bentonites are a critical first step to establish a resolved stratigraphic framework for the DPF in DPP and increase the accuracy of estimates for timelines regarding dinosaur evolution and turnover in DPP.

# Understanding changes in caribou ecology in North America from the late Pleistocene to the Holocene using stable isotope analysis

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The Pleistocene epoch was dominated by a series of glacial cycles followed by warmer interglacial periods. Glacial events lasted between 40,000 and 100,000 years while interglacials were much shorter at 10,000-15,000 years, resulting in much of North America being covered in ice for most of the epoch. Perhaps the most recognizable aspect of Pleistocene ecology is the vast diversity of large mammals that occupied a wide array of niches across Earth's terrestrial ecosystems. By the end of the Pleistocene however, the majority of large mammal species in North America had gone extinct. Caribou diversified early in the epoch and are notable as one of the few large terrestrial mammals on the continent to survive the Pleistocene megafaunal extinctions. The mechanisms of these extinctions remain poorly understood with respect to the degree of influence between climatic factors and human predation. We measured stable isotope geochemical data on both a modern antler from Nunavut and a fossil antler from the Yukon in the late Pleistocene. Nitrogen data from collagen along with carbon and oxygen values from carbonates were measured to determine climatic and dietary information about the contrasting ecological conditions of the two caribou. We found that trends displayed from geochemical data indicate a shift toward an increased migratory behaviour in North American caribou following the end of the last glaciation of the Pleistocene, which is consistent with the current understanding of their evolutionary ecology. This research helped illustrate that stable isotope data from mammals of the Late Pleistocene can provide further resolution into many of the uncertainties still surrounding. Future research should further investigate fossil antlers using broader datasets and resolve the discrepancies found in isotopic data using differing preparation methods.

# Surviving Hell's aquarium: life and death in marine ecosystems during the Age of Dinosaurs

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Eighty-five million years ago, the middle of North America was covered by an ocean filled with massive sharks, bony fish, and marine reptiles. So how did animals that were not apex predators survive in this seaway? Looking at the internal structure of bones reveals growth rates that reflect an animal's evolutionary background, growth stage, locomotion, and environment. Using this technique on extinct *Protostega* sea turtle and *Hesperornis* bird bones uncovers different survival strategies among Late Cretaceous marine animals. In a world of big predators with big teeth, you better grow up fast or get the heck out of Dodge.

# Carnivorous reptile macrowear and tooth use, with implications for tyrannosaurid feeding behavior

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Tooth abrasion visible to the naked eye, or macrowear, is produced by tooth-on-tooth and/or tooth-on-food contact, and can provide information regarding jaw mechanics, diet, and feeding behaviour. Unlike previous studies, we considered not only the type of macrowear and its location(s) on the tooth, but also tooth type and taxonomic identity. Three main macrowear categories were observed in extant reptiles and tyrannosaurids: facets (smooth, flat, typically oval surfaces with or without fine-scale scratches), spalling (removal of enamel with minor modification of overall tooth shape) and breakage (major modification of overall tooth shape, potentially with subsequent smoothing/wear). Facets were restricted to the labial and lingual tooth surfaces, whereas other wear types were observed on all tooth surfaces. We ran generalized multiple linear regressions on the extant dataset using the Akaike information criterion and an exhaustive search to identify wear types that best explained wear distribution relative to taxonomic identification or tooth type. We then plotted the proportions of the returned wear types relative to the number of teeth sampled to visualize distributions. The same model was returned at the subfamily and lower levels, with lateral facets, tip spalls, lateral spalls, tip blunting, mesial blunting and lateral blunting emerging as important variables. Across tooth surfaces, mesial blunting is more frequent than tip spalling in varanids while crocodylians and teiids typically exhibit the reverse; macrowear of any kind was rare in gavialids. Tyrannosaurid teeth show high levels of both mesial blunting and tip spalling. The preponderance of mesial blunting over tip spalling in varanids reflects progressive wear of the mesial carinae as the teeth are drawn through flesh, while the opposite pattern in crocodylians and teiids reflects frequent tooth breakage under oblique forces as chunks of flesh are ripped off during shaking and death rolling. Wear patterns in tyrannosaurids suggest that flesh was penetrated in a tip-mesial fashion, as in varanids, but that the head was then twisted to rip off chunks of tissue. Facets were not observed in teiids, but were observed in some varanids and crocodylians as well as in tyrannosaurids. The proportions of blunting and spalling features returned by the model differ between dietary categories: taxa that frequently consume large and/or semi-soft prey (e.g., Komodo monitors) have more blunting relative to spalling, while those consuming hard prey (e.g., Dracaena) have more spalling relative to blunting. Mixed prey consumers (e.g., Caiman) plot intermediately, and more piscivorous taxa (e.g., Gavialis) have relatively little wear of either type. Most tyrannosaurid genera generally plot with consumers of large/semisoft prey, but Gorgosaurus shows greater variability. These results suggest that tyrannosaurids typically consumed the flesh of large prey, and that tooth-bone contact and bone consumption were likely occasional or accidental rather than habitual in tyrannosaurids, including Tyrannosaurus.



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