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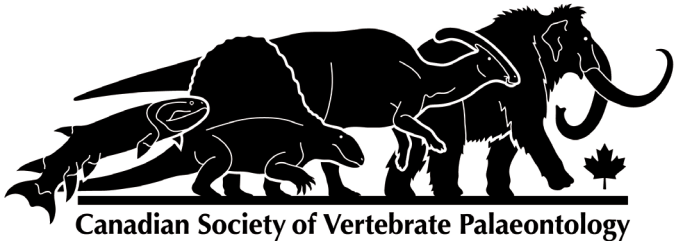
This year's logo is courtesy of McGill undergraduate student Alex Anderson. It features Québec's fleur-de-lis with important fossils representing Québec's contributions to vertebrate paleontology: *Bothriolepis*, *Elpistostege*, and *Hylonomus*.



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Taxonomy versus ontogeny — variation in the snout morphology of Early Permian trematopids at Richards Spur, Oklahoma

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Trematopids were an impressive group of Late Pennsylvanian and Early Permian terrestrial temnospondyls from North America and central Germany. These impressive predators have a largely unresolved phylogeny and poorly understood ontogeny due to a lack of substantially informative fossils representing several taxa. Recent discoveries of numerous skulls of trematopids at the famous Richards Spur (Ft. Sill) locality have allowed for the use of non-invasive imaging analysis, known as "neutron computed tomography" (The Dingo Beamline at ANSTO, Australia), for taxonomic and ontogenetic analysis on these new, well-preserved partial and complete trematopid skulls from the cave infills at the Dolese Brothers Limestone Quarry, Richards Spur, Oklahoma. Hydrocarbon impregnation of these skulls make them ideally suited for neutron tomography, resulting in very high quality data for segmentation. Representing various ontogenetic stages, these skulls can be used to address interesting challenges that can arise from distinguishing ontogenetic variation from taxonomically relevant features. We have already been able to produce detailed anatomical reconstructions of these skulls and have identified features that are both ontogenetically variable and ontogenetically independent among these specimens. This new dataset will create a more accurate representation of both the taxonomy and ontogeny of this clade at Richards Spur. It will also resolve some of the questions regarding whether or not ontogenetically influenced characters were appropriately considered in previous taxonomic interpretations of juvenile and adult specimens of trematopids from this famous locality. Our preliminary data indicate that at least two, possibly three, distinct trematopid taxa can be identified based on the combined features of skull shape, internarial fontanelle size and shape, and the presence of lateral exposures of the palatine and ectopterygoid bones beneath the orbits. This pattern conforms well to the level of taxonomic diversity found among various tetrapod taxa in the Richards Spur terrestrial vertebrate faunal assemblage, including multiple species of dissorophid and amphibamid temnospondyls, recumbirostran microsaurs, acleistorhinid parareptiles, and captorhinid eureptiles.

‘Big Sam’: A new large skull of *Pachyrhinosaurus lakustai* from Alberta’s Campanian (73 Ma) Wapiti Formation, with implications for bonebed taphonomy and intraspecies variation

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The Pipestone Creek Bonebed (PCB), located near Grande Prairie, Alberta, is one of Canada’s largest and densest dinosaur bonebeds, producing an average of 100 to 300 fossils per square metre. Since the discovery of this monodominant bonebed in the 1970s, a series of excavations by the Royal Tyrrell Museum of Palaeontology, Grande Prairie Regional College (now Northwestern Polytechnic), the University of Alberta, and the Philip J. Currie Dinosaur Museum (PJCDM) have yielded nearly 8000 specimens. The PCB represents a mega-herd of the endemic centrosaurine ceratopsian species *Pachyrhinosaurus lakustai*, which likely died in a single catastrophic event. The PCB represents a cross-section of a *P. lakustai* community from a single point in geologic time. The huge sample size, which includes individuals of all ages, makes the PCB invaluable in the study of ceratopsian morphology, ontogeny, ecology, intraspecies variation, and social structure.

The PCB has yielded more than a dozen complete and partially complete skulls of *P. lakustai*. However, due to extensive taphonomic crushing and warping, the scientific significance of many of these specimens is limited. In 2024, the palaeontology team from the PJCDM discovered a very large skull in the bonebed, the first to be found in over a decade. The excavation and extraction of this specimen (PCB.2024.666), nicknamed ‘Big Sam’, took five months to complete, with a subsequent field jacket weighing over 450 kg (1000 lbs). The skull consists of the complete cranium, including the occipital condyle and braincase, an articulated left squamosal, and the parietal bar. Though somewhat dorsoventrally compressed, ‘Big Sam’ is among the largest skulls collected from the PCB, measuring 138 cm in length and with a massive nasal boss measuring 43 cm in diameter. Unusually for the PCB, the skull was preserved upside-down, with the ventral side facing the surface. Due to this, this skull is the first *P. lakustai* specimen in which the palatal and rostral region are well preserved and are relatively free of lateral crushing or warping. While the specimen is currently being prepared, some interesting features have already been identified. An autapomorphy of *P. lakustai* is the parietal ‘unicorn’ spike(s) on the parietal bar, which can vary in number from one to three. Despite its size, ‘Big Sam’ appears to have an extremely reduced parietal spike, calling into question the theory that these were display features in the oldest and most mature animals. The taphonomy of the skull, as well as the 100+ bones jammed in against it (of *P. lakustai*, but from different individuals), has also led to interesting questions about how the bonebed deposit formed. Subsequent preparation work and study of this specimen is likely to yield interesting insights in the morphology, intraspecies variation, and ecology of *P. lakustai* specifically, and ceratopsians in general.

The evolution of ceratopsian feeding: an exercise in 3D biomechanical modeling

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Ceratopsians were a widely successful clade of Jurassic to Cretaceous dinosaurs. The first ceratopsians were diminutive herbivores with apparent adaptations for high fibre herbivory and relatively complex mastication cycles. Over time, some highly derived euceratopsians, the ceratopsids, attained very large body sizes and developed shearing tooth batteries with a simple orthal bite stroke. However, to this day, no study has ever produced quantitative and absolute estimates of ceratopsian feeding performance through their evolution.

For this study, we 3D modelled the cranial adductor musculature of eight ceratopsian taxa throughout their evolutionary radiation (*Psittacosaurus lujiatunensis, Protoceratops andrewsi, Leptoceratops gracilis, Centrosaurus apertus, Chasmosaurus belli, Styracosaurus albertensis, Triceratops horridus, Pachyrhinosaurus lakustai*). We estimated bite force, jaw gape, bite volume, and shear in all these taxa, providing some of the first absolute and quantitative data on the evolution of feeding performance of this clade.

Our results reveal a significant change in ceratopsian feeding performance from the earliest basal ceratopsians to the most derived ceratopsids. Early ceratopsians and neoceratopsians had high relative bite force and shear. Ceratopsids had lower relative bite force and shear, but their high absolute size resulted in high bite force and high shear. Incidentally, this study also shows ceratopsians were amongst the strongest biting taxa to have ever existed, rivaling and even surpassing some carnivorous taxa. Among herbivorous taxa, *Triceratops horridus* was found to be the strongest biting taxon to have ever existed, with an estimated bite force around 30,000 N.

Comparison of the feeding performance of ceratopsians to modern megaherbivores reveals that ceratopsians likely played a unique role in their ecosystems, analogous to some modern herbivores, but not exactly like any of them. We also discuss the implications of these findings for the permanence of ecological niches and the drivers of evolutionary change in feeding performance.

How do ecosystems evolve? Analysis of 264 ecosystem networks across the Cenozoic of North America

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Ecosystems are inherently complex systems, shaped by dynamic interactions between species, environmental factors, and evolutionary processes. Ecosystem change often proceeds abruptly, displaying stable behaviour until critical "tipping points" are exceeded, leading to potentially irreversible changes. Thus, developing methods to fully capture ecosystem complexity and evolution through these transitions is essential.

To this extent, quantitative ecosystem networks are an emerging approach thanks to their potential to combine biodiversity, species interactions, and ecosystem function. Yet, application of these methods to deep time are limited, fraught with several biases. Compared to modern ecosystems, ancient Phanerozoic ecosystems were more diverse, environmentally broader, and evolved across multiple sweeping transformations. These latter factors bring the study of ancient ecosystems to the forefront of exploring how these complex systems evolve and respond to environmental and biotic perturbations.

In this study, we reconstruct 264 fossil mammalian trophic networks in North America that are concentrated in the Western Interior and span relatively evenly throughout the entire Cenozoic Era. Our model uses extant mammal community observations to predict interactions using matching species traits like body size, broad dietary category, and life habit, and refines these predictions using phylogenetic comparisons.

Each trophic network is used to track changes in network properties over the Cenozoic. Although some network properties change monotonically, others have nonlinear trajectories, and some remain constant. This suggests that some network properties are constrained or insensitive to fluctuating biotic and abiotic conditions, while others are labile to fluctuating biotic and abiotic conditions. We also cluster networks based on their properties, revealing the existence of at least three "states": a post-K-Pg extinction recovery state, a warm Paleogene state, and a post-Paleogene cool state. We discuss the biotic and abiotic factors that possibly mediated these state shifts.

Finally, we discuss the best approaches and heuristics to study ecosystem evolution, with a focus on ecological networks. We draw parallels to evolutionary biology, including the use of evolutionary landscapes to track how ecosystems might optimize certain properties such as stability through time. We also discuss how studying time-series of past ecological networks and associated biodiversity metrics like the rate of interaction rewiring might help predict and even detect impending state shifts in extant ecosystems.

The southernmost occurrence of Arctic cloud forests: insights from the Maastrichtian—Danian Scollard Formation of northern Alberta

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It is no secret among palaeontologists that biodiversity once flourished on an Earth far warmer and more humid than *Homo sapiens* has ever known, despite the negative effects of anthropogenic climate change on modern ecosystems. One such warm interval, spanning the Late Cretaceous and early Paleogene, was the first to have occurred after the global diversification and radiation of angiosperm plants, the dominant primary producers in terrestrial ecosystems since the Cretaceous. During this interval, unique ecosystems thrived under climate regimes that would appear alien today. For instance, broad-leaved angiosperm trees adapted for months without sun, nearly perpetual cloud cover, and extreme humidity spread to latitudes as far as 80 ºN, beyond the range of even the most extreme boreal forests in the present day. The analysis of a moderately high latitude palaeoflora (palaeolatitude ~61.5 ºN) from the Scollard Formation of northern Alberta yields insights into the southernmost and warmest extents of the now-extinct polar broadleaf deciduous forests. Palaeoclimate parameters calculated using the Climate Leaf Analysis Multivariate Program (CLAMP) indicate that the dinosaurs, reptiles, mammals, amphibians, and invertebrates that once inhabited these forests would have enjoyed warm winters averaging >13.5 ºC, hot summers averaging >20 ºC, and intense fog, rain, and humidity year-round. This climate regime is in sharp contrast to that of cities near 61.5 ºN today, such as Yellowknife in the Northwest Territories, whose residents regularly experience winter temperatures lower than -45 ºC.

Estimating body mass in extinct mammals: evaluating the predictive power of dental, cranial, and postcranial proxies

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Body size is a fundamental biological parameter that profoundly influences the ecology, physiology, life history, and evolution of organisms. Estimating body size in extinct species, though not directly measurable from the fossil record, is possible through allometric relationships between skeletal dimensions and mass in extant taxa. Prior research has produced various scaling equations, but the choice of proxy can result in highly variable estimates. This study addresses this challenge by compiling a diverse dataset of dental, cranial, and post-cranial measurements from extant mammals. We generated a set of scaling equations and rigorously tested their suitability and predictive power for estimating body mass by comparing several performance metrics, such as the coefficient of determination and residual standard error. Subsequently, we applied these equations to estimate the body mass of a wide range of Paleocene mammals. Our findings highlight the strong predictive performance of postcranial proxies, offering reliable estimates. Particularly, long bones and tarsals showed strong predictive performance and hold great potential as a proxy due to their good preservation potential and highly diagnostic morphology. Conversely, dental proxies exhibited reduced efficacy, substantial variability, and unreliability. Additionally, our research revealed that predictive performance improves significantly across all proxies when species are divided into size classes, specifically separating those above and below 10 kg. This underscores the importance of this threshold in future body mass estimation studies. These results contribute significantly to our understanding of body mass prediction in mammalian species and provide valuable guidance for researchers aiming to estimate body size from fossil remains.

A new genus and species of acanthothoracid placoderm (stem-group Gnathostomata) from the Early Devonian of Arctic Canada

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The origin of jawed vertebrates was a pivotal episode that established defining characteristics of nearly all living vertebrates, from jaws, teeth, and paired fins, to myelinated nerves and adaptive immune systems. Placoderms (armoured Silurian-Devonian gnathostomes) represent the only known jaw-bearing members of the gnathostome stem-group and are thus crucial to our understanding of the origin of this group. However, their phylogenetic interrelationships are much debated. Furthermore, much of our anatomical understanding of placoderms derives from

late-occurring (Devonian) taxa. Among the most enigmatic placoderms are the so-called 'acanthothoracids', a likely paraphyletic array of poorly understood placoderms. Despite their incompleteness, 'acanthothoracids' have figured prominently in debates on the origin of jawed vertebrates. Arguably the best-preserved examples of 'acanthothoracids' come from the Early Devonian Drake Bay locality in Nunavut. Until recently, however, this group was considered to host only a single genus, *Romundina*. Here we present a new genus and species of 'acanthothoracid' from this locality. We investigated the specimen using high-resolution synchrotron tomography. The new specimen consists of a three-dimensional partial braincase, comprising the orbits, nasal capsule, and brain cavity. The exquisite preservation of the endocranial cavity provides evidence of a complex hypophyseal and lymphatic system — the latter previously unknown in a placoderm. This system is evidenced by compact bony clusters permeated by reticulating canals and connecting to the internal carotid arteries. The cranial nerve canals have a unique bulbous profile, resembling the shape of ganglia; this suggests that the cranial nerve ganglia may have been housed within the braincase cartilage, rather than external to it as in chondrichthyans. We show that 'acanthothoracids' exhibit a previously unappreciated combination of ancestral and derived gnathostome features. Moreover, we highlight significant problems with current hypotheses of placoderm interrelationships, in particular the evolution of craniofacial geometry across the 'agnathan-gnathostome' transition.

The chemical composition of pterobranch (Hemichordata) tubes

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Graptolite tubes are so ubiquitous in the Palaeozoic fossil record that they are used as index fossils for dating rocks. These tubes represent one of the most disparate extracellular secreted structures in nature and are found in thousands of graptolite species, including the extant *Rhabdopleura recondita*. The chemical composition of graptolite tubes is a topic of enduring debate since their major component is hypothesized to be either chitin, keratin, protein, cellulose or collagen. We integrated bioinformatics and spectroscopic analysis to reject the keratin and cellulose hypotheses. Instead, we found eight chitin synthase genes in the *R. recondita* genome. The spectroscopic analyses of the tubes revealed the presence of a composite of a chitin polysaccharide with calcium carbonate along with protein and fatty acid. As a continuation of this study, we are determining the chemical composition of tubes referred to *Cephalodiscus*, the sister taxa to graptolites, which revealed the presence of silicates, calcium carbonates and undefined polysaccharides. To characterize a chitin polysaccharide, we are employing infrared spectrometry, X-ray diffraction, Raman spectroscopy and a specific colorimetric method. This study will be the first to characterize the origin and evolution of graptolite tubes.

Acorn worm ossicles and the origin of the echinoderm skeleton

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Calcium carbonate ossicles are the foremost morphological innovation of echinoderms. Their origin was with an acorn worm ancestor to the Ambulacraria (Echinodermata and Hemichordata). This hypothesis finds support from comparative morphology, elemental analyses, and comparative genomics. Like those of echinoderms, acorn worm ossicles are ectodermal, formed in an extracellular occluded space bordered by a sheath of sclerocyte cells, but are microscopic, monotypic, and composed of calcite, aragonite or vaterite with low to high magnesium concentrations. Echinoderm ossicles are made of calcite with a high Mg concentration. Acorn worm transcriptomes include echinoderm matrix metalloproteases, carbonic anhydrases and ossicle specific MSP130 proteins. We have failed to develop an ossicle proteome, and have not found any MSP130 transcripts in the acorn worm trunk where ossicles occur. These findings suggest that the MSP 130 gene family had not yet been co-opted for ossicle development in the ambulacrarian ancestor. Ambulacrarian ossicle biomineralization may have appeared before its genetic regulation.

According to molecular clock data, the origin of Ambulacraria was 559 mya. From around this date, the evolution of the echinoderm endoskeleton began with ossicle polymorphy, followed by intercalation, and then the development of a rigid skeleton by ~ 520 mya. High Mg calcite hardens ossicles and thus may be regarded as a skeleton coaptation. By 510 mya echinoderms had diversified into four distinct body plans. One of these was the bilaterally symmetric fossil Ctenoimbricata, which has a dorsal surface of monotypic non-intercalated ossicles, reminiscent of acorn worms. The origin of the porous microstructure called stereom, and the function of acorn worm ossicles are exciting avenues for discovery.

Thecate stem medusozoan polyp from the Upper Ordovician of Quebec

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The fossil record of Cnidaria is scarce and often disputed. A new genus and species of an exceptionally preserved, soft-bodied, tubicolous medusozoan is described as a new species of *Paleocanna* from the Upper Ordovician (Katian) Neuville Formation in Québec. These fossils, preserved as carbonaceous compressions, occur alongside typical shelly assemblages. Fifteen slabs of shaly limestone containing approximately 135 specimens were examined. Individual polyps occupied upright tubes, which were found either solitary or clustered at the base. Some tubes exhibit a striated periderm near the base. The polyp is elongated, with a rounded aboral end and a proximal ring of tentacles that consistently protrude from the tube. A phylogenetic analysis of 51 taxa and 304 discrete morphological characters indicates that this species lies along the stem of Medusozoa. Specimens on single slabs display uniform orientation, suggesting rapid burial. This new species constitutes an exceptionally preserved member of an Ordovician deposit that exhibits Burgess Shale–type soft-tissue preservation.

New ichthyosaur from Colombia reveals high ecological disparity in Cretaceous ichthyosaurs

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With an evolutionary history spanning nearly 160 million years, ichthyosaurs represent one of the best examples of secondarily aquatic marine adaptation. Despite their early ecological diversity, Cretaceous ichthyosaurs experienced a decline in morphological disparity, with reduced niche differentiation compared to their Jurassic predecessors. However, this perspective is largely shaped by an incomplete fossil record. The Lower Cretaceous Paja Formation Biota of Colombia, home to one of the richest marine assemblages of the Neotropics, provides a critical window into this understudied evolutionary phase of ichthyosaurs. We describe a newly discovered ichthyosaur that challenges traditional views of Cretaceous ichthyosaur ecology. This taxon exhibits an unprecedented combination of cranial and postcranial traits, including a rostrum wider than high, highly labiolingually compressed dentition, a unique configuration of the dorsal skull, and unique bone patterning in the hindfin, occupying a novel ecomorph within ophthalmosaurians. Our comparative, ecomorphological and phylogenetic analyses reveal unexpectedly high craniodental ecological disparity among Paja ichthyosaurs, comparable to the best-documented and highly diverse Early Jurassic Posidonia Shale lagerstätten. These comparisons indicate that the Paja ichthyosaur assemblage evolved toward a prevalence of macropredatory adaptations. Across seventeen examined taxa, we document a spectrum of feeding strategies, suggesting complex niche partitioning and trophic interactions in the Paja ichthyosaurs. These findings not only expand the known ecological range of Cretaceous ichthyosaurs but also indicate a broad shift while maintaining an equally diverse ecomorphospace in these taxa. The new taxon is one of many examples of Cretaceous ichthyosaurs evolving a broader ecology in their environments.

An elusive bird and non-avian dinosaur fauna from the latest Cretaceous (Campanian/Maastrichtian) Kanguk Formation of Bylot Island, Nunavut

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Polar ecosystems of all geological periods attract palaeontological interest since they are often a crucial component of our understanding of deep-time changes in latitudinal climate and biodiversity gradients. However,

high-latitude fossil localities remain elusive due to several geographical and logistical constraints, such that a few select localities provide a disproportionate amount of data. Here, we describe dinosaur (including bird) fossils collected from the Late Cretaceous Kanguk Formation of Bylot Island, Nunavut. As the age of this unit is estimated as latest Campanian to early Maastrichtian, it provides one of the few glimpses into vertebrate life in the Eastern Canadian Arctic at palaeolatitudes of nearly 80°N, slightly south of the better-known Prince Creek Formation biota in Arctic Alaska. The first palaeontological expeditions to Bylot Island took place in 1987, 1988 and 1989, with their collections now curated at the Canadian Museum of Nature. The last expedition took place in 2007, and its specimens were deposited in the Nunavut fossil vertebrate collections. All terrestrial dinosaur remains collected during these surveys were allochthonous to their burial setting since their depositional environments varied between delta mouths, beaches and lagoons. This taphonomy is further supported by the occurrence of shark and ratfish teeth, marine bivalves and hesperornithiform bird bones in the 2007 collection. We describe additional hesperornithiform specimens from the latter collection, with an assortment of vertebrae and tibiotarsi that widen the body size distribution represented in the fossil record of these local marine bird populations since the initial description of *Canadaga arctica* from earlier collections. Another significant find consists of the first tyrannosaurid bone reported from Arctic Canada, tentatively identified as a tibial shaft belonging to a juvenile individual of indeterminate species due to its small proportions relative to adult skeletons. This occurrence, together with that of juvenile hadrosaur remains, bolsters evidence from Alaska suggesting that dinosaurs likely survived year-round within sufficiently productive polar ecosystems, despite an extreme photoperiod regime. These two collections significantly expand the non-avian dinosaur and bird fossil record from the Canadian High Arctic and consolidate a hypothesis of relatively equable latitudinal climate and biodiversity gradients during one of Earth's 'greenhouse' periods.

Exceptional preservation of acanthomorph fishes within a regurgitated pellet

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Within the Lethbridge Coal Zone of the upper Dinosaur Park Formation, Alberta, Canada, a 6 m thick unit of marine mudstone preserves a diverse assemblage of aquatic organisms from the transgressing Western Interior Seaway. Bony fish fossils from this unit are typically found as isolated elements, most often teeth or fragmented vertebrae. However, a recent and rare fossil discovery provides a unique opportunity to examine multiple bony fish elements preserved together. The specimen, a compact pellet 22 mm long and 11 mm wide, contains minute fish bones held together by an iron-rich matrix. Identified as a regurgitalite (fossilized regurgitated material), it is the first documented occurrence of this fossil type in the Dinosaur Park Formation. Unlike previously reported coprolites (fossilized feces), the regurgitalite lacks a calcium phosphate matrix, and its exceptionally well-preserved skeletal elements suggest that it was expelled before digestion was completed. A high-resolution micro-CT scan reveals a delicate aggregation of fish remains, including teleost vertebrae, acanthomorph spines, and toothed dentaries and premaxillae. Many of the vertebrae retain their fragile processes, revealing an unusually high level of preservation among isolated fossils from the Lethbridge Coal Zone. The presence of two distinct centrum sizes, along with duplicated mandibular elements, indicates that at least two individuals are represented. An estimate of the number of fish elements preserved within the regurgitalite was derived by multiplying the number of elements visible in a

single CT scan slice by the thickness of the specimen, then dividing by the average thickness of the elements. The detection of roughly 1,200 elements further supports the conclusion that multiple individuals are represented in the pellet. Nonetheless, the similarity in size of numerous toothed elements suggests that some elements may be associated. This regurgitalite provides a glimpse of an organism's meal along the shores of the Western Interior Seaway. It contributes valuable insight into acanthomorph anatomy and enhances our understanding of Alberta's Late Cretaceous ecosystem.

New tracks from the Peace Region of British Columbia show that ankylosaurids were present in the Cenomanian of Laramidia

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The ankylosaurian ichnospecies *Tetrapodosaurus borealis*, first described from the Gething Formation of the Peace River Canyon in British Columbia, is now known from multiple localities across North America and further afield, and is particularly abundant in the area around Tumbler Ridge. Comparatively rare tracks with a pentadactyl manus and tridactyl pes from the Dunvegan and basal Kaskapau formations in the Tumbler Ridge area are identified as a new thyreophoran ichnogenus, *Ruopodosaurus clava*. These trackways have a narrow gauge, and pes tracks typically have a bilobed heel, rounded or bluntly-pointed unguals, and are outwardly rotated. Among ankylosaurs, only ankylosaurids have three pedal digits rather than four, making this the first known track morphotype for ankylosaurid ankylosaurs. *Ruopodosaurus clava* is found in the same localities and deposits as *T. borealis*, indicating that both ankylosaurid and non-ankylosaurid ankylosaurs co-existed in the mid Cretaceous of the Peace Region. All known *Ruopodosaurus* pes tracks are around 30 cm long, and are thus significantly smaller than the largest *Tetrapodosaurus* pes tracks that approach 50 cm in length. The presence of *Ruopodosaurus* in the Cenomanian is significant, as the presence or absence of ankylosaurids in Laramidia between the Albian and Campanian was previously unclear. The identification of a distinct ankylosaurid track morphotype also provides the potential for testing the antiquity of ankylosaurids in North America with future discoveries.

Testing trade-offs in the fossil record: socio-sexual vs. natural selection in the cranial evolution of duck-billed dinosaurs (Ornithischia: Hadrosauridae)

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Exaggerated cranial structures have repeatedly evolved in vertebrates, with numerous groups developing prominent bony structures for display and/or combat. In extant taxa, the evolution of these structures is typically discussed in the context of an evolutionary trade-off with socio-sexual selection, where their presence increases reproductive success at a cost to other functions. Studies of evolutionary trade-offs in the fossil record have focused almost exclusively on functional traits (e.g., jaw closing speed vs. strength), but trade-offs also likely occurred between osseous socio-sexual cranial display structures and other functions of the skull, notably feeding. Lambeosaurine hadrosaurids provide an ideal case-study to test for trade-offs in skull evolution in fossil vertebrates. Lambeosaurines exhibit extreme modifications to their facial skeleton, where the premaxillae, nasals, and prefrontals are modified to form prominent supracranial crests that developed through ontogeny. In addition to visual display, these crests also likely facilitated intraspecific communication via sound production. Oddly, lambeosaurine crests are extensions of the premaxillae and nasals onto the skull roof, where stress from feeding is usually dissipated in amniotes. Their sister group, Hadrosaurinae, 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 an evolutionary trade-off between lambeosaurine supracranial crests and feeding mechanics, we used finite element analysis (FEA) to perform three distinct ecological and evolutionary comparisons. First, we tested for changes in feeding mechanics through ontogeny as the crest developed in the lambeosaurine *Corythosaurus casuarius*. Second, we tested for differences in feeding mechanics between *C. casuarius* and the contemporaneous crestless hadrosaurine *Gryposaurus notabilis*. Third, we tested for changes in feeding mechanics in association with crest evolution using a suite of 10 lambeosaurines, hadrosaurines, and non-hadrosaurid iguanodontians. Taken together, the results of these comparisons demonstrate that changes in skull shape associated with lambeosaurine crest evolution significantly impacted cranial biomechanics. Lambeosaurines tend to have smaller jaw muscles and lower bite forces than non-crested hadrosaurines, but higher mechanical advantage due primarily to posterior reduction of the temporal chamber, though interspecific variation is present. Hadrosaurine skulls behave similarly to non-hadrosaurid iguanodontians during feeding, with stresses distributed throughout the skull and snout. In contrast, lambeosaurine skulls experience little stress and strain in the preorbital region, and stress during feeding is instead concentrated posteriorly in the braincase and palate. We interpret this as an adaptation to reduce unnecessary bending in the delicate supracranial crests. Notably, the patterns of stress and strain observed in crestless juvenile *C. casuarius* are more similar to hadrosaurines and non-hadrosaurid iguanodontians, suggesting that these differences in skull biomechanics are not due exclusively to diet specialization, but relate to the size and position of the supracranial crest. In conclusion, this study demonstrates that lambeosaurine supracranial crests altered jaw muscle architecture and the distribution of stress and strain during feeding, resulting in the compensatory evolution of cranial biomechanics.

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A new "*Stegoceras*-like" pachycephalosaurid from the Santonian Milk River Formation of Alberta, Canada

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Despite the continued identification and description of new pachycephalosaurid species, their early evolutionary history and diversity continues to be poorly unknown. The vast majority of material and known species are restricted to the latest Cretaceous (Late Campanian and Maastrichtian), despite presumably diverging from ceratopsians in the Late Jurassic. Only a handful of pre-Campanian pachycephalosaurid specimens are known from Asia and North America. Perplexingly, these geologically oldest specimens, such as the type series of *Acrotholus audeti* and *Amtocephale gobiensis*, tend to have a mixture of plesiomorphic and derived traits. They are typically recovered within Pachycephalosaurinae in phylogenetic analyses, implying a number of ghost lineages within Pachycephalosauridae and undiscovered early-diverging taxa. Here, we present a new pachycephalosaurid specimen (TMP2015.044.0001) from the Santonian Deadhorse Coulee Member of the Milk River Formation (83.6–83.7 Ma) Alberta, Canada. It is the most complete (albeit heavily worn) pachycephalosaurid from the Milk River Formation, represented by an almost complete frontoparietal, with articulated portions of the nasals, prefrontal, palpebral, and posterior supraorbital, all of which are incomplete. All preserved elements are completely fused to each other, suggesting an advanced ontogenetic stage. These fused contacts are identifiable in micro-CT images. This allowed us to segment the frontoparietal from the peripheral elements and include it in a morphometric analysis with other pachycephalosaurids from Alberta, including *A. audeti* (the other known pachycephalosaurid from the Milk River Formation).

Despite its incomplete condition, TMP2015.044.0001 can be readily distinguished from *A. audeti* by the presence of a groove separating the frontonasal boss and supraorbital lobe(s)—likely a plesiomorphic trait. Instead, TMP2015.044.0001 is morphologically consistent with UCMP 130051 (Campanian Judith River Formation, Montana), which is typically regarded as a mature *Stegoceras* sp. These two specimens possess an unusual dorsal depression along the peripheral margin of the frontals at the contact with the palpebral and posterior supraorbital that results in separate anterior (prefrontal and palpebral) and posterior supraorbital lobes (hemilobes) of the cranial dome. This is not apparent in any other pachycephalosaurid specimen (including *Stegoceras validum*). TMP2015.044.0001 and *S. validum* are morphometrically distinguished from *A. audeti* by a narrower frontoparietal at the prefrontal-palpebral contact relative to the frontoparietal width at the posterior supraorbital-postorbital contact. Given the incomplete condition of TMP2015.044.0001, we conservatively refer it to a *Stegoceras*-grade pachycephalosaurid, and suggest that more detailed analyses may allow it to be referred to a new taxon. Discovery of this new specimen begins to fill the ghost lineage of *Stegoceras*-like pachycephalosaurids as predicted by previous studies, but long ghost lineages for early diverging pachycephalosaurs still remain.

Post-Eocene rhinocerotid dispersal via the North Atlantic

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Biotic interchange (i.e., the movement of organisms among regions and continents) among Europe, Asia and North America over the last 66 Ma shaped global mammal biodiversity. However, for most clades, the number and timing of dispersals remain poorly understood. Herein, we aim to reconstruct the biogeographic history of rhinocerotids, a clade with considerable past diversity and a geographic range that encompassed much of the globe. Using a fossilized birth-death approach, we estimated the largest time-calibrated phylogeny of Cenozoic rhinocerotids to date. We then used the maximum likelihood approach in BioGeoBEARS to fit an array of biogeographic models (e.g., Dispersal-Extinction Cladogenesis (DEC), DEC+jump dispersal) and stochastic character mapping to infer the number of biotic interchange events among Asia, Europe, North America, and Africa. We found that the highest rates of biotic interchange, unsurprisingly, occurred between Europe and Asia. However, the next highest number of exchanges occurred between Europe and North America. Furthermore, we show that dispersal between Europe and North America occurred during the Oligo-Miocene, suggesting that the North Atlantic route may have been passable for mammals millions of years longer than previously proposed; typically, the North Atlantic route has been considered passable for terrestrial vertebrates only from the Paleocene to early Eocene. Recent geological and palaeoclimatological evidence, however, suggests that waterways that now prevent terrestrial dispersal via the North Atlantic (e.g., the Fram Strait, Barents Sea) were shallow until the Miocene and, potentially, bridged by seasonal sea ice as early as the late Eocene. We therefore hypothesize that rhinocerotid dispersal between Europe and North America post-Eocene may have occurred via the North Atlantic. Our study reveals the complex history of a charismatic mammalian clade and provides insight into the importance of the Arctic as a persistent connector of otherwise geographically disparate faunas.

Diverse inner ear morphology in early Miocene Thryonomyoidea (Rodentia) from Napak, Uganda

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Rodents, specifically thryonomyoids, constitute the most abundant fossils found at the Miocene-aged sites of Napak, Uganda (20 Ma). The past diversity of thryonomyoids was much greater than current diversity, which is now limited to two extant species of cane rat (T*hryonomys gregorianus* and *Thryonomys swinderianus*). The Napak sites have yielded several thryonomyoid crania, in addition to numerous isolated auditory bullae that have not yet been described. Here, we present the first descriptions and shape analysis of the inner ear morphology of three fossil

thryonomyoids (*Diamantomys luederitzi, Paraphiomys pigotti*, and a smaller species that we tentatively identify as Thryonomyoidea indet.). Our results show that there is considerable morphological diversity among fossil thryonomyoids, with notable morphological characteristics defining each species. Fossil inner ear morphology also supports previous thryonomyoid phylogenies obtained from tooth morphology. *Diamantomys luederitzi* is the only species that has a secondary common crus, an ancestral placental mammal trait. In most phylogenies of fossil thryonomyoids, *D. luederitzi* is placed within Hystricognathi at the divergence between thryonomyids and bathyergids. *Paraphiomys pigotti* inner ear shape is similar to the two modern day *Thryonomys* species, and is an intermediate between them. This supports previous phylogenetic analysis of placing *Paraphiomys* within Thryonomyidae, suggesting that *Paraphiomys* is closely related to the modern forms. The external bulla morphology of Thryonomyoidea indet. is similar to the type specimen of *Kenyamys mariae* (Kenyamyidae, Thryonomyoidea) from Rusinga, Kenya, but is larger in size. It is possible that Thryonomyoidea indet. should be referred to *Simonimys genovefae*, a larger kenyamyid with similar tooth morphology as *K. mariae*, but there are no fossil crania for comparison. Internally, Thryonomyoidea indet. has oblong anterior canals and an angled common crus, unlike the other thryonomyoids with round anterior canals and a vertical common crus. The diversity of inner ear morphology uncovered in this study bolsters the morphological and phylogenetic diversity found within fossil Thryonomyoidea.

"Innies" and "outies": quantifying morphological variation among nasal bosses of *Pachyrhinosaurus lakustai* (Ceratopsia: Centrosaurinae) from the Pipestone Creek Bonebed in the Upper Cretaceous Wapiti Formation of northern Alberta

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Phenotypic variation within dinosaur species is best observed in monodominant bonebed assemblages, which many authors interpret as representing single populations of the dinosaur species therein. Any such population is expected to display intraspecific phenotypic variation, which may reflect differences in genotype, life experience, sex, or ontogenetic stage within the species. Variation is well-documented in many ceratopsid bonebeds, such as the extensive Pipestone Creek Bonebed near Grande Prairie, Alberta, Canada. This fossil site preserves potentially hundreds (MNI = 33) of individual *Pachyrhinosaurus lakustai*, a centrosaurine dinosaur known for the presence of nasal and postorbital bosses rather than horns. This massive monospecific sample reveals extensive individual variation; for example, study of ontogenetic changes in the eponymous nasal boss of *Pachyrhinosaurus lakustai* has revealed its beginnings as a bladed demi-horn in juveniles and subsequent development into the full boss seen in adults. The nasal bosses of the largest specimens range from dorsally convex "outies" to dorsally concave "innies," with some seemingly intermediate or transitional forms. Few studies have explored the biological basis for this variation in boss morphology, or whether the variation is simply taphonomic noise. If natural, the coexistence of "innie" and "outie" morphs could be reflective of advanced age, degenerative pathology, or sexual dimorphism. Herein, we employ various methods to visualize and quantify the characteristics of these nasal bosses, including histology and a novel use of

Geographic Information Systems (GIS), in order to document and interpret the patterns of variation displayed by the fossils. Current data reveals an overall higher frequency of "innie" and intermediate morphs, and also suggests that "outies" tend to be more rugose than more invaginated bosses.

New cranial material and nuclear genome sequences clarify evolutionary relationships of *Haringtonhippus francisci*

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The reconstruction of evolutionary relationships among species is crucial for our understanding of both past and present biodiversity. The development of advanced molecular techniques capable of sequencing the genomes of extinct taxa has revolutionized our understanding of phylogenetic relationships even within clades whose evolutionary relationships were previously regarded as being well-resolved. Despite significant progress that has been made in rectifying the complex evolutionary relationships of equids (Perissodactyla, Equidae), the phylogenetic affinity of many species remains uncertain. Those of the Pleistocene North American stilt-legged horses are particularly contentious, with conflicting views regarding their placement within the genus *Equus*. The evolutionary relationships of *Haringtonhippus francisci* (also referred to as *Equus francisci*) to other equids have been the subject of considerable debate due to it being the only stilt-legged horse described from eastern Beringia (present-day Alaska and Yukon), and its frequent synonymization with other species in the literature. Here, we describe the first cranial material discovered from Yukon, Canada of eight *Haringtonhippus francisci* individuals and present the most complete nuclear genomes of the species to date. Although there exists variation among the specimens, all share several dental characters including pronounced styles, one to three plications on the fossettes, and arcuate protocones. However, overall tooth morphology is generally non-diagnostic and shares many similarities with the typical caballine dental morphology. Genomic data place all specimens within a monophyletic clade that falls definitively outside of crown *Equus*, indicating that *Haringtonhippus* represents a valid genus of stilt-legged horses. However, this calls into question the phylogenetic relationships of other stilt-legged horses, many of which have been placed within *Equus*, which may indicate that the so-called "stilt-legged horse" clade is polyphyletic and therefore does not represent a valid taxonomic group. Further research is required to resolve the complex evolutionary relationships of Pleistocene stilt-legged horses, but this study has provided a critical first

step in establishing that *Haringtonhippus francisci* represents a morphologically cryptic, yet genomically distinct species. It is highly likely that more specimens belonging to this taxon could exist in museum collections but have yet to be recognized due to morphological similarity with other species of Pleistocene equids. We emphasize the need for further investigation into potentially misidentified specimens of *Haringtonhippus francisci*, which in turn will contribute to the resolution of the long-standing debate regarding the true number and taxonomic identities of Pleistocene North American horses.

Return of the mummies: unique European pyxicephalid (Anura) revealed by Eocene mummies from the Quercy (SW, France)

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The Quercy Phosphorites area provides more than 200 fossiliferous karstic infilling localities in southwestern France, ranging from the Lower Eocene up to the Miocene. While exploited for phosphates in the 19th century, thousands of vertebrate fossils were discovered. These fossils are assigned to a variety of clades (arthropods, birds, amphibians, turtles, crocodilians, etc.), with mammals constituting a majority of fossils and diversity. This makes the Quercy area a major site for the evolution of European fauna during the Eocene and Oligocene. Anurans are present within the Quercy, but a single taxon, *Thaumastosaurus*, was named after Quercy specimens. However, in the early stages of industrial exploitation (1873), exceptional amphibian specimens with the external surface of the unmineralized tissues preserved were discovered and referred to as mummies. Since 2012, the mummies started to be scanned, revealing preserved internal soft tissues and articulated skeletons. One mummy was assigned to *Thaumastosaurus*. A second mummy, previously identified as another species, was scanned, and its osteological characteristics allow an attribution to *Thaumastosaurus*. Both mummies provide essential information on the postcrania of *Thaumastosaurus*, previously known only by cranial bones. This new anatomical information was used to test the phylogenetic affinities of *Thaumastosaurus*, previously considered close to South American frogs. Phylogenetic analyses proposed *Thaumastosaurus* as a member of Pyxicephalidae, a clade endemic to sub-Saharan Africa. Its presence in Europe highlights a faunistic exchange with Africa during the Eocene and the presence of an African component in European herpetofauna before the environmental changes at the Eocene-Oligocene transition.

Functional morphology of *Leptoceratops gracilis* teeth and their role in plant processing

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Ceratopsians were herbivorous dinosaurs that dominated Late Cretaceous ecosystems, with their success often attributed to dietary niche partitioning facilitated by specialized plant-processing adaptations. While derived ceratopsians evolved complex dental batteries, the feeding mechanics of basal forms like *Leptoceratops gracilis* remain uncertain. Their unique dentition, featuring heterodont teeth and vertical shearing surfaces, may represent

an intermediate strategy for processing tough vegetation. To explore this possibility, 3D models of *Leptoceratops* (CMN 8889) dentition were reconstructed and tested in a mechanical simulating jaw motion and bite forces. Two key dental adaptations were suggested: (1) heterodonty with anterior teeth for food manipulation and posterior teeth with specialized shearing surfaces, and (2) apical points to pierce and separate fibers. Mechanical testing demonstrated bite forces of 840 N (anterior) to 2520 N (posterior) were sufficient to process woody material up to 15 mm in diameter. These results suggest that paired with circumpalinal chewing, its dentition allowed *Leptoceratops gracilis* to occupy a distinct dietary niche, feeding on low-growing woody plants that complemented the diets of contemporaneous larger dominant herbivores. This study uses functional morphology of teeth to reconstruct potential feeding adaptations of the *Leptoceratops* and to examine their possible role in the evolution of ceratopsian herbivory.

Regional variation in the relative abundance of dinosaurs during the latest Cretaceous of North America

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Exposures of the latest Cretaceous Period stretch for nearly 1500 km across western North America, representing the best terrestrial fossil record preceding the end-Cretaceous mass extinction. Although exposures vary in nomenclature and lithology, they are all paracontemporaneous and can be constrained to the Lancian age, representing roughly the last million years of the Cretaceous Period. The temporal control and geographical spread of Lancian strata in North America create a rare opportunity to study dinosaur assemblages on a regional scale. However, most studies have focused on the well-sampled Hell Creek and Lance formations, while few studies have been conducted on the Scollard, Frenchman, and Denver formations. Fewer still have compared dinosaur assemblages across the entire region, leading to conflicting hypotheses on the distribution and provinciality of Lancian dinosaurs. Earlier studies have argued that the latest Cretaceous dinosaur assemblages were subdivided into distinct assemblages along a latitudinal gradient, whereas recent studies have suggested a more homogeneous assemblage with low provinciality, driven by warm temperatures and a shallower climate gradient.

In this study, we compare Lancian dinosaur assemblages across the above-mentioned strata using data collected from over 20 institutional databases. This extensive dataset provides the best opportunity to address the question of dinosaur provinciality at the end of the Cretaceous Period. The preliminary results of ordination methods such as Non-dimensional Metric Scaling (NMDS) and Correspondence Analysis (CA) suggest some notable trends in dinosaur distributions at the family level. NMDS recovers formations along an axis generally consistent with latitude, suggesting that latitudinally correlated variables may have influenced the distribution of dinosaur assemblages. Leptoceratopsidae are comparatively abundant in the northernmost Scollard Formation, supporting the hypothesis of a northern assemblage typified by *Leptoceratops*. Other herbivore groups like Ankylosauridae, Pachycephalosauridae, and Thescelosauridae, are also relatively abundant in northern regions, whereas Hadrosauridae, represented solely by *Edmontosaurus annectens*, become increasingly abundant in the south. Interestingly, some small theropods (Troodontidae, Dromaeosauridae, *Richardoestesia* sp., and *Paronychodon* sp.) plot along a separate axis in the CA, suggesting that another factor—potentially interspecific competition or some

unrecognized environmental variable—influenced their distributions. We suggest that Lancian dinosaur assemblages showed some regional variation, although not to the extent of endemicity reported earlier in the Cretaceous Period. Therefore, not all Lancian dinosaur assemblages may be comparable, and we emphasize the need for more focused studies on poorly sampled formations (e.g., Scollard, Frenchman, and Denver). Data collection is ongoing and will provide more refined results, shedding more light on factors that influence the distribution and structure of dinosaur communities at the end of the Cretaceous Period.

Multi-isotope dietary reconstruction of Modern and Beringian Gray Wolves

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Understanding how species adapt to environmental change is critical as many of them are threatened by extinction under ongoing climate changes. Beringia, the landmass that connected Yukon and Alaska with eastern Siberia throughout much of the Late Pleistocene (~129–12 ka), experienced significant climatic warming during the terminal Pleistocene (~16–11.7 ka) coincident with a widespread North American megafaunal extinction event. However, species like the grey wolf (*Canis lupus*) survived, possibly due to dietary flexibility. We are revisiting this hypothesis by combining existing and novel palaeodietary proxies.

Stable isotopes in animal tissues reflect the consumers' diet, making them a powerful tool for dietary reconstructions of modern and extinct species. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes are commonly used in palaeodiet studies but are vulnerable to the degradation of organic molecules and to environmental baseline shifts. Calcium isotopes ($\delta^{44/42}Ca$) have been proposed as a complementary and potentially more robust dietary proxy.

We radiocarbon dated and analyzed $\delta^{13}C$, $\delta^{15}N$ and $\delta^{44/42}Ca$ in the remains of modern and Pleistocene wolves (n=15 and n=14, respectively) and their potential modern and Pleistocene preys (n=20 and n=22, respectively). Using Bayesian stable isotope mixing models (BSIMMs), we reconstructed gray wolves' prey preferences and dietary strategies over the past 50,000 years.

As expected, BSIMMs relying on $\delta^{13}C$ and $\delta^{15}N$ data showed that Pleistocene wolves primarily consumed large ungulates, with pre-LGM and LGM wolves having a hypercarnivorous, horse-specialized diet whereas modern wolves had a more generalist diet. When adding the $\delta^{44/42}Ca$ values as a third dimension, BSIMMs showed evidence of an even greater dietary shift with Pleistocene wolves consuming almost exclusively horses, whereas modern wolves showed a more diverse and small prey (i.e., snowshoe hare and Arctic ground squirrel) dominated diet.

Calcium isotopes reinforce the hypothesis that Pleistocene wolves adapted to deglaciation and the extinction of Beringian horses during the terminal Pleistocene by shifting to a more generalist and flexible diet focusing on small prey. Our study provides key information on the palaeoecology of Beringian mammals and underlines the importance of diet in biodiversity conservation, which can help inform effective management strategies for at-risk species in the face of current and future climate change. Besides the palaeoecological insights, our work also demonstrates a key methodological advance with the addition of calcium isotopes as a third, more robust palaeodietary dimension

less influenced by environmental baselines and diagenesis. This offers an intriguing glimpse into the relatively unexplored potential of calcium isotopes to further investigate palaeodiet and presents an exciting development in the integration of traditional (i.e., carbon and nitrogen) and non-traditional (i.e., calcium) isotope geochemistry into the field of palaeobiology.

Revision of a Paleocene catfish from Sanshui Basin, Southern China

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All Paleocene-Eocene catfish from East Asia were previously assigned to the extant family Bagridae (Siluriformes), leading to a long-standing ghost lineage. Two nominal species, *Mystus dalangshanensis* and *Mystus spinipectoralis*, from the Paleocene Buxin Formation in Sanshui Basin, south China represent a 30 Ma gap from the estimated mitogenomic divergence time for *Mystus*. These discrepancies suggest either problematic taxonomic assignment, and/or a 'morphology vs. molecules' conflict exacerbated by an incomplete fossil record. Based on our analyses of new materials from recent fieldwork, we propose a substantial revision of Paleocene Sanshui catfish by removing them from the suborder Siluroidei, and by extension, Bagridae based on key new observations. First, the principal caudal fin rays of Sanshui specimens have 18 (fin formula i,8,8,i), which is a basal character absent in extant catfish (i,7,8,i) except Diplomystidae. The Paleogene †Hypsidoridae and †Astephidae also have 17. Second, the coronoid process of the dentary is elevated and prominent. This condition is seen only in †Hypsidoridae. The moderately developed coronoid process is present in diplomystids and some bagrids, but not in the rest of the siluriforms. Third, interdigitation is absent at the suture of ceratohyal and epihyal, a known synapomorphy of Siluroidei. All these characteristics indicate Sanshui catfish belong to a basal lineage of catfish and suggest early morphological diversification hidden by previous taxonomic assignment. These new findings offer clarification critical to untangling puzzling aspects of the evolutionary history of catfish and highlights the importance of systematic review and revision as evidence of divergence times.

Captorhinid premaxillary dentition reveals the pathological phenomenon of tooth socket closure

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Captorhinid eureptiles are the most commonly found amniotes within the cave deposits of the Richards Spur locality

in Oklahoma, making them ideally suited for examining dental characteristics and identifying abnormalities and pathologies. To gain a better understanding of their feeding behaviours, we undertook a detailed study of 577 premaxillary bones through comparative dental histological analyses of both pathological and healthy elements, in combination with neutron computed tomography. We were able to identify morphological alterations of the dentition, alveoli, and internal dental canals, with two types of pathologies observed that had tooth sockets enclosed by secondary bone either due to: (1) infection, which resulted in the tooth falling out and modification of the internal and external premaxillary bone morphology; (2) breakage of the tooth crown, with partial roots retained under the secondary bone. We suggest that the latter is a reactive behaviour when a younger tooth, recently ankylosed to the jawbone, breaks and the sequential replacement cycle has not begun; thus, it appears to be a reparative response by the alveolar bone to trauma, preventing any other form of illness, such as infections, since the blood vessels of the pulp cavity would have been exposed. While we found that this type of pathology is present in each type of jawbone (premaxilla, dentary, and maxilla), 29% of the premaxillary bones had at least one enclosed tooth socket, with the first tooth position exhibiting the pathology most frequently. This phenomenon of the first tooth having an enclosed socket due to a higher chance of breakage may be related to the unique captorhinid feature of a greatly enlarged, posteriorly bent tooth crown that may have been exposed to the external environment. There is consistent external wear on the labial surface of the first tooth (65% of specimens had a wear facet), which is not associated with a tooth-on-tooth grinding or chewing feeding behaviour. The pattern of scratches on the wear facets supports the hypothesis that these large anterior teeth were not covered by labial scales, as is common in the vast majority of terrestrial vertebrates, but instead extended beyond the ventral lip of the mouth. We propose that a heavy price was paid for the exposure of these teeth and the unique, characteristic features of captorhinids in the form of widespread wear on the labial surface of the premaxillary teeth and exceptionally frequent dental pathology.

An Early Jurassic ichthyosaur skeleton from Fernie, British Columbia

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In the summer of 1916, an articulated, partial ichthyosaur skeleton was discovered along the banks of the Elk River near Fernie, British Columbia. It was promptly collected by the Crowsnest Pass Coal Company and donated to the Geological Survey of Canada in 1917. Although the discovery was featured in the local newspapers, the precise location of the site was never recorded, and the skeleton has since sat largely unexamined in the collections of what is now the Canadian Museum of Nature.

Interest in the find was renewed with the recent rediscovery of the original locality, based on a photo from an old newspaper clipping (Fig. 1). The host strata of the Fernie Formation are poorly exposed along the river, preventing precise stratigraphic correlation. However, it is possible to date the skeleton using associated ammonites, which suggest an early Pliensbachian age. The ichthyosaur skeleton (CMNFV 40398) is missing its diagnostic paddles, but features of the skull and coracoid suggest affinities with *Ichthyosaurus*, despite the somewhat larger size of the

skeleton. Although *Ichthyosaurus* has previously been documented from Canada based on less complete remains, the genus is known primarily from the Lower Jurassic of Europe. Thus, the Fernie skeleton possibly represents an important addition to the meagre North American record of the genus and is, in fact, the most complete ichthyosaur known from the Lower Jurassic of that continent.

Figure 1. Excavation of CMNFV 40398, with skeleton in foreground.

Description and phylogenetic analysis of a centrosaurine ceratopsid from the lower Judith River Formation, Montana

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Newly described centrosaurine ceratopsid species from the lowermost Judith River Formation have revealed an early rapid radiation of the subfamily during the early to middle Campanian. Early centrosaurines are characterized by low, ridge-like nasal ornamentation and long brow horns. The transition between these early diverging taxa

and later eucentrosaurines, namely the large-nasal horned subclade Centrosaurini, remains poorly understood. A new specimen from the upper part of the McClelland Ferry Member of the Judith River Formation of Montana, USA, is a rare example of an associated ceratopsian skeleton from this poorly sampled but key temporal interval. ROM 77588 consists of cranial and postcranial elements, including a well preserved nasal and ischium. The tall, near-spherical based, slightly recurved nasal horn bears resemblance to *Coronosaurus brinkmani* and *Centrosaurus apertus*; the presence of a deep overgrowth of bone associated on both the anterior and lateral margins of the nasal horn base closely resembles *Coronosaurus* and differentiates the specimen from known *Centrosaurus apertus* material. The postcrania show more potentially diagnostic morphology, particularly in the ischium where the distal end of the ischial shaft becomes mediolaterally compressed into a rectangular, paddle-like shape. Such expansion is observed in early, non-eucentrosaurine taxa like *Wendiceratops pinhornensis*, but differs from the distally tapered ischial shafts observed in Centrosaurini, namely *C. apertus*, as well as in Chasmosaurinae. Phylogenetic tests performed using TNT software found ROM 77588 to be nested within Centrosaurini as a sister taxon of *Coronosaurus brinkmani*, a genus previously known only from two bonebeds from the middle Oldman Formation in Alberta. ROM 77588 was discovered in strata that correlate to the Comrey Sandstone of the Oldman Formation, and therefore its age is also consistent with that of *C. brinkmani*. Given its combination of traits and stratigraphic position, ROM 77588 may represent the first record of *C. brinkmani* from Montana and thereby contributes new insights into the early evolution and distribution of centrosaurine ceratopsids and faunal turnover in the clade.

A new stem saurian reptile from the Karoo Basin of South Africa

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Sauria, the crown group of Diapsida, has an extensive and rich evolutionary history that reflects remarkable morphological and taxonomic diversity. Today, saurians are the most speciose group of amniotes and are represented by archosaurs (birds and crocodilians), lepidosaurs (squamates and rhynchocephalians), turtles, as well as numerous extinct taxa (e.g., dinosaurs, pterosaurs, and marine reptiles) that persisted until the end of the Mesozoic Era. The earliest stages of diapsid reptile evolutionary radiation are represented by a limited Paleozoic fossil record. Consequently, the phylogenetic relationships of many stem saurians remain unresolved, and the origin of the prolific clade Sauria—particularly that of lepidosauromorphs—remains poorly understood in contrast to the well-represented and extensively studied synapsid branch of crown Amniota. This considerable hiatus belies the extraordinary morphological diversification of saurians observed shortly after the end-Permian mass extinction. It is within this context that the postcranial anatomy of the widely known *Youngina capensis* is re-evaluated, and a newly named Late Permian, lizard-like stem saurian from the Karoo Basin of South Africa, *Akkedops bremneri*, is described based on two isolated skulls. The famous aggregation of "juvenile *Youngina*" (SAM-PK-K7710) is also shown to be referable to this species, thereby making it one of the best-represented stem saurians. *Akkedops bremneri* is most readily distinguishable from *Youngina capensis* by the following features: a saddle-shaped and posteriorly emarginated quadrate with a tympanic crest and unique medial process; a sliver-like supratemporal with a noticeable lateral flange that sutures to the postorbital, thereby contributing to the upper temporal fenestra; the absence of a lower temporal bar; a greater contribution of the postorbital to the upper temporal fenestra; a distinctly more heavily dentulous palate; a splint-like contribution of the lacrimal to the orbital margin; and an anteroposteriorly shorter rostrum. Our phylogenetic analysis recovered *Akkedops bremneri* as the sister taxon to Sauria and provides further evidence against a monophyletic "Younginiformes," as *Youngina capensis* is excluded from a clade with other "younginiform" reptiles and

is instead recovered as sister to *Akkedops bremneri* + Sauria. This is an intriguing result considering the relatively small size and slender, lizard-like morphology of *Akkedops bremneri*, which is most comparable to lepidosauromorphs even though it is currently recovered outside of Sauria. The available evidence suggests an underrepresented complexity surrounding the earliest diversifications of diapsid reptiles along the saurian stem, and new discoveries are bringing this pivotal episode of diapsid reptile evolution into greater focus.

Trait variation or a new species? A newly discovered chasmosaurine skull from the extreme uppermost Dinosaur Park Formation

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We report the discovery and partial description of a new specimen of chasmosaurine ceratopsid from the upper Lethbridge Coal Zone. The specimen in question, UALVP uncatalogued (identified here by the loan number L2018-07) collected from Quarry 300, is a fragmented but largely complete skull of a mature adult originally discovered in 2018, and subsequently excavated by the McGill University field crew in 2023. The skull was found 14 m above the Lethbridge Coal Zone (LCZ) lower contact at an elevation of 743.26 ± 0.48 m, making it the stratigraphically highest known dinosaur from the formation to date.

During preparation, it was noted that the anatomy of the skull shared many similarities with the chasmosaurine *Chasmosaurus* ('*Vagaceratops*') *irvinensis* known from the upper Dinosaur Park Formation (Holmes et al., 2011). UALVP L2018-07 was found higher in section than the highest known specimen of *C. irvinensis*, TMP 1998.102.8 (a partial posterior parietal bar; Campbell et al., 2019). Like *C. irvinensis*, UALVP L2018-07 possesses small posteriorly positioned parietal fenestrae, a transversely broad, rounded nasal horncore, no orbital horncores (instead replaced by small raised orbital bosses), a bony rugose swelling anterior to the nasal horncore, and triangular-shaped epiparietals that wrap posteriorly around the posterior parietal bar (Campbell et al., 2019).

Notably, UALVP L2018-07 possesses anatomy that falls outside the current specific diagnosis of *C. irvinensis* described by Campbell et al. (2019), including the following traits: (1) The posterior bar is not flat (180°) at the junction with the medial parietal bar, but instead it is Y shaped, with the posterior parietal forming an angle of roughly 125°, falling more into the angle range seen in *Chasmosaurus russelli*; (2) An extremely robust medial parietal bar, which contrasts with the typical 'strap-like' parietal bars of *Chasmosaurus*; (3) at least two distinct, broad anterior undulations on the medial parietal bar, similar to those seen in some other ceratopsians such as *Anchiceratops ornatus* and *Centrosaurus apertus* (Hieronymus et al., 2009; Mallon et al., 2011). The holotype of *C. irvinensis* (CMN 41357) may possess one such undulation on its thin medial parietal bar but it was difficult to discern because of the broken and distorted nature of this bar. Otherwise this trait is absent from all *Chasmosaurus* specimens (Campbell, 2014); (4) a bony protrusion on the medial posterior parietal bar could be interpreted as the epiparietal 'P0', and is similar in size to the P1 epiparietal.

As UALVP L2018-07 is still in preparation, specific taxonomic affinity cannot yet be determined. Further preparation, together with a subsequent specimen-based phylogenetic analysis, will yield greater insight into wheth-

er this specimen represents a morphological trait expansion of *C. irvinensis* (requiring a revision of the specific species definition), or is instead distinct enough to describe it as a new species. As chasmosaurine parietal anatomy can vary significantly within a single species, we refrain from making any concrete attributions at this date. Regardless of affinity, this specimen significantly expands the temporal range of chasmosaurine dinosaurs in the Dinosaur Park Formation up to the contact with the overlying Bearpaw formation. If further research attributes UALVP L2018-07 to *Chasmosaurus irvinensis*, it will significantly expand the temporal range of this dinosaur to encompass the entire indeterminate pachyrhinosaur-*Lambeosaurus magnicristatus* biostratigraphic zone.

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Are Cretaceous ganoid scales diagnostic for different taxa?

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Ganoid scales are commonly recovered in vertebrate microfossil sites. This is because they preserve well, as they are formed from hard materials (bone and enamel) and there are many scales on each individual fish, providing many elements for potential preservation. Ganoid scales recovered from Cretaceous and Cenozoic deposits are frequently identified as belonging to extant genera of fish that are currently found in the geographical region. These include the Lepisosteiformes (gars) *Lepisosteus* and *Actractosteus* in North America, and the Polypteriformes (bicher) *Polypterus* (the ropefish, *Erpetoichthys* has not been reported) in Africa. However, in some localities, non-scale remains of both Lepisosteiformes and Polypteriformes are known from the same deposits (e.g., the Maastrichtian of Madagascar). Few fossil scales have undergone rigorous examination to determine their taxonomic identity. While histological and microstructural differences among ganoid scales from some taxa have been documented, ganoid scales from other taxa have not been comprehensively assessed. Without a comprehensive understanding of the differences among taxa, it is difficult to determine the correct identity of individual specimens. Here, we document variation in histology and microstructure of ganoid scales of extant taxa, and then assess the utility of this variation in determining the identity of fossil ganoid scales from Cretaceous and Cenozoic deposits. This is a first step in determining to what taxonomic level fossil ganoid scales can be identified.

Narwhal migration and foraging behaviours in Baffin Bay: a multi-elemental approach using stable isotopes and trace metals

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Arctic marine ecosystems are changing rapidly due to anthropogenically-driven climate change and increased human presence in the Arctic. Faced with rapid degradation of marine habitats, many marine mammal species have modified their mobility and diet in response to the ongoing environmental changes. The narwhal (*Monodon monoceros*), with its restricted range, selective diet, and strong dependence on sea ice, may be particularly vulnerable to these environmental shifts and could experience behavioral shifts. Therefore, there is a need to improve our understanding of narwhal ecology in order to detect any potential alterations in their behavior in response to ongoing climate change. In this study, we investigate the use of several isotopic and elemental proxies to reconstruct narwhal diet and mobility over time, offering novel insights into whether narwhal migratory and foraging strategies have shifted in response to environmental change.

Narwhal tusks are continuously growing teeth, preserving geochemical signatures that potentially offer a chronological record of individual movement and foraging behaviors over multiple decades. Several isotopes vary spatiotemporally in seawater and are incorporated into marine mammal tissues. Oxygen isotopes ($\delta^{18}O$) reflect seawater temperature and proximity to sea ice, while carbon isotopes ($\delta^{13}C$) vary with net primary productivity, differentiating coastal from offshore habitats. Other geochemical markers are more directly linked to foraging ecology, such as nitrogen isotopes ($\delta^{15}N$), and to a lesser extent carbon isotopes ($\delta^{13}C$). These isotopes fractionate with trophic level and can reflect shifts in dietary sources. Other non-traditional isotopic and elemental markers (^{143}Nd, $\delta^{138}Ba$, ^{206}Pb, and Hg concentrations) are thought to reflect water mass origin, salinity gradients, pollution exposure, and trophic structure. Together, these proxies could offer a comprehensive approach to reconstruct narwhal mobility and habitat use over time.

In this study, we test the potential of these different tracers for geolocation and foraging reconstruction by analyzing isotopes in two modern narwhal tusks from individuals of known sex, origin, migratory patterns, and of estimated age through growth layer group (GLG) counts. We collected 24 annual samples and 10 seasonal samples from each individual to generate multi-isotope profiles. We then compared the isotope profiles of each individual to existing isotope baselines within the foraging range to assess the geolocation and foraging information reflected in each of these tracers.

Our preliminary results show that $\delta^{18}O$, $\delta^{13}C$, and $\delta^{15}N$ differ between the two narwhal individuals. This likely reflects the distinct isotopic environmental baseline and foraging strategy of each individual belonging to different populations. Indeed, the $\delta^{18}O$ values of the Baffin Bay population are lower, reflecting their year-round location

at higher latitudes and their longer residence in Baffin Bay open waters. The Hudson Bay population remains in southern coastal highly productive waters year-round, reflected in their higher $\delta^{13}C$ and $\delta^{18}O$ values. Elevated $\delta^{15}N$ values for the northern individual prior to 2003 indicate a diet dominated by higher-trophic level fish, consistent with the Baffin Bay population's winter reliance on Greenland halibut. Interestingly, its isotopic profile shifts after 2003 simultaneously with rapid and permanent losses of sea ice in the Canadian Archipelago and starts to resemble that of the southern population's diet with lower $\delta^{15}N$ values. This shift suggests that in response to climate change, the narwhals of the Baffin Bay population might be changing their foraging behavior, increasingly relying on bottom-dwelling prey as they spend more time in the ice-free coastal waters of the Canadian Archipelago.

These promising results suggest that multi-isotope profiling of modern and historical narwhals might provide key background data about the ecology of narwhal populations and their responses to loss of sea ice cover, progressive ocean warming, and other anthropogenic impacts.

Watch your step: caution in bridging the trackway—trackmaker divide in Carboniferous tetrapods

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The field of ichnology has been a branch of paleontology since the mid 19th century. Vertebrate tracks are a vast dataset compared to vertebrate body fossils: an individual organism will leave only one body, but will leave many tracks and only one body to potentially be preserved. Tracks are direct records of organismal behavior and can be used as proxies for biodiversity and paleoecology. The use of anatomy-consistent morphology in ichnotaxonomy incorporates trackmaker identity by correlating the morphology of the track with that of available trackmaker(s). Standard practice is to interpret ichnotaxa to a family level for trackmakers, but the Linnaean rank and cladistic status of trackmaker taxa actually varies greatly.

Our work aims to harmonize the ichnological and body fossil records of early Carboniferous tetrapods to better ground trackmaker inferences. For example, the Pennsylvanian-Permian ichnogenus *Limnopus* is referred to eryopid temnospondyls. However, large ichnospecies (e.g., *L. littoralis, L. waynesburgensis*) are 200% larger than small ichnospecies (e.g., *L. vagus*). It has been suggested that the different ichnospecies of *Limnopus* represent distinct ontogenetic stages of the trackmaker, including the similar but smaller ichnogenus *Batrachichnus*. Of the few Carboniferous temnospondyls for which the manus and pes are both known in detail, the morphology of the large *Limnopus* morph is consistent with that of *Eryops*, but edopid trackmakers cannot be discounted. This has minimal implications for reconstructing ecosystems, given the similarities between eryopids and edopids. However, this uncertainty in the identity of the trackmaker makes the use of *Limnopus* as a biostratigraphic appearance datum for Eryopidae problematic. The recent consolidation of *Limnopus* species into the type (*L. heterodactylopus*) ensures greater ichnotaxonomic consistency, but weakens the track-trackmaker link.

Interpretation of Carboniferous pentadactyl tracks must account for the presence of pentadactyly among multiple stem tetrapod families by the late Mississippian. Trackways and skeletal remains — specifically autopodia — are scant in the earlier Mississippian, but both hint at a reduction of pedal digit number to five by this time. The

timing of manual digit reduction remains uncertain, but coexistence of a probably hexadactyl manus (*Pederpes*, Whatcheeriidae) with pendatactyl and tetradactyl manual prints highlights the earliest Carboniferous as a time of diversity and dynamism in early tetrapod morphology.

The rich fossil marine reptile record from the Bearpaw Formation deposits of Southern Alberta, Canada: data on taphonomy, stratigraphy, palaeoecology

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The Bearpaw Formation deposits of Southern Alberta, Canada, near the Lethbridge area, have yielded numerous fossil marine reptiles over the past couple of decades, offering a unique window into the Late Cretaceous marine ecosystems of North America. These deposits are targeted by industrial mining for the abundance of the rare gemstone ammolite, which is produced by a unique fossilization process affecting ammonite shells. Collaborative efforts with local mining companies have significantly increased the number of discoveries, predominantly of mosasaur and plesiosaur specimens, which continue to grow the collections of the Royal Tyrrell Museum in Drumheller, Alberta. This study focuses primarily on the taphonomic processes and stratigraphic context of these fossil-rich deposits, providing new insights into the palaeoecological dynamics of the Bearpaw Sea.

The first goal is to present new data about the local stratigraphy of the Lethbridge deposits, detailing the specific layers within the dark-grey shales of the Bearpaw Formation where most of the new marine reptiles are being found. The stratigraphic framework of the Bearpaw Formation relies on the division into various ammonitic zones, each defined by the abundance of one or two species of ammonites. The marine reptile-rich layers of the Lethbridge area are dominated by the presence of oxyconic (i.e., flattened or compressed) *Placenticeras*, which is indicative of the upper parts of the formation, corresponding to a late Campanian to early Maastrichtian age. This, together with the characteristics of the sediment, which consists of smooth, fine-grained, dark-coloured, laminated mudstone, suggests deposition in intermediate to distal offshore marine environments.

Our second goal is to document the variety of non-diagenetic indicators preserved on the fossilized remains. This includes: 1) traces of scavenging, such as bite marks from various toothed vertebrates, like sharks, bony fish, and other marine reptiles; 2) the presence of isolated shark teeth, bony fish teeth, and mosasaur teeth around marine reptile carcasses or embedded within their bones; 3) a variety of traces produced by invertebrate organisms, from commonly known bioturbation around the marine reptile specimens to possible feeding traces on skeletal elements. Evidence of mechanical separation of skeletal parts in our specimens is also fairly common, with bone breakages and element losses that likely occurred shortly after death or perimortem. Additionally, the frequency of bone surface alterations resulting from peeling or exfoliation of the cortical bony layer suggests, for some specimens, prolonged exposure to environmental elements with a combination of physical, chemical, and biological weathering. In this respect, we can draw parallels between modern whale-fall communities and Late Cretaceous carcass falls. The large carcasses of mosasaurs and plesiosaurs may well have supported rich communities at the bottom of the Bearpaw Sea, similar to those observed in contemporary deep-ocean environments.

Beyond taphonomic indicators, we also identified various pathologies on several mosasaur specimens, including bite marks with evidence of healing, dental infections, and other types of bone traumas and disorders. This gives us

some insights into the life histories and ecological interactions of these ancient marine reptiles before their death.

Interestingly, the fossil marine reptiles from the Lethbridge deposits of the Bearpaw Formation seem to be predominantly of medium to large size, with little to no evidence of smaller or younger individuals so far. Whether this size distribution has specific ecological implications or is just the reflection of preservation biases within the formation will need further investigation.

In conclusion, the Bearpaw Formation's fossil deposits of Southern Alberta represent a rich source of information on Late Cretaceous marine environments. Our study provides invaluable insights into the dynamic interactions between marine reptiles and their ecosystem, and the processes that shaped the preservation of these remarkable specimens. Continued exploration and research in the area will nonetheless deepen our understanding of ancient marine biodiversity and, more specifically, marine reptile evolution.

Palaeoecological food webs through the Ordovician-Silurian extinction event of Anticosti Island, Quebec

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Québec's Anticosti Island preserves fossil assemblages representing the Late Ordovician biodiversification event, followed by the first global mass extinction, the Ordovician–Silurian extinction (~453-433 Ma). It was triggered by oceanic changes in temperature, oxygen, currents, and nutrients. We constructed paleo-ecological food web models of the late Ordovician and early Silurian fossils from Anticosti Island to assess how communities responded to these perturbations. Our Anticosti fossil fauna database now includes 661 species including algae, Chitinozoa, Acritarcha, Porifera, Cnidaria, Bryozoa, Ostracoda, Bivalvia, Monoplacophora, Gastropoda, Cephalopoda, Brachiopoda, Annelida, Trilobita, Crinoidea, basal echinoderms, Pterobranchia, Conodonta, ichnofossils, and incertae sedis species. These were grouped into feeding guilds including the predominant suspension feeders and carnivores. Less common guilds included detritivores, herbivores, and grazers. There were 218 species present during the Ordovician, and 243 for the Silurian. The lower trophic levels exhibited resilience, persistence, and ultimately facilitated the restoration of ecological balance following the extinction event. Understanding the ecological ramifications of rapid species loss in ancient ecosystems offers valuable insights into contemporary ecological dynamics.

Who was the ruler of Maastrichtian Mongolia? Taxonomic revision of *Tarbosaurus* provides insight into tyrannosaurid diversity of central Asia

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Tarbosaurus Maleev, 1955b is one of the largest tyrannosaurids known, commonly occurring in the Maastrichtian of Mongolia. The genus and species within have had a complex history dating back to when the original species, now known as *Tarbosaurus bataar*, was named. Four different species in three different genera have previously been named, although today only one is considered valid. Considered by many as the sister taxon to *Tyrannosaurus rex*, the species is known from several adult individuals with relatively complete skulls. One individual, ZPAL MgD I/4, has been described in great detail, and shows significant differences in cranial structure from the larger North American taxon. The Nemegt Formation and its large sample size therefore provide ample opportunity to study the variation in dimensions and discrete characters. A new species of tyrannosaurid is being proposed based on several complete crania, and has several consistent morphological differences, including an autapomorphy separating the taxon from *Tarbosaurus bataar*. Morphometric analysis of the diagnostic maxilla reveals a clear separation in morphology between the two *Tarbosaurus* species. Namely, in the new species, the most posterior point of the dorsal subcutaneous surface is far anterior to the lacrimal contact, and the maxilla is relatively deeper in the largest specimens. While the stratigraphy of the Nemegt Formation is contentious, the new taxon is found almost exclusively in the western Nemegt localities, whereas *Tarbosaurus bataar* is found almost exclusively in the eastern localities. The Nemegt Formation is already known for its diversity of small theropods at different localities within a relatively small area. This suggests temporal or palaeoenvironmental differences that we presently do not understand.

The relationships of the specimens were analyzed using an in-group tyrannosaurid character matrix based on discrete characters, rather than allometric characters. Ontogenetically invariant, discrete characters do not force potentially unrelated large taxa to clade together because of size. The resulting tree topologies suggest a more complex evolutionary history of Tyrannosauridae than previous analyses, including the existence of a potential monophyletic central Asian clade. The discovery of another giant tyrannosaurid underlines the value of constructing discrete characters for alpha taxonomic work and increases our knowledge of the evolution and distribution of Tyrannosauridae.

Unraveling linear evolution

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The rates and modes of evolution have been central focuses of paleontological and neontological analyses for nearly two centuries. Studies of fossil sequences have frequently argued that nonbranching linear evolution between species ('anagenesis'/'phyletic evolution'/'phyletic gradualism') exists in addition to branching evolution ('cladogenesis'/'speciation'). We critically examine the philosophy and methodology supporting linear evolution. Linear evolution originated from general observations of fossil sequences, later supported by morphometric and phylogenetic analyses calibrated to stratigraphy (stratophenetics and stratophylogenetics, respectively), becoming a popular model despite conflated terminology. In recent years, new data has largely rolled back the number of proposed linear evolutionary occurrences, but the philosophy at its root has remained a core concept of evolutionary theory. We test the base methodologies supporting linear evolution using a mixture of new and previously published fossil and modern data. Stratophenetic analyses of foraminiferans from the Miocene-Pleistocene South Pacific yield different linear evolutionary patterns depending on the chosen morphometric, yet all fail to capture at least three instances of branching evolution, and lambeosaurines from the Campanian Dinosaur Park Formation show a false linear stratophenetic pattern of cranial crest evolution in the absence of taxonomic data. Lambeosaurine stratophylogenetics recovers an inverse relationship between apparent instances of linear evolution and increased specimen inclusion. The bell curve model of population variation can indicate a single, split, or directionally-evolving population depending on which character is examined, as demonstrated by a sample of modern canids. These methods rely on the assumptions that morphological change in preserved characters accurately maps genealogical lineage structure, that first and last appearance data are accurate, and that species origins were congruent with preserved fossil-bearing rocks: we argue that none of these assumptions are scientific. We ultimately regard linear evolution to be a concept derived from sampling biases: the fossil record preserves a small fraction of the true data, and so phylogenetic estimations derived thereupon will inevitably reconstruct oversimplified relationships. These estimations have been historically interpreted as evolutionary processes, but are in fact generalized patterns from which an underlying process cannot be determined. We further note that combining extrinsic (environmental) and intrinsic (genetic) heterogeneities cannot produce the evolutionary homogeneity required to produce linear evolution. The inevitable branching structure of lineages through time can produce 'linear evolution' only if dissenting branches (of unspecified scale) are arbitrarily ignored, at which point 'linear evolution' becomes a simplification. The dichotomy of linear versus branching evolution is therefore false: evolution is self-similar in its ubiquitous divergent structure.

Chasing coal: a novel investigation of biostratigraphy in Dinosaur Provincial Park

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Stratigraphy in Dinosaur Provincial Park (DPP) has been a complicated and burdensome hurdle for field palaeontologists to tackle throughout the locality's research history. Determining the stratigraphic positions of fossil sites within the Belly River Group (BRG) is often quite challenging, primarily due to the lack of visible datum points and the inconsistent deposition of sediments making up the rock formations in the Park. The current method utilizes the contact between the Oldman Formation (OF) and the Dinosaur Park Formation (DPF), which often has a highly variable absolute elevation and can be difficult to identify along several outcrops. Here we propose to estimate the height of individual DPP fossils and quarries relative to the contact between the Lethbridge Coal Zone (LCZ) and underlying DPF horizons. We show that the LCZ contact constitutes a datum with a much more consistent absolute elevation than the OF-DPF contact throughout the Park. Furthermore, we develop a geospatial method that enables an interpolation of the height of the LCZ directly above/below the GPS coordinates of individual fossil quarries, thereby increasing the accuracy of fossils' stratigraphic position.

Analyzing aerial images and digital surface models from a prior airplane survey conducted in 2015, we recorded the contact between the LCZ and lower DPF horizons across the entire park for the first time. Using the newly generated DPF-LCZ contact points and OF-DPF contact data from a prior ground-based differential GPS survey, we produced interpolated surfaces in ArcGIS Pro using its trend analysis tool and geostatistical wizard. Both methods allowed us to generate results aligned with the expected geology and were easy to work with during analysis while minimizing error.

This study results in four novel interpolated digital elevation models of the OF-DPF and of the DPF-LCZ contact which extend throughout the park. For the first time, these contacts will be known at a reasonably high degree of accuracy for every GPS-marked location in the Park. To explore these methods' possible ecological and evolutionary implications for the DPP biota, stratigraphic distributions of all major dinosaur, mammal, turtle, and fish families were calculated using the new LCZ contact and maps and compared to the prevailing OF-DPF contact method.

Modeling the paleoecological trophic network of the Lower Ordovician Fezouata Shale (Morocco) fossil fauna

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The Fezouata Shale, a fossil Lagerstätte from the Lower Ordovician of Morocco, has a fauna composed of species typical of both the Cambrian Explosion and the Great Ordovician Biodiversification Event. This community is

directly comparable to that of the Cambrian Burgess Shale in that it was a shallow open-water marine community. An interesting comparison can also be made with the community of the Chengjiang Shale, which was located in a deltaic environment. Here, we reanalyzed species lists for the early Chengjiang fauna and later Burgess Shale assemblages. We then compiled a comprehensive species list for the Fezouata Shale and developed an empirical trophic network, including 15 of its comparable properties. These were compared to a model of the trophic structure of the three fossil faunas generated with the niche model, known for accurately representing modern trophic networks. An uncertainty analysis was also conducted to evaluate the presence of potential bias in the fossil data. The Fezouata trophic network was more speciose and larger (420 taxa and 18751 interactions; 178 trophic species and 4228 interactions) than that of Burgess (142 taxa and 771 interactions; 48 trophic species and 249 interactions) and Chengjiang Shales (85 taxa and 559 interactions; 33 trophic species and 99 interactions). The Fezouata network had a lower mean trophic level than that of Chengjiang due to a higher proportion of basal species following the Ordovician Plankton Revolution. The Fezouata network was similar to the Burgess Shale network as no property meaningfully differed between them. Thirteen properties of all three fossil networks showed little meaningful difference, except for a gradual increase or decrease from the oldest to youngest trophic networks. This is significant because it supports the hypothesis that there was a gradual slow-burn change in trophic complexity from the Cambrian Explosion through to the Late Ordovician, suggesting the Cambrian Explosion and the Great Ordovician Biodiversification Event were part of one single long-lasting diversification event.

Tournaisian trackways from the Albert Formation: Implications for the locomotion of Early Carboniferous tetrapods

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'Romer's Gap' is a geological time interval in the early Mississippian Period (Tournaisian stage; 350 Ma), and has a sparse terrestrial fossil record. 'Romer's Gap' is thought to be the interval when tetrapods transitioned from aquatic to terrestrial environments. Terrestrial fossils from this interval are known from only three localities worldwide, including the Albert Formation (a lacustrine paleoenvironment) in New Brunswick, Canada. The Albert Formation has recently yielded the earliest known tetrapod trackways in 'Romer's Gap', over 70 tetrapod trackways on a single surface.

Fossil footprints provide an alternative source of information to body fossils, allowing for the study of the behaviour and methods of locomotion of extinct animals. We will compare the morphologies and kinematics of early tetrapods to those of proposed extant tetrapods to determine the validity of these animals as analogs for Tournaisian-aged tetrapods. Extant tetrapod trackways will be registered in a saturated mud substrate to be analyzed according to standard ichnological methods of measurement and using photogrammetry 3D modelling. The results will be compared to the same measurements taken for select fossil trackways from the Albert Formation to ascertain the

diversity of locomotion methods and morphologies present at the onset of the Carboniferous Period. Preliminary results suggest that the early tetrapods of the Albert Formation were competent terrestrial locomotors of varying morphologies. By working at the intersection of biomechanics and paleontology, we will be able to gain a more robust understanding of Tournaisian-aged tetrapod locomotion and diversity during 'Romer's Gap'.

Floral diversity and environment of mixed coastal forests in the early Maastrichtian Horseshoe Canyon Formation

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The Horseshoe Canyon Formation (HCFm) of Alberta is home to one of the best sampled Late Cretaceous ecosystems in North America. It is famous for its many dinosaur skeletons collected from extensive badlands along the Red Deer River Valley over the last 150 years. The HCFm also produces exceptional plant fossils in preservation styles that range from leaf compressions retaining organic cuticle to silicified fossils that are perfect three-dimensional copies of once living tissues. Despite these incredible palaeobotanical resources, the flora of the HCFm has been largely understudied. This study provides a holistic view of Alberta's early Maastrichtian forests using compression fossils of leaves and reproductive structures from the Morrin Bridge Paleofloral Site (HCFm) with comparative material from the contemporaneous St. Mary Spillway (St. Mary River Formation). Together, these formations reveal a mixed coastal rainforest with a canopy composed of redwoods, ginkgoales and woody dicots. An understory of ferns, horsetails, and the bennettitalean *Nilssonia* with a diverse array of aquatic and semiaquatic plants in nearby wetlands. There are very few well-preserved early Maastrichtian floras in the world, as such, many of the fossil plants from these formations represent unique species or genera not previously recorded in the Late Cretaceous. A comprehensive understanding of the floral diversity contextualises the environment once inhabited by dinosaurs in Alberta's ancient past.

A description of dental histology and implantation geometry in Chamaeleonidae

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Chamaeleonidae is a clade of squamates distributed today across Africa and Madagascar. Chamaeleonids exhibit an acrodont dentition wherein the tooth is interpreted as attaching to the apex of the jaw and suturing directly

to the lamellar bone of the jaw. Mediolateral contact between the tooth and the supporting jawbone is absent in conventional descriptions, which distinguishes acrodont dentitions from the pleurodont and thecodont tooth implantations seen in other reptiles. Along with Agamidae, chamaeleonids form a monophyletic acrodontan clade of iguanians that all share acrodont implantation. While squamates present a diverse array of tooth implantation forms, chamaeleonids uniquely display the development and retention of solely acrodont implantation throughout ontogeny. According to historical terminology and understanding of dental tissue homology, chamaeleonids must lack the periodontal tissues otherwise described in mammals, crocodilians, pleurodont iguanids, and agamids, among other amniotes. However, a body of recent literature has re-interpreted the homology of tooth attachment tissues across thecodont, pleurodont, and acrodont amniotes. Therefore, current research underlines the primacy of describing the implantation geometry of extant clades, so that the same definitions may be communicated to fossil specimens.

Here we describe chamaeleonid tooth implantation and attachment tissues using serial histology and micro-computed tomography. In this study, we identify a previously unrecognized mediolateral contact between the teeth and supporting jaw bone, and found evidence of a calcified periodontal ligament through the presence of abundant Sharpey's fibres between the teeth and the supporting bone. With the observations produced in this paper, we define acrodont geometry as the implantation of the tooth to the apex of the parallel and equivalent walls of the supporting lamellar bone. Our description of extant chamaeleonid tooth histology has implications for the study of fossil acrodontan lizards, such as the Changjiangosauridae of the Mongolian Eocene. Changjiangosaurid dentition displays a similar apical implantation to chamaeleons, and in the absence of described attachment tissues, they are diagnosed as acrodont solely based on geometry of implantation. Evidence for tooth replacement in the Chiangjiangosauridae is conflicting. Neither wear nor resorption pits associated with their apical teeth have been described in the literature. Regardless of the reality of tooth replacement in changjiangosaurids, the family shares affinities with the acrodontans, and particularly the Chamaeleonidae, based on both dental and jaw characteristics. This interpretation would have implications for the origins of Chamaeleonidae from Asia prior to the establishment of their current distribution in Africa.

Altogether, this work contributes to the present trend in research towards describing a mammal-like tripartite periodontium in squamates, rather than a single 'bone of attachment'. This trend can subsequently characterize our observations of tooth attachment in extant and fossil taxa alike.

More mini bosses: new surveys of juvenile *Pachyrhinosaurus lakustai* material from the Campanian Wapiti Formation provides insight into boss development

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Ceratopsians are well known for elaborate cranial ornamentation, including nasal and orbital horns, parietal frills, and frill ornamentation, especially during the Late Cretaceous period. The ontogenetic development of

these features is unknown in most species, as most ceratopsian species are solely known from adult specimens. The scarcity of juvenile material means that the understanding of ceratopsian ontogenetic development relies heavily on species for which juveniles are well represented, such as the chasmosaurine *Triceratops* and the centrosaurine *Centrosaurus*. The Pachyrhinosaurini sub-clade of centrosaurines displays cranial orientation unique to ceratopsians in the form of large, bony nasal, orbital and/or naso-orbital bosses. These bosses form broad, rugose lumps over the nose and eyes in adult animals. Among Pachyrhinosaurini, only *Pachyrhinosaurus lakustai* and *P. perotorum* are represented by juvenile specimens that can hint at the ontogenic development of these unique features. Previous work by Currie et al. (2008), Kruk (2015), and Fiorillo and Tykoski (2013), suggests that bladed 'demi-horns' form instead of true horns that fuse, accrete lateral bone, and possibly partially resorb in patterns that create the nasal boss of *Pachyrhinosaurus*. In *P. lakustai*, similar 'demi-horns' form over the orbits into a postorbital boss in adulthood. However, the scarcity of juvenile specimens in the smallest/youngest age classes has made this hypothesis difficult to prove.

The Pipestone Creek Bonebed in northwest Alberta represents hundreds or possibly thousands of *P. lakustai* specimens at several ontological stages (Currie et al., 2008). Bamforth et al. (2024) presented a preliminary study into how new discoveries from this bonebed increased the current understanding of *P. lakustai* boss development. Herein, we describe what expanded surveys of juvenile *P. lakustai* material from the Philip J. Currie Dinosaur Museum and the Royal Tyrrell Museum of Palaeontology tell us about intriguing patterns in the size and orientation of postorbital demi-horns as they develop into bosses. Preliminary measurements of these features have already led to interesting conclusions about the development of these unique cranial elements. Of the 29 isolated postorbital demi-horns measured, 18 were from the left-hand side and 11 were from the right. The size of these demi horns ranged from 4.5 to 18.2 cm long and from 3.1 to 11.9 cm deep, but most were between 6-10 cm long and 4-6.5 cm deep. Of the postorbitals measured, 15 out of 29 had a demi-horn that was more vertically oriented when observed from the proximal end of the blade relative to the angle of the orbit. There were eight horizontal horns and six with boss-like textures that were flatter. The postorbitals with a boss-like texture were either from adults with a fully formed orbital boss or from subadults with a boss that exhibited the loss of a defined blade, and were mostly horizontal with pitting in the middle directly dorsal of the orbit with rugosity along the edges. Interestingly, the angle of the blade was not correlated to the size of the individual, though a boss-like texture was only found on the largest specimens. These preliminary results suggest a late and possibly rapid ontogenetic shift from the demi-horns on the postorbital of *P. lakustai* to the adult form orbital boss. This may suggest an ornamentation and display function that is only present in adult animals for these orbital bosses. Better understanding of the ontogenetic pathway of *Pachyrhinosaurus* cranial ornamentation will help us understand the differences between ontogenetic and taxonomic variation in ceratopsians.

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A preliminary study on development of the paratympanic pneumatic system in embryonic *Alligator*

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Extant crocodylian middle ears are elaborated with air-filled spaces lined with epithelium, known as the paratympanic sinus system. This elaborated complex system is also present in birds, suggesting the possibility of shared characteristics of some morphologies throughout Archosauria. However, due to the soft tissue nature of this pneumatic system, developmental studies in both taxa are needed to better understand the shared characteristics between crocodylians and birds. Our previous work focused on establishing a developmental pattern of the paratympanic sinus system associated with its surrounding soft tissue structures in an embryonic series of quail using 3D reconstruction datasets. In contrast, 3D ontogenetic studies of the paratympanic sinus system in *Alligator* have been limited to post-hatching series with little information on the surrounding soft tissue structures. Early studies of crocodylian embryos using histological sections limited the accurate 3D morphologies of the complex paratympanic sinus system. Here, we present our preliminary examination of the embryonic alligator data using 3D reconstructions based on high-resolution CT scan data. I2KI-stained *Alligator mississippiensis* scan data were acquired using a Zeiss Xradia 520 Versa at Multiscale Correlated Imaging Laboratory (MSCIL), McGill University to visualize the soft tissue structures. The 3D reconstruction data show that the complex paratympanic system develops at stage 19 in *Alligator*. A particularly interesting observation at this stage is that a small ventral portion, derived from the primary otic sinus, extends directly towards the Meckel's cartilage without passing through the cartilaginous quadrate, which has not been reported previously as far as we know. In contrast, in the posthatchling alligator, a ventral diverticulum from the tympanic sinus extends within the ossified quadrate first and then extends into the Meckel's cartilage derived articular via the siphoneal tube. This suggests that the ventral diverticulum observed in the stage 19 *Alligator* is either a de novo structure not observed before or presents a primary development of the siphoneal diverticulum that later becomes incorporated into the ossifying quadrate. With the limited *Alligator* embryonic data we examined, we discuss the implication of the presence of the ventral diverticulum in the embryonic *Alligator* by comparing it to the embryonic quail and a range of stem and basal archosaurs.

Faunal and functional diversity in a freshwater vertebrate community from the Tournaisian (earliest Mississippian) of New Brunswick, Canada

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The Albert Formation of southern New Brunswick (NB), Canada, is dated to the Tournaisian (earliest Mississippian; ~ 358.9 Ma–346.7 Ma) and is thought to have been deposited in a continental freshwater lacustrine setting and in associated fluvial-deltaic systems. Unlike most other Tournaisian-aged deposits, the Albert Formation has produced hundreds of articulated fish fossils. The Albert Formation, thus, provides a unique taphonomic window to study a continental, freshwater ecosystem from shortly after the end-Devonian mass extinction event.

Recent collection efforts and museum collection surveys have resulted in an improved understanding of faunal diversity across the Albert Formation. Fluvial-deltaic and shallow-water lacustrine deposits near Bloomfield and Norton, NB, and at Irishtown Quarry yield representatives from most major vertebrate groups, including Actinopterygii, Sarcopterygii, Chondrichthyes, and "Acanthodii". The deeper-water lacustrine faunas at Albert Mines and Apohaqui Government Quarry, on the other hand, are almost entirely comprised of actinopterygians (although a single "acanthodian" fin spine is reported from Albert Mines). These differences may reflect true organismal distributions, taphonomic biases, collection biases, or a combination thereof.

Although genus and species-level taxonomy in the Albert Formation fauna remains largely unresolved, quantitative analyses of functional traits using 2D morphometrics provide evidence that Albert Formation osteichthyans (i.e., Actinopterygii + Sarcopterygii) were morphologically variable, to a degree not unlike that seen in other late Paleozoic aquatic faunas. Thus, study of the Albert Formation fauna provides evidence that vertebrate communities were morphologically and potentially ecologically diverse by the earliest stage of the Mississippian.

Unexpected mosaic anatomy in a new genus and species of Early Carboniferous actinopterygian

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Early actinopterygian evolution and diversity flux remain poorly understood. A direct reading of the fossil record implies a profound shift occurred between Devonian and Carboniferous actinopterygian faunas. Devonian actinopterygians are known from a handful of lineages in a single body plan, but Carboniferous actinopterygians are diverse and morphologically disparate. This transition has been interpreted as an explosive diversification enabled by a mass extinction affecting vertebrates. However, new fossil data from both sides of the Devonian-Carboniferous boundary, phylogenetic results suggesting substantial actinopterygian survivorship, and analysis of actinopterygian fossil record completeness have challenged this interpretation. This suggests that a direct reading of the incomplete actinopterygian fossil record is misleading.

Fossils from the Early Carboniferous (Tournaisian; late Tn2 to early Tn3 palynomorph stages) Horton Bluff Formation of Nova Scotia have helped to fill in the actinopterygian fossil record despite being significantly incomplete. We report an articulated actinopterygian skull, pectoral girdle, and fin, representing a new genus and species, from the Horton Bluff Formation at Blue Beach, Nova Scotia.

This new taxon appears to have an unexpected combination of character states. For example, the pectoral girdle and fin appear plesiomorphic: an interclavicle is present, the notch for the pectoral fin is directed posteroventrally and overlain by a triangular process of the cleithrum, and the pectoral fin endoskeleton is strongly reminiscent of

Moythomasia. By contrast, the hyomandibula bears an opercular process, the lower jaw has a small coronoid process, and there appears to be a second intermediate element in the hyoid arch between the hyomandibula and the ceratohyal. This potential second intermediate element seems to contact the articular, and interpreting its identity could be critical in resolving controversy over actinopterygian hyoid arch evolution. In our phylogenetic analysis, this new taxon is recovered among a grade of otherwise Devonian taxa in an overall topology that implies significant actinopterygian survivorship across the Devonian–Carboniferous boundary.

Thus, our results continue to blur the distinction between Devonian and Carboniferous actinopterygians both in terms of morphology, by revealing an unexpected combination of character states, and phylogeny, by recovering an additional boundary-crossing lineage.

Experimental recreation of tooth marks: what information can tooth mark morphology actually capture?

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Contact between carnivores' teeth and the bones of other animals during feeding and predation can occasionally leave the bones with visible marks which may be preserved in the fossil record. Fossils of tooth-marked bones provide relatively direct information regarding how an extinct animal behaved while it was still alive, like footprints and many other traces, and can also be used to draw inferences about the tooth shape of the carnivore responsible for producing the tooth marks. Such inferences rely, to varying degrees, on a researcher's ability to directly associate a particular behaviour and/or tooth shape with a given tooth mark morphology. Feeding experiments with modern carnivores (e.g., alligators) have yielded many insights into the tooth marks produced by different taxa, but the fact that the animals typically perform multiple kinematically disparate types of biting action while eating makes it nearly impossible to associate particular mark morphologies with particular behaviours by simply examining the tooth-marked bones after the fact. Using a mechanical biting apparatus, we experimentally recreated various tooth mark morphologies on wooden dowels with full-sized ceramic composite and conventional resin tyrannosaurid teeth, scaled to the average adult *Tyrannosaurus* lateral maxillary/dentary tooth. The apparatus is designed so that a single 3D printed tooth is mounted on an articulated arm (≈lower jaw), which can be gradually closed along a hinge (≈articulation between the surangular and quadrate) connecting it to a fixed arm (≈upper jaw) where the wooden dowel is secured; the metal plate where the tooth is mounted can also be slid horizontally (≈anteroposteriorly) to alter the tooth-dowel contact angle. For mechanical convenience, the articulated arm is positioned above, and descends towards, the fixed arm, even though the former represents the lower jaw and the latter the upper. The marks produced on the dowels closely replicate some types observed on modern and fossil bones. By varying the angle of contact with the dowel, we were able to use a single tooth to produce marks exhibiting a range of widths and various internal and external textural combinations described by the recently developed Category-Modifier system of tooth mark classification (e.g., smooth-edged and internally smooth, smooth-edged and internally striated, rough-edged and internally smooth). Our results call into question some previous attempts to use tooth mark characteristics to infer behaviour, tooth morphology, and/

or tracemaker identity. For example, some researchers have interpreted relatively narrow, V-shaped marks as the result of contact with the edge of a small, narrow tooth (e.g., a dromaeosaurid's) and relatively broader, U-shaped marks as the result of contact with the edge of a larger, wider tooth (e.g., a tyrannosaurid's). Marks produced by a single tooth in our experiments not only included V- and U-shaped variants, but spanned an order of magnitude in width. However, not all past inferences surrounding mark formation mechanisms are problematic. Related experiments using plaster teeth and plasticine support previous assertions that raked tooth marks (i.e., tooth marks showing numerous, parallel fine grooves) are the result of denticulated mesial/distal edges being dragged across the bone surface. Our results suggest that individual tooth marks capture information about dental morphology, tracemaker body size, and biting kinematics, in varying combinations and with varying degrees of specificity.

First report of vertebrate body fossils from the West Bay Formation of Nova Scotia

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Shoreline outcrops of the Minas Basin, Nova Scotia provide a critical window into vertebrate evolution during the Carboniferous Period. The late Viséan-Serpukhovian-aged West Bay formation preserves abundant invertebrate fossils, plant material, and tetrapod tracks, but no vertebrate body fossils have ever been reported. Here, we report the first vertebrate material from the West Bay formation, collected from outcrops near Partridge Island in the municipality of Parrsboro. This material comprises the articulated remains of small fish including trunks, median and caudal fins, vertebral columns, and partial shoulder girdles belonging to a single actinopterygian morphotype. These specimens have elongated trunks and their anal and caudal fins are nearly confluent, creating an eel-shape (anguilliform) outline. The overall fin and elongate body shapes are strongly reminiscent of *Phanerosteon ovensii*, which was previously known only from Scotland. This first occurrence of *Phanerosteon* in Canada would provide a further example of the continuity of the Maritimes-West-European province during the Carboniferous. However, the incompleteness of the specimens and the confused nature of Palaeozoic actinopterygian taxonomy warrant caution in this interpretation. As for functional morphology, the nearly confluent anal and caudal fin and elongate bodies observed in these specimens are among the earliest found in the actinopterygian fossil record. Thus, these specimens provide insight into how actinopterygians evolved to explore new body plans and locomotory modes after the Devonian period. Most broadly, the changes in actinopterygian tail shape revealed by these specimens likely record changes in ecology; further study of actinopterygian tail shape evolution should result in deeper understanding of how actinopterygians expanded into new environments and ecosystems on their way to becoming the most diverse vertebrate group.