## CANADIAN SOCIETY OF VERTEBRATE PALAEONTOLOGY

8th annual meeting June 6-8, 2020 Victoria, BC



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

## June 6–7, 2020

## Victoria, B.C.

## Abstracts



## Message from the Host Committee

#### 20 April 2020

2020 has proven to be a strange and disruptive year for the Canadian vertebrate palaeontology community. A novel coronavirus, Covid-19, began circulating in China in December 2019, and had made its way to North America in January 2020, with the first cases reported in Canada on January 25th. Although concern about the impacts of this new virus were mounting throughout February, business seemed to be moving ahead as usual in most of our lives. By mid March, however, the severity of the disease and its rapid escalation into a global pandemic caused a seismic shift in our collective work and personal lives. Travel restrictions were put into place (both internationally and interprovincially), universities and museums were shuttered indefinitely, and many of us began working from home full time (as I write this introduction, I'm sitting on my balcony overlooking James Bay and the waters of the Salish Sea, my office view for the past five weeks).

Most relevant to this abstract volume, the Canadian Society of Vertebrate Palaeontology annual meeting was also called off because of Covid-19. Originally scheduled to be held in June 2020 at the Royal BC Museum in Victoria, BC, the conference was officially cancelled on March 18th. This was only a few days after the March 15th registration and abstract deadline, which had a robust turnout despite the rapidly increasing uncertainty around conference travel because of the pandemic. CSVP has opted to proceed with publication of this abstract volume in recognition of the efforts of our members to create and submit these abstracts, and to provide a record of the state of Canadian palaeontological research during what will no doubt be looked back on as a tumultuous and uncertain time for our field. CSVP members were given an additional extension to submit abstracts to this volume, in order to accommodate those who had been holding off on abstract submissions because of uncertainty about their ability to travel to the conference, and members were also given an option to withdraw abstracts from consideration for the volume given the cancellation of the in-person meeting.

The CSVP 2020 meeting would have been held from June 6–7th, 2020, at the Royal BC Museum in downtown Victoria, located on the traditional territory of the Lekwungen peoples, today represented by the Songhees and Xwsepsum (Esquimalt) Nations. The 2020 meeting logo features an illustration of *Ferrisaurus sustutensis*, a recently described leptoceratopsid from the Sustut Basin of northern BC. Many thanks to artist Francisco Riolobos for permission to use his artwork in our logo! The conference would have kicked off with a welcome reception and icebreaker at the Museum Happy Hour on June 5th, and would have closed with a banquet dinner at the Sticky Wicket Pub on June 7th. A field trip on June 8th would have taken us to the Courtenay & District Museum, a few hours up island, to view fossils from the Cretaceous Nanaimo Group of Vancouver Island and to visit a nearby locality where an elasmosaur skeleton was collected.

I am hopeful that the society will be able to reconvene in person in 2021, either at the Royal BC Museum or at another equally wonderful venue elsewhere in Canada. Until then, I hope that all CSVP members and those who had planned to attend the 2020 meeting are keeping healthy and happy.

Dr. Victoria Arbour, Curator of Palaeontology, Royal BC Museum Chair of the CSVP 2020 local organizing committee

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## A revised description of *Calligenethlon watsoni* based on computed tomography and the resulting implications for the taxonomy of the genus *Calligenethlon*

### Gabrielle R. Adams, and Hillary C. Maddin

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The Joggins Fossil Cliffs locality in Nova Scotia, Canada, is well known for its exceptional preservation of Pennsylvanian ecosystems and early tetrapod communities. One enigmatic but major constituent in these paleoenvironments are embolomeres, which were moderately-sized semi-aquatic to aquatic predators. *Calligenethlon watsoni*, originally described by Steen in 1934, is the only embolomere known from Joggins. This taxon was identified based on a skull table and disarticulated postcranial remains preserved in an upright lycopsid tree stump. Since this first discovery, several specimens have been attributed to this genus. All of these have been similarly disarticulated and found within fossilized lycopsid stumps with the exception of the most recently found, specimen NSM 94GF1.1, an articulated anterior half skeleton found as beach float on the tidal flats. NSM 94GF1.1 was described by Holmes and Carroll in 2010 and remains the best-preserved and most complete specimen known for *Calligenethlon*. Together this material is united under the genus *Calligenethlon* on the basis of its small size and distinctively gracile ilium, the former of which has since been challenged as diagnostic for the taxon. As such, any small but otherwise indeterminate embolomere material has since been tentatively assigned to *Calligenethlon*.

Here we provide an updated analysis of the genus *Calligenethlon* based on a revised external anatomical description of NSM 944GF1.1 and the first-ever description based on micro-computed tomography. This specimen provides for the first time, postcrania unequivocally associated with a skull, and is therefore uniquely able to permit assessment of other specimens currently attributed to *Calligenethlon*. Preliminary results of this analysis reveal that the skull of NSM 944GF1.1 is consistent with that of RM 2.1122, the type specimen, as well as those referred to *Calligenethlon* by Carroll (1967). These all display a similarly narrow skull table with parallel lateral margins, rather than concave ones seen in *Archeria* (Holmes 1989), *Proterogyrinus* (Holmes 1984) and other embolomeres. All the skull tables attributed to *Calligenethlon* also show long, slender tabulars that contact the parietals, as is diagnostic for embolomeres, but that also bear elongate tabular horns that extend posteriorly parallel to each other and to the skull roof lateral margins. Tabular horns of this morphology seem to be unique to this genus. Assessment of the postcrania is in progress but one feature present in NSM 944GF1.1 and other tentatively referred *Calligenethlon* specimens is a strongly developed olecranon process of the ulna. This feature of the ulna distinguishes *Calligenethlon* from other embolomeres like *Proterogyrinus* (Holmes 1984) and is most similar to the ulna described for *Archeria* (Romer 1957). Further examination will hopefully address questions of variation and reveal new features to replace size as the main diagnosis of this important early embolomere genus.

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## New insights on the temnospondyl fauna from Joggins Fossil Cliffs

#### Thomas Arbez, Arjan Mann, and Hillary C. Maddin

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The Joggins Fossil Cliffs, classified as a UNESCO World Heritage site, yields a long history of scientific research with more than 100 publications in over 150 years of research. The significance of this site can be attributed to the record of key fossil groups as well as the diversity of the flora and fauna, with about 150 species described the palaeoenvironments within which they lived (eco-lagerstätte). For vertebrate palaeontology, the importance of Joggins also resides in the fact that the locality contains many early or earliest occurrences of several diverse tetrapod clades, e.g., *Dendrerpeton* for Temnospondyli (only *Balanerpeton* occurs earlier), *Hylonomus* for Amniota, the oldest 'Microsauria' (e.g. *Hylerpeton, Leiocephalikon, Smilerpeton*) and *Asaphestera* (a former microsaur) for Synapsida. Thanks to the application of new tools to historical material and to the discovery of new material, new insights into tetrapod species diversity at Joggins are now available.

A CT-scan and redescription of the most complete tetrapod specimen found in Joggins, the temnospondyl amphibian currently referred to *Dendrysekos* (Schoch and Milner 2014) but formerly referred to *Dendrerpeton*, allowed access to the internal anatomy revealing new anatomical structures for this specimen including the stapes, a sclerotic ring and a partial braincase. Ongoing anatomical comparisons suggests that the genus *Dendrysekos* is a synonym of *Dendrerpeton*, where the morphological variations among *Dendrerpeton/Dendrysekos* specimens can be interpreted as intraspecific variations since no distinct characters other than proportional ratios can be found. This interpretation is supported by the results of an updated phylogenetic analysis which fails to resolve discrete relationships between specimens assigned to either *Dendrerpeton* or *Dendrysekos*. The results also show that early temnospondyl relationships are more uncertain than previously thought due to the low number of shared derived characters distinguishing the main early temnospondyl groups (Edopoidea, Dvinosauria, Eryopidae and Dissorophoidea).

However, a tetrapod skull, thought to belong to the same taxon as the articulated skeleton of *Dendrerpeton*, was recently discovered. The CT-scan of this skull shows that at least one other temnospondyl genus cohabitated with *Dendrerpeton* at Joggins. The specimen is clearly distinct from Dendrerpeton based on the shape of the skull and the location of orbits. The preliminary identification based on the 3D model suggests affinities with either Dissorophoidea or Dvinosauria (ongoing manual preparation of the specimen will hopefully resolve this). This would be the second distinct temnospondyl known from Joggins and makes it the oldest representative of either Dissorophoidea or Dvinosauria. Together this works is allowing us to better understand the temnospondyl amphibians diversity in Joggins and address questions of early temnospondyl phylogenetic relationships.

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## New vertebrate fossil localities in Spatsizi Plateau Wilderness Provincial Park, northern British Columbia

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The recently described Maastrichtian-aged leptoceratopsid *Ferrisaurus sustutensis* originated from outcrops along the Sustut River in the southern portion of the Sustut Basin in north-central BC. However, thick vegetation in this region makes the search for additional vertebrate fossil discoveries difficult. In contrast, outcrops of the Sustut Group in the northern part of the Sustut Basin occur in high alpine plateaus with less vegetation, which have much greater rock exposure that is also easier to traverse on foot. Fragmentary dinosaur remains were discovered at two sites within Spatsizi Plateau Wilderness Provincial Park by a Royal BC Museum botanical team in 2013: the western portion of the east-west oriented unnamed ridge north of the Hyland Post hunting camp, and Tomias Mountain. We revisited these sites in August 2019.

A tyrannosaur tooth crown and indeterminate bone fragment were collected from Hyland Post in 2013. We spent four days prospecting in this area and found only one small possible bone fragment. The 2013 field team collected a cross-section of a large ornithischian limb shaft and a thin tubular bone that may be a crocodylo-morph mandible at Tomias Mountain. This site proved to be very fossiliferous in 2019: we collected a small hollow limb shaft from a possible small theropod, an indeterminate small flat bone, and observed several larger bones, including a nearly complete large rib, in boulders that were too large to collect during this reconnaissance work. Unfortunately, unseasonably heavy snow meant we only had one afternoon of prospecting time at this promising locality. A return visit is planned for summer 2020.

The geology of both sites on the Spatsizi Plateau differed significantly from Sustut Group outcrops along the Sustut River. At Hyland Post, we observed thick units of coarse conglomerate, consistent with descriptions of the Laslui Member of the Brothers Peak Formation (BPF). Conglomerates were absent from the fossiliferous site at Tomias Mountain, and bones were found in pebbly sandstone, consistent with descriptions of the overlying Spatsizi Member of the BPF. The Brothers Peak Formation conformably overlies the Tango Creek Formation; palynomorphs at the Ferrisaurus holotype locality within the Tango Creek Formation suggest an age of ~68 Ma. Additional work is needed to determine the age of the dinosaurs of the Spatsizi Plateau.

# Geometric morphometrics as an informative tool in understanding mammalian development evolution

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Heterodonty (i.e., possession of different tooth morphologies) is considered a hallmark of mammalian evolution. Recent literature describes genetic mechanisms thought to pattern heterodonty during early dental development in mammals. However, these studies are unable to address changes in developmental mechanisms at macroevolutionary scales, due to exclusive reliance on extant taxa. Therefore, there is a pressing need for an understanding of dental development that incorporates both extant and extinct taxa. We hypothesize that analysis of cusp-shape disparity at the premolar/molar boundary will elucidate pivotal evolutionary changes in mammalian dental region patterning. We are developing a landmark scheme to capture shape disparity at the premolar/ molar boundary for both extant and extinct artiodactyl and perissodactyl species. We predict that more derived taxa should show higher levels of integration across the premolar-molar boundary. The current landmark scheme includes type II landmarks (protoconid, entoconid, metaconid, hypoconid, and others) and type III landmarks (cusp outlines) for both the fourth premolar and first molar. Geometric morphometric analysis is expected to provide a proxy of integration in developmental programs of premolars and molars. In this way, we can formulate further questions about trajectories of dental development evolution throughout ungulate lineages. This study aims to use dental morphology to elucidate evolutionary patterns to provide another outlook on dental development evolution in mammals. The final landmark scheme will be designed to be applicable to most other mammalian taxa, allowing further investigation into the evolution of variation existent in mammalian heterodonty.

## New and ancestral morphologies in lissamphibians produced by perturbing Hox gene expression domains

### Jade B. Atkins<sup>1</sup>, Robert R. Reisz<sup>2</sup>, and Hillary C. Maddin<sup>1</sup>

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The fossil record reveals a long history of morphological transformations throughout evolutionary time. Less well understood are the mechanisms that drove these morphological transformations. To study these underlying mechanisms, a more integrative approach is required combining developmental and paleontological methods. Such integrative approaches have improved our understanding of certain transformations (e.g., fin-to-limb) and their underlying mechanisms, whereas others, such as the evolution of the skull-neck boundary in tetrapods, remain poorly understood. Recent work synthesizing palaeontological, phylogenetic, and developmental data reveals that the extant amphibian condition is the product of an anterior shift in the location of the skull-neck boundary along the axis relative to their fossil ancestors and other tetrapod lineages. Here, we aim to further understand the mechanistic basis of this transformation through the experimental manipulation of factors regu-

lating the axial patterning in amphibians. The application of exogenous retinoic acid (RA) and an RA inhibitor to salamander (*Ambystoma mexicanum*) and frog (*Xenopus laevis*) embryos result in the translocation of the skullneck boundary anteriorly and posteriorly, respectively. These experiments reveal a similar capacity in both salamanders and frogs to respond to changes in late-stage axial patterning. These experimental phenotypes are consistent with homeotic transformations of the axial skeleton leading to a change in the location of the skull-neck boundary. In salamanders, a posterior translocation of the skull-neck boundary additionally results in a broader and more robust skull and vertebral elements in experimental animals compared to controls. Conversely, an anterior translocation of the skull-neck boundary results in reduced, anteriorly compressed palatal elements compared to controls. Significantly, details of the resulting phenotypes in salamanders, from skeletal, muscular and nervous tissue perspectives, mimic variation observed in their closest fossil relatives. This suggests such homeotic transformations, and their underlying genetic basis, may have played a role in the evolution of the tetrapod skull.

## Unusual ceratopsian frill morphologies from the late Maastrichtian Frenchman Formation (66 Ma) of Saskatchewan, Canada

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Large-bodied ceratopsians from the latest Maastrichtian Frenchman Formation (66 Ma) of Saskatchewan are traditionally classified into two genera, the common Triceratops and the rare Torosaurus. Debate exists as to whether these two groups belong to a single ontogenetic series, represent one taxon with taphonomic/pathologic variances, or truly represent distinct taxonomic groups. The Frenchman Formation represents a northern extension of the upper Hell Creek Formation into Canada, and is also coeval with the lower Scollard Formation of Alberta. Ceratopsian material accounts for approximately 70% of all dinosaur fossils recovered from the Frenchman Formation, with the majority of identifiable specimens being referred to Triceratops prorsus. Although not necessarily reflective of taxonomic diversity, two unusual ceratopsian specimens under Royal Saskatchewan Museum (RSM) curation suggest an underappreciated morphological diversity in ceratopsians from this time period. 1) Specimen EMP 16.1 was collected in the 1920s near Climax, SK and was originally identified as 'cf. Torosaurus'. It is represented by a parietal-squamosal frill and associated post-cranial material. The frill is large, broad and quadrangular in shape, lacking epiossifications. Re-preparation of the frill in 2001 revealed the parietal bar is not preserved. However, the parietal fenestrae are suggested to be symmetrical, and larger and more oblong than what is typical for Torosaurus. The specimen also displays smaller symmetrical, oblong squamosal fenestrae. EMP 16.1 may represent an atypical morph of Torosaurus, an undescribed ontogenic stage of the same, or possibly a new species. 2) Specimen RSM P3218.1, collected from Grasslands National Park, SK in 2017 and 2018, consists of a partial frill, nasal horncore, nasals and partial rostrum. Immediately adjacent to the parietal-squamosal suture, the parietal frill displays a distinct thinning of the bone, ending in defined, crenulated margins less than one centimeter thick. These margins form the edge of two partially preserved oblong fenestrae. In other ceratopsian studies, thinning out of the bone surrounding fenestrae has been suggested to represent ontogenic parietal thinning in older ceratopsian animals. Interestingly however, RSM P3218.1 also appears to display sub-adult characters, such as partially fused nasal bones. The recovery of more of this specimen may help to elucidate these unusual features. The anomalous characters displayed in EMP 16.1 and RSM P3218.1 may be reflective of ontogenic/morphological variations in Triceratops and/or Torosaurus, could represent northern regional variants, or may be new species. Future research will help to establish ceratopsian taxonomic diversity in the Frenchman Formation, as well as the range of phenotypic plasticity that may be expected in ceratopsian skulls from a single taxon.

# Stable isotopes analysis of caribou antlers as ecological indicators

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Rangifer tarandus groenlandicus (Barren-ground Caribou) are of both ecologic and socio-economic importance to the North. However, given pronounced Arctic climate change, many major caribou populations in Canada are in decline, including a significant number of Nunavut's populations. This study aims to determine whether Rangifer tarandus antlers can be used as effective ecological indicators relative to other hard tissues such as bone and teeth using stable isotopes of oxygen, carbon, and nitrogen. Variation in the rate and timing of tissue development should create different stable isotope profiles for each tissue. Antlers are unique in that they grow over a protracted period of time and unlike bone and teeth regrow annually. Antlers should therefore reflect the isotopic composition of food and water taken in during the spring and summer of a single year, providing a high-resolution record of ecological conditions. Bones and teeth form and mineralize over a different time frame, therefore reflecting averages of diet and water intake over months to years. Fifteen males were selected from the Canadian Museum of Nature based on geographic location, sex, maturity, and collection date. Approximately 30 samples were taken for each specimen from the mandible, third molar and every 3 cm along the length of the antler, some of which neared 1 m in length. Samples were then processed using standard procedures for both collagen and carbonate extraction. The carbon and nitrogen stable isotope compositions for collagen along the antlers show a significant pattern of variation, demonstrating the potential of such data as ecological indicators during antler growth period. Similarly, the carbonate results showed patterns of variation for stable carbon, potentially providing another signal of ecological variation during antler growth. This study helps to provide a better understanding of the utility of stable isotope analysis of antler tissues for understanding the ecology of Canadian caribou. Moving forward, antlers, which are commonly preserved in Pleistocene sediments and comprise a large portion of the CMN Pleistocene collections, can be used to address the ecological changes that characterized their survival through the extinction of 88% of North Americas megafauna during the Pleistocene-Holocene transition.

## Fish from the Late Cretaceous Prince Creek Formation, North Slope of Alaska

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The Prince Creek Formation (PCF) of northern Alaska provides exceptional insight into terrestrial high latitude ecosystems of the latest Cretaceous. This formation preserves a rich assemblage of vertebrates, of which, to date, all named species are endemic to this polar fauna. In addition to the dinosaur and mammals, a diverse assemblage of fishes is present, largely represented by isolated elements preserved in vertebrate microfossil localities. Here we present a taxonomic assessment of fish remains in the Prince Creek Formation based on both macro- and microfossil remains, and compare these data to Campanian to Maastrichtian-aged deposits at lower latitudes.

Elasmobranchs are represented by a single dermal denticle. It differs from the dermal denticles from southern localities so relationships are unknown. Chondrosteans are represented by both sturgeon and paddlefish. In addition to macro-remains, such as skull elements and fin spines, denticles of both of these fish are present in microfossil assemblages. The presence of two kinds of paddlefish is indicated by variation in the denticles present in the microfossil assemblage.

The only basal neopterygian present is *Belonostomus*, which is represented by a single fragment of a scale. Lepisosteids and amiids, which have long been considered the hallmark of Late Cretaceous vertebrate microfossil assemblages, are absent. Similarly, the presumed semionotiform referred to by Brinkman et al. as Holostean A, which is abundantly represented by scales in vertebrate microfossil localities of Alberta and has been interpreted as being more northern in its distribution, is absent.

A diverse assemblage of teleosts, most of very small size, is represented by isolated elements from vertebrate microfossil localities. Two teleosts can be identified on the basis of dentaries. These are the esocid *Oldmanesox* and the clupeomorph *Horseshoeichthys*. Dentaries and other tooth-bearing elements indicate that a minimum of seven additional teleosts are present in the assemblage. Two of these can be included in the Esocidae on the basis of similarities in the tooth-implantation. Two are tentatively included in the Salmonidae on the basis of comparison with extant members of the group. At least one acanthomorph is present. A fish represented by relatively large tooth-bearing elements with multiple rows of teeth is tentatively included in the Osteoglossomorpha. Toothbearing, branchial elements indicate the presence of a minimum of one, and possibly three, additional fish of uncertain relationships. Among extant teleosts, these branchial elements are most similar to cyprinids, although they also bear similarities to those of more basal teleosts, and the possibility that they are from one of these, although unlikely, cannot be excluded at this time.

Compared to other Campanian to Maastrichtian-aged assemblages in the Western Interior, overall species richness is lower in the PCF, in part due to the conspicuous absence of groups common at lower latitudes such as *Myledaphus*, lepisosteids, and amiids. The assemblage is also distinctive in the high abundance of salmoniformes, with both esocids and salmonids being present, and the possible cyprinid. This taxonomic composition demonstrates the existence of a distinct polar ichthyofauna in this region in the Late Cretaceous.

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# Variation in braincase morphology and palaeoneurology within Ceratopsia

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High-resolution CT scanning and 3D reconstruction has transformed the study of braincase anatomy and palaeoneurology in dinosaurs and other extinct vertebrates. The palaeoneurology and development of cognitive abilities is of particular interest in Ceratopsia, a group of non-avian dinosaurs for which many behavioural theories have previously been posited. Ceratopsian studies generally focus on the development of cranial ornamentation and braincases are often neglected because of the high level of bone fusion and consequent obscurity of sutures.

We use several taxa from across Ceratopsia to study morphological disparity in ceratopsian palaeoneurological architecture. Through the examination and segmentation of high-resolution CT scans of taxa across the clade, we found that, while general braincase arrangement remained the same, the morphology of individual elements altered significantly as the group evolved. The paroccipital processes are long and thin in basal forms such as Yinlong and Psittacosaurus and become taller and distally flared to accommodate the large frills of ceratopsids. These changes also increase the area of attachment for neck muscles such as *m. obliquus capitis magnus*. Similarly, the basal tubera of the basioccipital grow and develop, which increases the size of neck muscle attachment sites. On the ventral surface of the braincase, the morphology and orientation of the basipterygoid processes change dramatically leading to an overall transformation in appearance of the basisphenoid. The processes project anteroventrally in basal taxa and shift caudally through evolution of the clade so that ceratopsids, such as Medusaceratops and Triceratops, have caudoventrally projecting basipterygoid processes. There are some exceptions to this rule which is possibly a result of geographic separation and allopatric speciation. On the dorsal surface of the braincase, the frontal and parietal undergo drastic changes, in part due to the development and expansion of supracranial sinuses, brow horns and the parietal frill. Additionally, we explore semi-circular canal plasticity and find that there is a decrease in the size of the anterior semicircular canal relative to the posterior semicircular canal mirroring the shift from bipedal to quadrupedal locomotion through the clade.

This project has provided a suitable basis to collect synapomorphic braincase characters to complement previous phylogenetic research. In further work, these characters will be added to a grand ceratopsian phylogeny which will be analysed to determine the congruence of braincase characters.

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## A gigantic recumbirostran from the Carboniferous of Nova Scotia, reveals adaptations to herbivorous feeding

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Currently, it is thought that the establishment of a modern trophic structure with widespread herbivory occurred in the Permian. Herbivorous adaptations in tetrapods that allow for expanded niche exploitation include modifications to craniodental morphology and expansion of the postcranial skeleton (ribs, girdles) to accommodate large guts stocked with microbial endosymbionts to aid in digestion of cellulose. The earliest tetrapod clades to experiment with herbivory (e.g., diadectids, edaphosaurids, and captorhinids), have their origins in the terminal Carboniferous but do not diversify until the Permian. Here we present a new large pantylid recumbirostran 'microsaur' known from a single skull found in a lycopsid tree stump from the Pennsylvannian-aged Sydney Mines Formation on Cape Breton Island, Nova Scotia. Phylogenetic analysis recovers the new taxon as sister-taxon to Pantylus. MicroCT analysis reveals complex craniodental specializations that are interpreted as adaptations related to an herbivorous lifestyle. The morphology of the marginal and palatal teeth is similar to the durophagous dentition of fossil tetrapods including Pantylus, Euryodus, Opisthodontosaurus, but are also similar to that of modern omnivorous squamates (e.g., Tiliqua tiliqua). However, the palatal teeth are further organized into dense dental fields that together with dentition on the coronoids of the lower jaw form occluding dental batteries, similar to those seen in Permian-aged animals interpreted as herbivorous, such as other pantylids, moradisaurines and edaphosaurids. This suggests that the dental apparatus seen in the new taxon functioned similarly in facilitating both grinding and shearing of plant material, consistent with the interpretations made for the other taxa. Our new taxon, however, substantially predates these later occurrences, thus providing the earliest evidence for tetrapod herbivory, and possibly represents the first example of an herbivore for amniotes if recent phylogenetic hypotheses that recumbirostrans are reptiles are accurate. The early occurrence and extent of development of a complex dental apparatus in this unexpected data point indicates a far earlier diversification of diet and niche exploitation by early tetrapods than previously recognized.

## New plesiosaur (Reptilia: Sauropterygia) material from the Haslam Formation of Vancouver Island

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In North America, plesiosaurs are well known from Jurassic- and Cretaceous-aged strata of the Western Interior Basin. Conversely, plesiosaur remains from the Pacific margin are exceedingly rare, and are limited to a small number of Jurassic- and Cretaceous-aged deposits in Alaska, British Columbia, Oregon, California, and Oaxaca, and include elasmosaurids, pliosaurids, and one cryptoclidid. In British Columbia, indeterminate pliosaurid and elasmosaurid specimens have been documented from the upper Albian Haida Formation of Haida Gwaii and the lower Campanian Pender Formation (Nanaimo Group) near Courtenay, Vancouver Island, respectively. Apart from producing British Columbia's official fossil (the Puntledge River elasmosaurid), the Pender Formation has also yielded other aquatic reptiles including the mosasaurine mosasaurid *Kourisodon puntledgensis* and possibly an indeterminate trionychid turtle.

This study reports on new plesiosaur material collected from the Englishman River, near Parksville, Vancouver Island. This specimen preserves a tooth, a rib, gastralia, phalanges, and gastroliths, and was found in an associated state, possibly belonging to a single individual. The tooth is labiolingually compressed as in elasmosaurids, unlike the more rounded condition in polycotylids – the only other plesiosaur family currently known from post-Turonian rocks. Gastroliths are also common among elasmosaurid remains but rarely occur amongst polycotylids. Therefore, this specimen is considered to belong to an indeterminate elasmosaurid.

The marine strata that yielded these elasmosaurid fossils are assigned to the Haslam Formation of the Nanaimo Group. Inoceramid bivalves associated with the elasmosaurid remains are identified as *Sphenoceramus* sp., indicating that the fossil locality is within the uppermost Santonian to lowermost Campanian *Sphenoceramus* spp. zone of the group. Stratigraphically-adjacent exposures of the Haslam Formation contain the ammonites *Pseudoschloenbachia* and *Canadoceras yokoyamai*, suggesting that the interval can be refined further to the lowermost Campanian. This elasmosaurid specimen contributes to the marine reptile assemblage from the Haslam Formation, which presently also includes an indeterminate mosasaurid and the desmatochelyid turtle *Desmatochelys lowi*. This elasmosaurid specimen also extends the fossil record of plesiosaurs on Vancouver Island into the lowermost Campanian and helps to fill in the fossil record of this group on the Pacific margin of North America.

## Investigating the competition hypothesis: did carnivoramorphans drive creodonts to extinction in North America?

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Carnivoramorpha and "Creodonta" are both groups of ancestrally carnivorous mammals, which emerged in the Paleocene. Creodonts, comprising the Oxyaenida and Hyaenodontida, are polyphyletic and went extinct in North America during the Oligocene, and globally in the Miocene, while the monophyletic carnivoramorphans have survived to today. The "Competition Hypothesis" posits that carnivoramorphans drove creodonts to extinction through competition in North America during the Eocene. This study aims to further investigate the cause of the creodont extinction in North America. By assessing dietary niche overlap between carnivoramorphans and creodonts at early and late Eocene localities, we aim to determine how niche overlap changed, and whether or not this supports the Competition Hypothesis. Support has been found previously for the Competition Hypothesis at the genus level when specimens from multiple localities across the contiguous United States were analyzed together. Competition, however, does not occur among genera, and cannot occur among species that did not live together.

In this study, we tested for niche overlap among carnivoramorphan and creodont species from multiple early and late Eocene localities of Wyoming and South Dakota corresponding to the Wasatchian (55.4 - 50.3 Ma) and

Chadronian (38 – 33.9 Ma) North American Land Mammal Ages. Craniodental measurements, which correspond to preferred prey size in modern carnivorans, were taken for as many of the specimens as possible. These were combined with dental indicators of dietary preference (i.e., hypercarnivore, mesocarnivore, insectivore, herbivore), body mass, Prey-Focus Mass (a regression based on the body mass of the carnivore species to determine preferred prey size), and locomotory mode (i.e., digitigade, protodigitigrade, plantigrade) to estimate the dietary niche of each species. Using a Principal Component Analysis and Discriminant Function Analysis, we will compare the dietary niches of species within our focus localities to assess levels of niche overlap.

Preliminary results indicate that most of the species we examined were mesocarnivores, and that niche partitioning may have been facilitated through differences in body mass. Prey-Focus Mass Analyses indicate that during the early Eocene the oxyaenid creodonts may have exhibited niche overlap with contemporary carnivoramorphans; both likely focused on medium-sized herbivores. This indicates potential for competition between the oxyaenids and carnivoramorphans, which could have contributed to the complete extinction of the Oxyaenida by the middle Eocene. Hyaenodontid creodonts and carnivoramorphans focused on a variety of prey types with different body masses (small to medium) in the early Eocene, which could have led to competition between the them. During the late Eocene most hyaenodontids were hypercarnivores specializing on large-bodied herbivores, whereas carnivoramorphans focused on small to medium-sized prey. By the end of the Eocene, global climate had cooled significantly, and the lush vegetation of mid-Eocene North America had given way to more open, temperate ecosystems. This likely contributed to the extinction of the brontotheres and other large herbivorous prey. Carnivoramorphans were less dependant on large herbivores than hyaenodontids and were less affected by these changes. It is possible that carnivoramorphans competed with creodonts in the early Eocene, leading to oxyaenids going extinct and hyaenodontids hyperspecializing. It is unlikely that the carnivoramorphans were competing with creodonts at the end of the Eocene, however, and we propose that hyperspecialization was the ultimate driver of the extinction of creodonts in North America.

## Redescription and phylogenetic position of *Platypterygius sachicarum* (Reptilia: Ichthyosauria) from the Early Cretaceous of Colombia

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Ichthyosaurs were an enigmatic marine reptile lineage with an extensive evolutionary history spanning about 160 million years during the Mesozoic. The last surviving ichthyosaurs were the ophthalmosaurids, a group that was most taxonomically diverse during the Cretaceous, and represents a key clade for understanding diversity dynamics in Cretaceous marine ecosystems. For decades, *Platypterygius*, a Cretaceous ophthalmosaurid ichthyosaur, has caused persistent problems in ichthyosaurian taxonomy and phylogenetic analysis. It has been historically treated as a wastebasket taxon, with a stratigraphic range of 35 million years, and a type species *P. platydactylus* lacking a surviving holotype specimen, which was destroyed during WWII. This makes the type species a confusing and limiting resource of diagnostic characters for the genus (Fischer et al. 2016).

*Platypterygius sachicarum*, from northern Gondwana, is not an exception to this problematic taxonomy. *Platypterygius sachicarum* comes from the Hauterivian-Aptian-aged Paja Formation, one of the most complete lower Cretaceous sedimentary sequences from northern South America. This formation is a marine black shale unit deposited in a shallow sea. The extensive and well-exposed outcrops preserve almost 15 million years of Earth history (Etayo-Serna 1968). The region has already yielded several specimens of ichthyosaurs, fishes, turtles, plesiosaurs, a teleosaurid crocodylomorph, a fragmentary dinosaur, and abundant molluscan faunas (e.g., Schultze and Stöhr 1996; Cadena and Parham 2015; Carballido et al. 2015; Páramo-Fonseca 2015; Cortés et al. 2019). Nearly each new specimen represents a new species, indicating extremely high endemicity levels in this place and time. *Platypterygius sachicarum* has been incorporated into phylogenetic analyses for years resulting in poor phylogenetic resolution (e.g., Moon 2019). Some of the reasons are that *P. sachicarum* was originally defined based on a single skull, lacking a phylogenetic framework, and for more than two decades its characters were never reevaluated (Páramo-Fonseca 1997). Recently, an additional specimen along with the first documented postcranial remains of this species was reported, providing useful data including new characters for diagnosis and comparisons (Maxwell et al. 2019).

In this work, we aim to (i) review the morphological characters of both the holotype and the recently described specimen of *Platypterygius sachicarum*; (ii) revise and re-describe the skull of *P. sachicarum*; (iii) provide new cranial characters based on comparisons; (iv) re-diagnose and evaluate the validity of *P. sachicarum* through comparative morphology and phylogenetic analysis; and (v) discuss the implications for ophthalmosaurid phylogeny and diversity. Although phylogenetic analysis by maximum parsimony method is ongoing, preliminary results show that the holotype of *P. sachicarum* represents a valid taxon from the Barremian-Aptian of Colombia. Based on a dozen new characters of the mandible and narial region, P. sachicarum is distinct from P. platydactylus. The differences include a suite of characters attributable to hunting ecology. *Platypgerygius platydactylus* has a presumed deep water hunting ecology with large orbits and a thin, sigmoid mandible. *Platypterygius sachicarum* has a presumed shallow-water hunting ecology with relatively smaller orbits and a robust mandible. Together, the large number of character differences are used to remove the Colombian taxon from *Platypterygius* and recognize it as a new genus. These characters include a relatively straight ventral margin of the mandible (unlike in P. platydactylus and P. australis); short projection of the nasomaxillary pillar (unlike in *P. hercynicus* and *P. australis*); well-defined, precise base of the tooth enamel layer (unlike in *P. americanus*); more than half lateral contribution of the angular (unlike in *P. australis* and *P.* platydactylus). The redescription of this taxon opens questions relating to the diversity and paleobiogeography of the Early Cretaceous marine biota from northern Gondwana, and highlights the importance of individually assessing each *Platypterygius* species to better tackle the long-standing problem of its validity.

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## New fossil primate material from the Lothidok Formation, northern Kenya

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The Lothidok Range is located west of Lake Turkana in northern Kenya and is best known for its Miocene fossil apes. Paleontologists first visited the area in the 1930s, and short expeditions took place again in the 1940s (Madden 1972) and the late 1950s (Leakey et al. 2011). Meave and Richard Leakey led field campaigns there in the 1980s, and described three new species of fossil apes – *Afropithecus turkanensis, Turkanapithecus kalakolensis*, and *Simiolus enjiessi* (Leakey and Leakey, 1986a,b, 1987). All three species are unique to the Lothidok Range and are found at the early Miocene localities of Moruorot and the Kalodirr Site Complex (~17 Ma). There are also two known middle Miocene sites, Esha and Atirr (~13 Ma; Boschetto et al. 1992; Leakey et al. 2011), but these have been only minimally prospected to date.

The West Turkana Miocene Project (WTMP) began in 2008 with the goal to explore the Miocene deposits of the Lothidok Range. Our work to date has included paleontological survey, efforts to refine the geochronology of the Lothidok sequence, study of mammalian fossils collected by our team and previous teams, and paleoclimate and paleoenvironmental reconstruction. Of particular importance has been the recovery of new ape fossils. Since 2008, we have found new craniodental and postcranial material of each of the three species of fossil apes at Kalodirr and Moruorot (Rossie et al. 2012; Rossie and Cote 2017). To date, all of our new specimens can be comfortably assigned to the existing species, but further documents metric and morphological variation in each. Furthermore, we have re-evaluated previously collected specimens curated in the National Museums of Kenya. Newly identified dental material of Turkanapithecus from Moruorot is particularly important because it demonstrates that this species is found at both early Miocene localities, and not just at Kalodirr. Furthermore, our new material of Turkanapithecus and Simiolus at Kalodirr comes from the same fossiliferous horizon, clearly demonstrating that these taxa are sympatric and not time-successive. A new mandible of *Turkanapithecus* displays features reminiscent of nyanzapithecines, including a teardrop-shaped m3, deep lingual notch on m1, rounded and conical cusps, and a mesiodistally elongate p4 with tall trigonid. New material of Afropithecus turkanensis reveals an odd variant of its premolar morphology. A lower p4 associated with four other teeth exhibits a strange crown outline, unlike previous specimens (Rossie and MacLatchy 2013), or other apes. In occlusal view, the crown margin buccal to the trigonid is concave instead of being convex and bearing the usual cingulum, as though the latter had been somehow suppressed.

The most impressive specimen we've found to date is a partial skeleton of the smallest Lothidok Range ape, *Simiolus enjiessi*. The specimen preserves most elements from the arms as well as a set of teeth that confirm the taxonomic identification. The limbs are slender and elongate, with moderate curvature of the phalanges. The capitate

and hamate are configured to form a ball and socket joint very like that seen in modern gibbons, indicating a strong ability to rotate at the wrist. Overall, the morphology is consistent with a suspensory mode of locomotion.

The future goals of the WTMP are to focus on paleoclimate and paleoenvironmental reconstruction in order to better understand the adaptive pressures on these fossil apes, and to systematically collect fossils at the middle Miocene localities of Esha and Atirr, and to survey for new localities within the Lothidok Range.

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## A comparison of molding and casting compounds used for dental microwear analysis

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Dental microwear analysis has been used throughout the years to reconstruct the diets of extant and extinct animals. To study microwear, negative impressions of teeth are made with a molding compound. These negative molds are filled with a casting compound, often an epoxy resin, to produce transparent casts. Using various techniques such as high dynamic range imaging (HDRI), low magnification microscopy, and scanning electron microscopy (SEM), casts are then imaged for microwear analysis (i.e., quantification of the numbers of pits and scratches). The employed impression and casting materials vary in cost to researchers and, potentially, in the fidelity with which they record microwear on tooth surfaces. Here, we investigate whether two molding compounds in combination with two casting compounds are significantly different in their ability to capture microwear. The compounds are Regular Body President microSystem polyvinylsiloxane and Sinclair Dental VPS Impression Material (molding compounds), and EpoKwick and EpoTek (casting compounds). The combinations of compounds being compared are President/EpoTek, President/EpoKwick, Sinclair/EpoTek, and Sinclair/EpoKwick. A comparison of these compounds has never been done despite being commonly used in microwear studies. Our sample includes the upper second molars of extant ungulate (hooved) species with known diets: the moose (Alces alces), bighorn sheep (Ovis canadensis), and horse (Equus ferus). Results from a previous experiment using HDRI low magnification microscopy comparing total microwear counts and pit-to-scratch ratios suggest that the Sinclair and President molding compounds do not capture significantly different microwear signals. We are now using SEM to increase our resolution and expanding our statistical analysis to include the two different casting compounds. This comprehensive analysis to determine if there is a significant difference between commonly used molding and casting compounds will help inform researchers of the best compounds for microwear studies. However, what we have found so far, is that the compounds differ in their ease of use. The President molding compound has a shorter setting time than the Sinclair compound (2 minutes and 3.5 minutes respectively), and President has a higher viscosity. Because of these properties, President does not flow as well around the tooth cusps. More product is then wasted from having to redo molds and from the compound setting while still inside the applicator wand. We have also noticed that President does not interact well with the EpoTek and EpoKwick casting compounds. When poured into President molds, the epoxy retains many more small bubbles than it does with the Sinclair molds, which leads to more discarded casts and wasted epoxy.

## Morphometrics and biostratigraphy reveal theropod biodiversity patterns in the Dinosaur Park Formation (Late Cretaceous: Campanian) of Alberta

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Over a century of ongoing research on the extremely fossil-rich deposits of the Dinosaur Park Formation (DPF) has facilitated many detailed studies of dinosaur ecology and evolution. However, taphonomic size-biases and other factors have resulted in a dearth of skeletal material for theropod dinosaurs, particularly small-bodied species. The number of named theropod taxa in the DPF has also fluctuated, with taxonomic assessments often founded on isolated fragmentary remains. To ameliorate some of these issues, we combine comparative morphology with high-resolution biostratigraphy, and geometric morphometric analyses of diagnostic frontals to analyze patterns of theropod evolution and biodiversity in the DPF, with a particular interest in testing potential faunal turnovers and material of debated taxonomic affinity.

2D geometric morphometric analyses with 6- and 5-landmark variants were performed on a broad sample of frontals from small-bodied theropod taxa of the DPF and several non-DPF theropods. These analyses were used

to test the taxonomic identification of highly fragmentary and/or contentious specimens (e.g., cf. *Erlikosaurus*, CMN 12355). In our analyses, frontals of DPF troodontids, dromaeosaurids, and ornithomimids are readily distinguishable in morphospace, and when individual PC axes are plotted against centroid size. The frontal referred to cf. *Erlikosaurus* plots most similarly in shape and size to troodontids, an assessment which is also supported qualitatively, as CMN 12355 shares a suite of troodontid characters. Postcranial skeletal material referred to cf. *Erlikosaurus* in the DPF is qualitatively re-assessed and found to be most similar in morphology to co-occurring caenagnathids. Recent taxonomic revisions among DPF troodontids are also assessed here. Our results challenge the recent description of *Latenivenatrix* as a distinct taxon from *Stenonychosaurus*. In particular, new data, incorporating troodontid frontals not assessed in the initial description of *Latenivenatrix*, results in variable distribution of putatively autapomorphic characters and stratigraphic overlap between taxa. This together with morphospace overlap of frontals referred to both genera in our analyses calls into question the validity of this species.

With respect to broader evolutionary trends among DPF theropods, whereas some isolation exists in biostratigraphic distributions among identified theropod material from DPF, there is no distinct pattern of faunal zones as previously documented in ornithischians, and most theropods appear to range throughout most of the stratigraphic extent of the DPF or overlap extensively (e.g., *Gorgosaurus* and *Daspletosaurus*). This may reflect a greater sensitivity of herbivorous ornithischians to environmental change and associated shifts in plant distributions when compared to the generally faunivorous to omnivorous theropods or other cryptic ecological or evolutionary factors.

## Histology of *Prosaurolophus maximus* (Hadrosauridae: Hadrosaurinae) reveals possible ontogenetic variability between hadrosaur species

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Due to their abundance, hadrosaurs are one of the most common groups used to study dinosaur ontogeny. Traditionally, studies have focused on examining the ontogenetic changes that occur in the skull, and how they affect our understanding of hadrosaur taxonomy, with more recent studies also determining the growth rates of individual species using histological techniques. While these studies have provided a wealth of information regarding the ontogenetic changes that occur in several hadrosaur species, a lack of comparative ontogenetic studies leaves us with little understanding of the large-scale ontogenetic trends occurring within Hadrosauridae.

In this study, we examine the ontogenetic changes that occur in the hadrosaur *Prosaurolophus maximus* using four specimens curated at the Royal Tyrrell Museum as well as specimens from other North American institutions, and compare these changes to those observed in other hadrosaurid taxa to identify ontogenetic trends within the clade Hadrosauridae. To examine these trends two analyses were performed. Firstly, the skull material of the various *P. maximus* specimens were used to reconstruct an ontogenetic series of the skull and compare it to that of other hadrosaur species, namely the hadrosaurine *Saurolophus angustirostris*, and the lambeosaurines *Corythosaurus casuarius*, *Lambeosaurus lambei*, and *Hypacrosaurus stebingeri*, to determine variability in the timing

of cranial ornamentation development within Hadrosauridae. Secondly, using histological sections of the tibiae of available specimens, growth marks were identified and used to determine the biological ages of those specimens. These ages were then plotted against tibial circumference, which can be used as a proxy for body mass, to estimate the growth rate of *P. maximus*. This growth rate was then compared to that of other hadrosaur species, namely the hadrosaurines *Maiasaura peeblesorum*, *Probrachylophosaurs bergei*, and *Kamuysaurus japonicas*, and the lambeosaurine *Hypacrosaurus stebingeri*, to determine how hadrosaur growth rates vary between species.

Our results show the cranial ornamentation of *Prosaurolophus maximus* starts developing at approximately 40 to 45 percent of the animal's maximum size, and is fully developed by 66 percent maximum size. In contrast, most lambeosaurine cranial ornamentation starts developing when the individual is between 50 and 60 percent of the species maximum size. Additionally, the reconstructed growth rate of *P. maximus* exhibited a slower rate than other hadrosaurines, but close to the growth rate of the lambeosaurine *Hypacrosaurus stebingeri*.

The results of both analyses indicate that growth rates differ between hadrosaur species, suggesting that there is greater ontogenetic variability within Hadrosauridae than previously thought. While the number of species we examined is currently limited, our results suggest several possible hypotheses that could explain the observed variability. First, the fact that both *P. maximus* and *H. stebingeri* have overlapping temporal and geographic ranges, suggests that palaeoenviromental factors, such as climate and availability of resources, may have strongly influenced species growth rate in hadrosaurs. Additional factors, such as the extent of cranial ornamentation development and presence of gigantism within a species, may also have played a role in the variability of ontogenetic trajectories observed in hadrosaurs. However, as there are currently few hadrosaur species for which the ontogenetic series has been thoroughly examined, it is unknown if the trends observed in this study are representative of all Hadrosauridae. Therefore, additional hadrosaur species will need to be examined using both histological and morphometric techniques to test the hypotheses presented in this study.

## The endosseous labyrinth of *Champsosaurus* (Diapsida: Choristodera) and its phylogenetic and ecological implications

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*Champsosaurus* was a gharial-like reptile that lived from the Late Cretaceous to the Paleocene in what is now western Canada and the United States. At present, little is known about their inner ear anatomy, primarily due to poor preservation of their gracile skulls, yet clarification of this structure promises to inform phylogenetic, functional, and ecological reconstructions. Here we describe the inner ear of *Champsosaurus* using computed tomography (CT) scanning of two well-preserved skulls housed at the Canadian Museum of Nature (Ottawa). The CT data were digitally segmented to produce three-dimensional models of the inner ear. The phylogenetic position of Choristodera within Diapsida is uncertain, so inner ear segmentations of 61 extinct and extant members of

Lepidosauromorpha and Archosauromorpha were included to adequately bracket *Champsosaurus*, with *Youngina* included as an outgroup. The semicircular canals of these species were landmarked, aligned and scaled using Generalized Procrustes Analysis, and projected into morphospace using principal component analysis (PCA) and canonical variates analysis (CVA).

The CT segmentations demonstrate that the semicircular canals of *Champsosaurus* are approximately orthogonal, and circular in outline. The PCA indicates a phylogenetic signal in semicircular canal shape, where taxa cluster into three distinct groups in morphospace: lepidosauromorphs, non-avian archosauromorphs, and avians. *Champsosaurus* and *Youngina* plot among the non-avian archosauromorphs, suggesting that *Champsosaurus* and archosauromorphs may have retained the ancestral semicircular canal morphology. The CVA demonstrates that the semicircular canals of *Champsosaurus* are most similar in shape to the other aquatic taxa, suggesting that *Champsosaurus* was adapted for sensing movement in an aquatic environment. Overall, this study represents the first morphometric analysis of semicircular canals across Diapsida, and the results are consistent with the hypothesis that *Champsosaurus* was a specialized aquatic predator. These data also support previous interpretations that *Champsosaurus* was behaviourally similar to modern crocodilians, and likely occupied a similar niche.

## Ecological niche modeling supports fossil evidence for an Appalachian population of neochoristoderes

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Four neochoristoderan vertebral centra were recently recovered from the latest Cretaceous deposits of New Jersey. These vertebrae represent the first evidence of neochoristoderes from the Atlantic Coastal Plain, extending the geographic range of this group in North America over 2000 km further east. Three of these vertebrae were recovered from the basal lag of the Navesink Formation (uppermost Campanian to the lowermost Maastrichtian) in the area of Holmdel, NJ, and the fourth was recovered from the Marshalltown sequence (upper Campanian) of Ellisdale, NJ. These vertebrae suggest that a population of neochoristoderes was present in Appalachia during the latest Cretaceous, but they raise the question of why neochoristoderes appear to have been so rare in Appalachia, while they were quite common in contemporaneous Laramidia.

It has previously been suggested that *Champsosaurus*, the only neochoristoderan genus known from the Late Cretaceous of North America, was latitudinally restricted between approximately 40 and 60 degrees North in Laramidia, in which case New Jersey (palaeolatitude of 37-38 degrees north) is slightly too far south to preserve a population of *Champsosaurus*. It is perhaps unsurprising that these animals are so rare here; however, Appalachia likely presented different environmental conditions than Laramidia, and it possible that the ideal habitat range of this taxon in Appalachia differed from that in Laramidia.

To test this, we implemented ecological niche modeling (ENM) to predict the ideal habitat range of the neochoristodere *Champsosaurus* in North America during the latest Cretaceous. Maastrichtian occurrence data for *Champsosaurus* from the palaeobiology database were verified for accuracy, and palaeorotated using GPlates. The rotated coordinates were then run through a BIOCLIM model in R using the dismo package, with Maastrichtian near-surface (2 m) air temperatures during the warmest and coldest seasons set as predictor variables. These climate data were output from the fully coupled GCM HadCM3L Atmospheric–Ocean General Circulation Model, and kindly made available by A. Farnsworth.

Preliminary results suggest that the ideal habitat for *Champsosaurus* in Laramidia was restricted between approximately 40 and 60 degrees North, supporting previous habitat range hypotheses; however, these results suggest that the ideal habitat range for *Champsosaurus* in Appalachia was restricted predominantly to the Atlantic coast, extending South to approximately 35 degrees North. These estimated ideal habitat ranges suggest that the vertebrae recovered from New Jersey may represent the southern margin of a potentially large population of neochoristoderes along the Atlantic coast of Appalachia, and the majority of their ideal habitat likely extended further North into what is now Canada, where latest Cretaceous sediments are not preserved. This makes it unsurprising that neochoristoderes appear to be so rare in the Appalachian fossil record, but if accurate, suggests that their fossils are to be expected in New Jersey and neighbouring regions. In the future, we will implement the more rigorous ENM program MaxEnt (Maximum Entropy Distribution Modeling), run a second analysis using Campanian occurrences and climate data, and include additional climate predictors to bolster the analyses.

# Osteological changes with growth of the alestid fish *Petersius conserialis* (Characiformes: Alestidae)

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Traditional classifications of the African characiform family Alestidae are largely based on features of the dentition and body size. The alestid tribe Petersiini, as traditionally classified based on reduced multicuspid teeth and a "small" body size, is now recognized to be a non-monophyletic group. It is known that dentition in Alestidae can change with growth, and therefore, the reduced dentition described in petersiins may be the result of a small body size. The first described petersiin, *Petersius conserialis*, has been an enigma as a result of limited specimen availability, contradicting information in the literature regarding the presence or absence of a parietal fontanelle, and its relatively large body size in comparison with other petersiins. We examined the osteology of a growth series of *P. conserialis*, using cleared and stained specimens, to address the conflicting information available in the literature for this species. We found there to be negative allometric growth between the standard length and the length and width of the parietal fontanelle. Morphological and osteological changes that occur throughout growth in *P. conserialis* were also found. Based on this research, we provide one of the few detailed osteological descriptions of a small alestid; this work will be useful for future comparisons to other species of Alestidae (and Characiformes). A strong understanding of morphological and osteological changes throughout growth in fishes is important to aid in the assessment of fossil fishes that may represent different ontogenetic stages.

## The problematic pachycephalosaurid *Gravitholus albertae*: synchrotron imaging facilitates reappraisal of taxonomic validity

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The only known specimen of *Gravitholus albertae* – TMP 1972.027.0001 – represents a heavily fused, incomplete pachycephalosaurid skull roof form the Oldman Formation of Alberta. The validity of *G. albertae* has been contentious due to the exceptional amount of fusion and extensive pathologies over much of the dorsal surface. More recent studies now consider TMP 1972.027.0001 as pachyephalosauridae indet., although a few studies retained *G. albertae* as valid. To test the taxonomic validity of *G. albertae*, we utilized Synchrotron imaging to study TMP 1972.027.0001 to define sutural contacts between the cranial elements for a detailed description of the specimen. Segmenting the separate elements within the skull roof of TMP 1972.027.0001 will allow comparisons and morphometric analyses with other pachycephalosaurids.

Synchrotron images reveal TMP 1972.027.0001 is one of the most complete pachycephalosaurid skulls known from Alberta. TMP 1972.027.0001 comprises a frontoparietal dome, partial right nasal, partial right prefrontal and anterior supraorbital, left and right posterior supraorbitals and postorbitals. The type closely resembles *Stegoceras*-grade taxa in possessing a tall and broad frontonasal boss separated from the supraorbital lobes by a groove, prefrontal and anterior supraorbital not incorporated into the dome, and a "pear shaped" dome in dorsal view. The fusion of peripheral elements to the frontoparietal and to themselves indicate TMP 1972.027.0001 is an ontogenetically mature individual. Virtually all differences we observe between TMP 1972.027.0001 and *Stegoceras validum* are reflective of ontogeny: degree of inflation of the posterior supraorbital, absence of a parietosquamosal and lateral shelves (dome inflation has reached posterior and lateral margins of the skull), and the incorporation of the prefrontal into the frontonasal boss. The absence of ontogenetically independent differences suggests TMP 1972.027.0001 represents an ontogenetically mature *S. validum*.

A Principal Component Analysis of Belly River Group pachycephalosaurids was performed using 13 linear measurements. Measurements were size standardized using frontoparietal width. PC 1, PC 2, and PC 3 account for 43%, 22%, and 16% of the total variation respectively. TMP 1972.027.0001, Hanssuesia sternbergi, and Stegoceras validum do not overlap, but form a continuum along PC 1, TMP 1972.027.0001 being the most negatively placed and the cluster of S. validum the most positively placed. The range of variation for S. validum across PC 1 if TMP 1972.027.0001 were to be treated as a specimen of S. validum, however, completely encompasses the range observed for *H. sternbergi*. TMP 1972.027.0001 falls within the range of *S. validum*, and *H. sternbergi* for PC 2 and PC 3. The relative length of the frontal, width at the prefrontal/anterior supraorbital contact, width at the anterior/posterior supraorbital contact, and length of the postorbital all strongly loaded positively (>0.3) in PC 1. The first three of these are known to scale with negative allometry (compared to frontoparietal width) in Stegoceras validum, thus the position of TMP 1972.027.0001 and H. sternbergi support the hypothesis that these specimens may represent later ontogenetic stages of S. validum. The range of size observed for H. sternbergi based on frontoparietal width, is clustered around the largest S. validum (excluding TMP1972.027.0001, the largest specimen in the analysis), and no juvenile specimens for H. sternbergi are described currently. Reduced Major Axis (RMA) regressions of these negatively allometric, non-size standardized measurements (log transformed; frontoparietal width as independent variable) were performed on specimens of S. validum only, followed by iterations including TMP 1972.027.0001 and H. sternbergi. Inclusion of the latter two increased r values and tightened slope confidence intervals (maintaining negative allometry) and explains the diagnostic wide frontoparietal of *H. sternbergi* as the result of negative frontal length allometry. Similarly, including TMP 1972.027.0001 and *H. sternbergi* with *S. validum* in RMA regressions of other purported diagnostic features of *H. sternbergi* (height and width of the frontonasal boss) increased r values and tightened slope confidence intervals. Given the available specimens and the trends observed for the pachycephalosaurid domes in this study, the taxonomic validity of *G. albertae* and *H. sternbergi* are challenged. Thus, we propose synonymy of *G. albertae* with *S. validum*, support previous studies synonymy of *H. sternbergi* and *S. validum*, and refine our understanding of ontogeny within *S. validum*.

# Using tooth enamel microstructure to identify mammalian fossils at an Eocene Arctic forest

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Early Eocene (ca. 50-55 Ma) sediments of the Margaret Formation on Ellesmere Island, Nunavut preserve evidence of a rainforest inhabited by alligators, turtles, and a diverse mammalian fauna. The mammalian fossils are fragmentary and often poorly preserved. Here, we offer an alternative method for identification. Among the best preserved and extensive of the Eocene Arctic forests is the Strathcona Fiord Fossil Forest, which contains permineralized in situ tree stumps protruding from a prominent coal seam. However, this forest yields a paucity of vertebrate fossils. In 2010 and 2018, we recovered mammalian tooth fragments at the fossil forest, but they are so incomplete as to be undiagnostic by using their external morphology. We used a combination of light microscopy and SEM analysis to study the enamel microstructure of two tooth fragments from the fossil forest - NUFV2092B and 2092E. The results of our analysis indicate that NUFV2092B and 2092E have Coryphodon enamel, which is characterized by vertical bodies that manifest as bands of nested chevrons or treelike structures visible in the tangential section under light microscopy. This enamel type is not found in other mammals known from the Arctic. Additionally, when studied under SEM, the enamel of NUFV2092B and 2092E has rounded prisms that open to one side and are surrounded by interprismatic matrix that is nearly parallel to the prisms, which also occurs in Coryphodon enamel, based on prior studies by one of us (WvK). The tooth fragments reported here, along with some poorly preserved bone fragments, are thus far the only documented vertebrate fossils from the Strathcona Fiord Fossil Forest. However, fossils of Coryphodon occur elsewhere in the Margaret Formation, so its presence at the fossil forest is not surprising. What is novel in our study is the way in which we identified the fossils using their enamel microstructure. The presence of Coryphodon also supports that the strata containing the Strathcona Fiord Fossil Forest are temporally correlative with the early Eocene (Wasatchian) fossil-bearing strata of the Margaret Formation approximately 25 km further north at Bay Fiord, a conclusion reached independently by lithologic correlation.

## Identification of damage and agents of deterioration in the paleonichnological site of La Virgen del Campo in Ensico (La Rioja, Spain)

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La Rioja, Spain has one of the best paleoichnological fossil records in the world, with almost 10,000 dinosaur footprints and around 1000 trackways. We worked at one of the best-known sites, known as "La Virgen del Campo", found in the Enciso locality in La Rioja, Spain. This site has many agents of deterioration that could be causing it harm.

Damage to the site has occurred because the site is exposed to temperature and humidity variation, in addition to rainfall erosion and other factors that are detrimental to the preservation of the footprints. We realized that we could change the restoration materials and methods that had been previously used in the site to preserve and protect the footprints. We decided to try materials that are normally used in the conservation and preservation of stone monuments.

For the identification of deterioration, we installed two data loggers on the site, and used ICOMOS-ISCS (Illustrated Glossary on Stone Deterioration Patterns) which is a guide with photographic records for the identification of damage in the field. Once the fossil damage has been identified and environmental conditions of the site are known, the degradation agents that are most harmful can be determined.

According to the above-mentioned guide, the conditions most likely to damage fossils in this site are the following: cracks (fractures, hair cracks, splitting), delaminations, disintegrations, fragmentations, erosion, missing parts, crusts, deposits, efflorescences, graffittis and biological colonization (lichens, moss, and other plants).

As for environmental conditions, our data loggers showed that humidity is very high most of the time. With these data we determined that water is one of the most harmful degradation agents in the area. With the information obtained thanks to these two tools, the intervention materials necessary for the correct restoration and preservation can be evaluated. To determine these materials, the Coremans Project of stone restoration criteria are taken into account.

## New information on the rise of mammals

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The extinction of the dinosaurs and subsequent rise of the mammals at the K-Pg boundary is among the most profound transitions in the history of terrestrial life. Dinosaur ecosystems and the mechanisms of their downfall are intensely studied, but considerably less is known about the ascent of mammals to key terrestrial niches. It is clear that within 10 million years, placental mammals flourished in diversity, size, and ecology, but a poor fossil record has made the details of this radiation unclear. In the last decade, a collaboration between the New Mexico Museum of Natural History and the PalM team at the University of Edinburgh has uncovered a wealth of fossils from the Nacimiento Formation in New Mexico that fill this critical gap. This new material is providing insights on physiology, sensory adaptations, diet, and locomotion that drastically improve our understanding of the dynamics of placental mammal diversification. The team is using these data to disentangle the phylogeny of the problematic 'archaic' placentals-those with no apparent extant descendants, but which played dominant roles in Paleocene ecosystems. Our work shows that early Paleocene mammals had relatively small brains, but rapidly developed a diversity of unique plantigrade to subdigitigrade locomotor styles that are non-analogous to extant mammals. These animals also diversified in body size, which is possibly related in some groups to environmental shifts associated with hyperthermal events. The skeletons of some early Paleocene mammals display a range of unique robust morphologies, most similar to those associated with burrowing lifestyles in extant mammals. Others, like small-bodied pantodonts, appear to have exhibited gregarious behaviour like in later forms, as inferred from relative abundance within a bonebed. The relationships of early Paleocene mammals are tested in an expansive new phylogenetic dataset including 693 characters scored for a broad range of 194 taxa (of which 125 are Paleocene species). This analysis allies some Paleocene taxa with major extant clades (e.g., 'condylarths', pantodonts and meridiungulates within Euungulata), whereas others fall outside of Placentalia (e.g., taeniodonts). Combined with improved stratigraphy from the Nacimiento Formation, these analyses show that many major placental groups likely originated by the earliest Paleogene.

# Drone remote sensing: new opportunities for dinosaur fossil discovery

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#### Summary

Spectral measurements of dinosaur fossil bone were acquired using a laboratory spectroradiometer. Unique spectral signatures were derived from multiple fossils, including fossils recently colonized by lichen, and from sediment samples. The results indicate a strong potential to detect new areas of abundant dinosaur fossils and bonebeds based on their distinct spectral signatures using RPAS ('drone') airborne remote sensing.

#### Introduction

The science of palaeontology provides a unique and direct perspective of the history of life and biological evolution. Dinosaur Provincial Park (DPP) and the Dinosaur Park Formation (DPF) in Alberta are internationally recognized and unique fossil resources, with over 45 species of dinosaur discovered dating to 77 million years ago (Currie and Koppelhus 2005; Brown et al. 2014; Alberta Parks 2017; UNESCO 2019). Designated as a UNESCO World Heritage Site in 1979, DPP has proved to be a major source of fossilized material, with over one hundred years of research accumulating in the best-sampled, most well understood Mesozoic terrestrial assemblage in the world (Currie and Koppelhus 2005). Given the extensive DPF outcrop across southern Alberta, the remote and rugged terrain and the high erosion rates, significant time and resources are invested in prospecting for new sites each year. The detection of identifying markers indicating the presence of fossil material using remote sensing offers the potential to increase the efficiency of prospecting. The markers used in our study included weathered fossil bone, modern lichen colonies (associated with characteristic fossil areas), as well as a distinctive sandstone channel lag sediment (Fig. 1). Of particular interest are larger area (10–100 m), high density (10–100 bones/m2) accumulations of large bones, representing attritional multi- taxic bonebeds or monodominant mass-death assemblages, which, given their size and density, are likely discoverable using remote sensing.



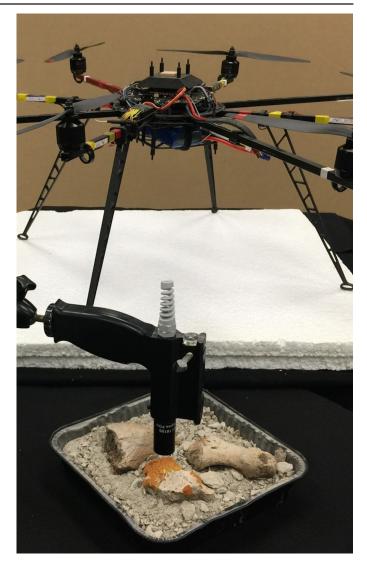
#### Laboratory Spectral Measurements

Remote sensing uses platforms like satellites, airplanes, helicopters, and drones to fly over a specified area and acquire images in a relatively short amount of time and has revolutionized the acquisition of large area, georeferenced ecological data and resource exploration. The sensors on these platforms measure the amount of reflected solar radiation in different wavelengths as reflected by the ground surface to provide

**Figure 1.** Unexcavated horned dinosaur bone bed in Dinosaur Provincial Park, Alberta, showing predominantly sandstone sediment with a clear layer of ironstone and lichen-encrusted fossils distributed on top. information about the unique reflectance patterns of the target. Due to the nature of fossil material becoming exposed via erosion, the target size will often be smaller than the typical pixel size of most sensors. Thus, in anticipation of needing a sub-pixel scale analytical approach such as Spectral Mixture Analysis (SMA; e.g., Peddle and Smith 2005), the goal of this first study was to create and assess a sufficiently comprehensive library of spectral measurements of fossil bones and related material, and to build an initial reference endmember spectral library for use in SMA as an integral part of our analysis of these fossils and other targets from DPP.

Representative fossils from the DPF were borrowed from the Royal Tyrrell Museum of Palaeontology (RTMP) for spectral measurements. Sediment was also retained from the fossil preparation process at the RTMP to provide representative samples of sediment types located at DPP as part of the DPF. Also, fossil bone exposed at the surface is often preferentially colonized by a specific lichen species or species complex. Samples of bone covered in these lichens were isolated in the lab and served as an additional potential fossil marker target. An example of a dinosaur fossil with lichen set on sediment from DPP is shown in Figure 2. The set of different dinosaur bones and other vertebrate fossil types measured in our initial lab experiment is listed in Figure 3 [see legend].

Spectral measurements were acquired in the ATIC Remote Sensing Lab at the University of Lethbridge using an Analytical Spectral Devices (ASD) Fieldspec-3 High-Resolution Full-Range Spectroradiometer [350– 2500 nm]. Reference spectra to derive reflectance were



**Figure 2.** Laboratory-based measurements of fossils combined with RPAS imagery make this research unique and exciting.

acquired using a white Spectralon panel (pressed polytetrafluoroethylene – PTFE). Due to noise in the shortwave infrared detectors of the spectroradiometer, the longest wavelength considered was 1900nm and a low-pass filter was applied beyond 1000 nm to all spectral curves, for illustration purposes only. ATIC has acquired a new drone system and this will be used to measure these samples in the lab and will be deployed over DPP for imaging during the summer 2020 field season with the same drone-based camera system as in the lab.

#### Results

Initial results from this first laboratory experiment are presented in Figure 3. Amongst the nine samples, there are four distinct patterns of reflectance. Each shows that these representative targets are sufficiently different spectrally and suitable to enable spectral separation within pixel-scale targets from Remotely Piloted Airborne System [RPAS, a.k.a. drone] missions planned for summer 2020 at DPP. The unique reflectance signatures of fossil bone, sediment, and lichen also show that these can serve as suitable endmember spectra for input to a SMA.

#### Conclusion

In the ATIC Remote Sensing Laboratory at the University of Lethbridge, spectra of various fossil specimens, as well as lichen and sediment, were measured and assessed. The unique spectral signatures obtained indicate (i)

these are spectrally distinct targets; (ii) they are suitable for use in SMA; and (iii) there is strong potential to detect areas with abundant dinosaur fossils and bonebeds in DPP from RPAS remote sensing missions planned for summer 2020. If this proof of concept is successful for these smaller areas, it may have significant implications for prospecting in expansive and poorly-accessible outcrops.

#### Acknowledgements

We are grateful to the Royal Tyrrell Museum of Palaeontology and Mr. Brandon Strilisky for facilitating the loan of fossil material and sediment. We also thank Ms. Cassandra Kimmen for her assistance with lab measurements.

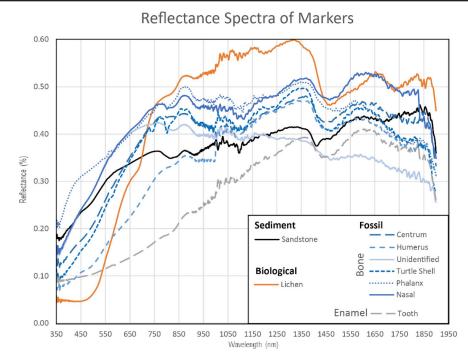


Figure 3. Reflectance spectra of markers from the Dinosaur Park Formation.

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## New thescelosaurid (Dinosauria, Ornithischia) material from the Wapiti Formation (Campanian) of northern Alberta

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The basal neornithischian dinosaur clade Thescelosauridae flourished from the Aptian to the Maastrichtian. This diverse, but in some respects poorly studied, group of small-bodied herbivores existed in both North America and Asia and is divided taxonomically into Orodrominae and Thescelosaurinae. In the Campanian-Maastrichtian of southern Alberta, orodromines typically occur in the Belly River Group and thescelosaurines in the younger Edmonton Group. The two stratigraphic groups are separated by shale deposits of the Bearpaw Formation, laid down during a Campanian transgression of the Western Interior Seaway, which obscures the pattern of thescelosaurid evolution during this interval. However, the Wapiti Formation, a non-marine fluvial deposit exposed in northern Alberta, includes strata that correlate with the transgressive Bearpaw Formation. Recent fieldwork in the Grande Prairie area has yielded new thescelosaurid material from the DC (Dinosaur-Chelonian) Bonebed, which lies within Unit 3 of the Wapiti Formation and roughly corresponds in age to the transition between the Bearpaw Formation and the overlying Edmonton Group in southern Alberta. The thescelosaurid material from the DC Bonebed includes a number of disarticulated postcranial and cranial elements. Some of the DC thescelosaurid specimens, including a femur, two fibulae, and a quadrate, show morphological similarities to the equivalent bones in North American and Asian thescelosaurine taxa. However, preliminary phylogenetic analysis of the DC specimens, using a previously published character matrix and assuming that they all belonged to a single species, tentatively places the fossil material in a polytomy with Orodrominae and Thescelosaurinae. The DC thescelosaurid specimens represent the first record of a thescelosaurid in the Wapiti Formation and of the thescelosaurid fauna that existed during, or perhaps just after, the deposition of the Bearpaw Formation.

### Baryonychine (Theropoda: Spinosauridae) remains from the Lower Cretaceous Enciso Group of La Rioja (Spain)

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The Riojan sector of the Cameros Basin in Spain is highly known for the abundance and good quality of Lower Cretaceous ichnite sites. Nonetheless, skeletal remains have been limited to isolated discoveries. In recent years, the performed explorations and diggings have led to the finding of new theropod material in Igea (La Rioja). Amongst these remains, twelve isolated teeth and a fragment of a left maxilla are known.

The teeth show typical baryonychine features such as elliptical to subcircular cross-section, chisel-shaped denticles, fluted enamel surface and veined enamel texture. Two tooth morphotypes can be distinguished. The first morphotype has denticles on both mesial and distal carinae whereas the second one lacks denticles on the mesial carinae. Furthermore, unlike the first morphotype, the teeth belonging to the second morphotype show mesial carina that run from the apex to slightly further than mid-crown. Both morphotypes have been previously identified in the Maestrazgo Basin, but not in the Cameros Basin, where the first morphotype has only been reported

A left maxilla was previously assigned in 1995 to *Baryonyx* sp. It bears eight subcircular or elliptical alveoli which lack teeth. The alveoli are not paired and anteriormost alveoli are angled anteriorly. In ventral view, the maxilla shows a wavy lateral surface. The lateral and lingual half of the maxilla are separated by a groove that isolates the alveoli to the labial half. These features suggest that the Igea maxilla can be attributed to Baryonychinae, but it is too fragmentary to be assigned to *Baryonyx* sp.

### Vertebrate faunal assemblages of the Late Cretaceous Western Interior Seaway in Manitoba

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Upper Cretaceous shallow marine sedimentary deposits exposed along the Manitoba Escarpment in eastern Saskatchewan and south-western Manitoba have been previously well-studied in terms of identifying foraminiferal biozones, hydrocarbon potential, and lithostratigraphic units, although data is currently lacking in terms of vertebrate biostratigraphy. An understanding of the distribution of vertebrates in Manitoba is essential in order to test hypotheses of faunal provinciality, habitat preferences, and temporal and spatial changes in faunal assemblages. In order to examine faunal occurrences, a dataset was compiled of specimens previously collected from Manitoba that are housed in museums across Canada and reported in the literature. The stratigraphic distribution of vertebrates in Upper Cretaceous deposits of the Manitoba Escarpment reveals several differences between the Cenomanian faunas of the Ashville and Favel formations and the Campanian faunas of the Pierre Shale, the most notable difference being the wide stratigraphic distribution of chondrichthyans and osteichthyans and the comparatively restricted stratigraphic ranges of reptiles and avians. The chondrichthyans Cretalamna and Squalicorax are represented in both Cenomanian and Campanian faunas, as well as the osteichthyans Apsopelix, Cimolichthys, Enchodus, Elopopsis, Ichthyodectes, Pachyrhizodus, Protosphyraena, Roulletia, and Xiphactinus. Reptile remains are mainly restricted to the Pierre Shale and most abundant in the Pembina Member, with the first appearance of mosasaurids in the lower Santonian Boyne Member of the Carlile Formation and last appearance in the middle Campanian Millwood Member of the Pierre Shale, as well as the first appearance of turtles in the Pembina, represented by Toxochelys and Protostega, and their last appearance in the Millwood. Exceptions to the restriction of reptiles to the Pierre Shale include the occurrences of the crocodile Terminonaris and a pliosaur in the Keld Member of the Favel Formation, and the relatively wide distribution of polycotylid plesiosaurs in both the Cenomanian and Campanian faunas. Avians are represented by two distinct faunas separated by a significant stratigraphic gap and they consist solely of the genera Pasquiaornis and Ichthyornis in the Belle Fourche Member of the Favel Formation and Brodavis and Hesperornis in the Pierre Shale. In terms of diversity, the Cenomanian faunas represented in the Belle Fourche and Keld members indicate a relatively high diversity chondrichthyan and osteichthyan assemblage and low diversity avian and reptile assemblage, whereas the early Campanian fauna represented in the Pembina indicates a high diversity osteichthyan and reptile assemblage and low diversity avian and chondrichthyan assemblage.

This initial investigation has revealed some collection biases that will need to be accounted for in future faunal analyses. The lower to middle Cenomanian Belle Fourche, upper Cenomanian Keld, and lower Campanian Pembina members have been more heavily sampled than other lithostratigraphic members exposed along the Manitoba Escarpment. Therefore, members that are poorly represented in museum collections, including the Morden, Boyne, Gammon Ferruginous, Millwood, and Odanah members, will be targeted in future field work in order to offset some collection biases or determine the cause of biases (e.g., poor outcrop exposure, poor preservation potential, and/or restricted land access). Future work will include biostratigraphic correlations between the Cretaceous marine units of Manitoba, Saskatchewan, Alberta, and USA, as well as paleoecological analyses and quantifying temporal faunal changes in order to address questions concerning evolutionary patterns, ecosystem function, and extirpation events within the Western Interior Seaway.

## Late Pleistocene bears of Vancouver Island: new insights from stable isotopes and radiocarbon

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Vancouver Island in the late Pleistocene was home to three coextant bear species: *Ursus arctos* (Grizzly Bear), *Ursus americanus* (Black Bear), and the now-extinct Short Faced Bear, *Arctodus simus*. New radiocarbon dates from Royal BC Museum (RBCM) specimens provide evidence that these three bear species overlapped chronologically on the island. The ecological implications of this overlap are being investigated using stable isotope analysis of the bone collagen found in their remains. Preliminary stable isotope results from bulk collagen tissue suggest niche partitioning between the bear species on the island. Going forward, this research will apply compound-specific isotope analysis to further investigate this niche partitioning and the resource group specializations of each species.

Preliminary results from compound-specific isotope analysis show that, although the bulk collagen nitrogen isotope signature of the Vancouver Island Short Faced Bear appears different from that of Short Faced Bear from the Yukon, these changes are likely due to differences in the environmental baseline isotopic composition of these regions and time periods rather than a difference in resource specialization. Unsurprisingly, compound-specific results further support the Short Faced Bears occupying a significantly higher trophic position than contemporary Black Bears. Upcoming compound-specific results will allow for a more detailed comparison of the trophic level occupations and resource specializations between Grizzly Bears and contemporary Short Faced Bears on the Island.

### The effects of uninformative and informative priors when applying Bayesian stable isotope mixing models to reconstruct the diets of eastern Beringian gray wolves (*Canis lupus*)

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During the Pleistocene, eastern Beringia was home to a diverse ecosystem rich in mammalian fauna that included both now-extinct and extant taxa of large bodied-carnivores and herbivores. Though many species have been discovered and described, reconstructions of ecosystem dynamics and predator-prey interactions are the focus of ongoing research. The extant gray wolf (Canis lupus) was among the large-bodied carnivores present in eastern Beringia during the late Pleistocene and is an apex predator in today's Arctic and Subarctic ecosystems. Accurate reconstructions of ancient wolf diets are important because they cannot be directly observed, and they provide valuable insights of the past dietary niche of this species to compare to modern individuals where direct observations are possible. To determine the relative contributions of various potential prey species to the overall diets of Beringian gray wolves, we used bulk carbon ( $\delta 13C$ ) and nitrogen ( $\delta 15N$ ) stable isotopes obtained from bone collagen of the wolves. We also obtained published isotopic data for nine eastern Beringian herbivore species. To determine the most probable dietary inputs for wolves, we used a Bayesian stable isotope mixing model (MixSIAR v.3.1.10), employing three models with different prior distributions. The first model, run with uninformative priors, weighted all potential prey species equally; all prey were equally likely to have contributed to the overall diets of the wolves. The posterior probabilities indicated that woolly mammoths (Mammuthus primigenius) constituted the majority of the diet (~39% ± 23%), followed by Yukon horses (Equus sp.; ~33% ± 20%) and mastodons (*Mammut americanum*;  $-5\% \pm 5\%$ ). We consider this model to be least likely, ecologically, given the large body masses of mammoths and mastodons. We therefore employed two additional models with

informative priors based on the known ecology of wolves and ungulates. The second model, run with informative priors based on previous dietary studies of wolves, suggested that Yukon horses were the most significant dietary contributor (~49% ± 18%), followed by woolly mammoth (~20% ± 19%), and muskox (*Ovibos moschatus*; ~7% ± 6%). The third model, run with informative priors based on models of prey abundance derived from body mass, produced results indicating that Yukon horse was the primary contributor to diet (~42% ± 20%), followed by giant beaver (*Castoroides* sp.; ~23% ± 16%), and dall sheep (*Ovis dalli*; ~20% ± 9%). Clearly, our choice of priors strongly influenced the posterior probabilities, likely because Pleistocene herbivores from the Yukon are primarily differentiated only by their values of  $\delta$ 15N and not  $\delta$ 13C (relating to the C3-dominated environment). Thus, caution must be exercised with regard to dietary interpretations of Pleistocene Arctic carnivores. Although there is very significant variability and high uncertainty among our model results, they are consistent with those of published literature in that large ungulates, especially Yukon horses, likely consistently contributed to the overall diets of Beringian gray wolves. They also suggest that Pleistocene wolves in Beringia potentially had diverse diets, including both now extinct and extant species. Although our findings are uncertain, they are valuable in improving the understanding of eastern Beringian trophic ecology, and, with further refinement, will provide novel insights about the dietary niche of gray wolves during the Pleistocene.

## Histological and developmental study of pleurodont squamate teeth reveals tooth attachment tissue homologues between reptiles and mammals

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Developmental biologists universally acknowledge that the dental tissues enamel and dentine are deeply conserved throughout the evolutionary history of amniotes. This consensus contrasts strongly with the disagreement and confusion surrounding the evolution of the tooth attachment tissues in mammals, crocodilians, and lepidosaurs. The traditional evolutionary model suggests that mammals and crocodilians have independently evolved a complex, three-part tooth attachment system consisting of tooth cementum, alveolar bone, and a suspending periodontal ligament (PDL). By comparison, modern lizards have a single, plesiomorphic 'bone of attachment' tissue that fuses tooth bases to the jaws. Over the last several years, we have challenged this hypothesis by demonstrating the presence of cementum, alveolar bone, and PDL in numerous fossil amniotes, and by constructing an alternative hypothesis for the evolution of dental tissues within Amniota. This alternative hypothesis states that all amniotes have homologous dental tissues that are found in all amniote clades. However, one of the major challenges to this hypothesis lies in the identity of the attachment tissues as extant crocodilians and mammals.

Here we provide a re-interpretation of extant squamate tooth attachment tissues in a histological sample spanning four squamate families (Iguanidae, Cordylidae, Teiidae, and Varanidae). Using new histological and micro-CT data, we compare the development of the attachment tissues in all of these groups to show that they do not conform to the classical model of 'bone of attachment' development, but rather that they all possess a three-tissue complex consisting of cementum, alveolar bone, and a transient PDL that completely mineralizes when the tooth is fused to the jaw. Moreover, we highlight a previously undocumented soft tissue component to the lizard attachment tissue system that we term the 'Interdental Connective Tissue' (ICT) that contains the bulk of the developing attachment tissues in modern pleurodont lizard teeth. The ICT resides in between adjacent teeth and has gone unnoticed in previous descriptions of lizard dental anatomy. Lastly, we demonstrate how variations in the degree of mineralization of the components of the ICT have given rise to the diversity of tooth implantation modes in modern squamates.

### Phylogenetic affinities of early European Passeriformes

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Passeriformes (passerines) is the most diverse and globally widespread order of living birds, consisting of two main suborders, the oscines and the suboscines. The passerine fossil record is limited, mostly represented by fragmentary skeletal material that lack phylogenetically diagnostic characters, which leaves few calibration points for divergence time estimates of passerine clades. Some researchers have thus used biogeographic events as a proxy, such as the separation of New Zealand from Antarctica, which has been used to propose the controversial late Cretaceous divergence between oscines and suboscines. There are three nearly complete passerine fossils from the early Oligocene of Europe that can be properly analyzed phylogenetically: Wieslochia weissi, Jamna szybiaki, and Resoviaornis jamrozi. We performed the first set of phylogenetic analyses of these fossils, combining osteological and genetic characters (for extant taxa) in maximum parsimony, maximum likelihood, and Bayesian inference methods. Wieslochia consistently falls within the crown suboscine clade Eurylaimides. Jamna is placed outside of crown-Passeriformes, either with stem passerine group Zygodactylidae, or sister to crown-Passeriformes. Resoviaornis was found to be an advanced oscine. This is the first study to place Resoviaornis into a phylogenetic context, and also the first to consider all three of these fossils together. Resolving the phylogenetic relationships of these early passerines provides us with a more reliable calibration point for divergence time estimates of passerines, as well as insight in the early radiation and biogeography of the most species-rich and widespread groups of birds on the planet.

## Ontogeny of a sexually selected structure in an extant archosaur *Gavialis gangeticus* with implications for sexual dimorphism in dinosaurs

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Despite strong evidence for sexual selection in various display traits and other exaggerated structures in large extinct reptiles, such as dinosaurs, detecting sexual dimorphism in them remains difficult. Their relatively small sample sizes, long growth periods, and difficulties distinguishing the sexes of fossil specimens mean that there are little compelling data on dimorphism in these animals. The extant gharial (*Gavialis gangeticus*) is a large and endangered crocodylian that is sexually dimorphic in size but males also possesses a sexually selected structure, the ghara, which has an osteological correlate in the presence of a fossa associated with the nares. This makes the species a unique model for potentially assessing dimorphism in fossil lineages, such as dinosaurs and pterosaurs, as it is a large, slow-growing, early maturing, egg-laying archosaur. Here we assess the dimorphism of *G. gangeticus* across 106 specimens and show that the presence of a narial fossa and pterygoid bullae diagnose adult male gharials. Males are larger than females, but the level of size dimorphism, and that of other cranial features, is low and difficult to detect without a priori knowledge of the sexes, even with this large dataset. By extension, dimorphism in extinct fossil reptiles should be very difficult to detect in the absence of sex specific characters, such as the narial fossa.

## A farewell to arms: amniote-like limb loss in recumbirostrans from Mazon Creek, Illinois

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Among modern tetrapods, many lineages have converged on a snakelike body plan, where extreme axial elongation is accompanied by reduction or loss of paired limbs. However, the fossil record of how and when this adaptive strategy evolved in various tetrapod groups remains poorly understood. For example, limb reduction and/or loss is known in a handful of early stem-group tetrapods and total-group lissamphibians, whereas the fossil record of limb reduction and loss within the amniote lineage is sparse. We here provide new insights into these questions by reporting a new molgophid recumbirostran from the Francis Creek Shale (309-307 Ma) of Illinois, USA, with extreme axial elongation and corresponding limb reduction. The new molgophid, represented by two exceptionally well-preserved specimens preserving complete body outlines, shows affinities with Brachydectes and Infernovenator. However, unlike in these taxa, the forelimb and pectoral girdle is entirely absent in the new molgolphid, thus representing the earliest occurrence of complete loss of a limb in a fossil amniote. The presence of a complete hindlimb and pelvic girdle in the new taxon contrasts with the condition seen in limb-reduced amphibians and certain limb-reduced reptiles. In these cases, the hindlimb-first reduction process is characterized by the loss and/or reduction in size of hindlimb elements and rudimentary pelvic girdle elements are often retained. Instead, the morphology of the new molgophid is consistent with a pattern of limb reduction seen in modern snakes, where the forelimb and pectoral girdle are lost first. In snakes, the loss of the forelimb is caused during embryonic development by the failure to form a discrete forelimb field due to homogenous Tbx5 expression over the entire pre-cloacal flank region, rather than a discrete Tbx5 domain to signal forelimb bud initiation (Woltering et al. 2009). The similar morphology between the new molgophid and snakes suggests a common limb-reduction mechanism may apply more broadly across the amniote tree.

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## Sexual dimorphism among polar bears from the Lancaster Sound subpopulation, Nunavut

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Polar bears (Ursus maritimus) are highly sexually dimorphic, with mature males being larger than females on average. Sexual size dimorphism within populations of Canadian polar bears has, to our knowledge, not been explored. Furthermore, numerous specimens in the Canadian Museum of Nature's (CMN) collections lack sex identification, limiting their utility for exploring the historical ecology of Canadian polar bears. Polar bear skulls of individuals of a known sex from the Lancaster Sound population (Nunavut, Canada) were studied to derive a model for assigning sex to specimens with incomplete collection data. We measured skull lengths, molar row lengths, skull width, and canine length for 55 specimens from the CMN. These were found to best reflect sexual size dimorphism in other carnivorans and have been employed in previous studies of polar bear skull morphology. Using discriminant analysis, we found that 75% of polar bears can be accurately classified based on skull size metrics. Juveniles are classified with less confidence based on size overlap among the sexes. The skulls and canines of males are significantly larger than females (p < 0.05). We modelled size dimorphism among Lancaster Sound polar bears using logistic regression to classify a specimen of unknown sex in the CMN collections. The unknown specimen was classified as a female with a 73.4% probability. We have improved the utility of CMN collections for our ongoing study of polar bear historical and paleontological ecology. In both contexts, identification of the likely sex of individuals is important, given significant behavioral and reproductive differences that likely influence the other ecological indicators we intend to use in future studies (e.g., stable isotopes).

## A juvenile pachycephalosaurid (Ornithischia: Pachycephalosauridae) from the Frenchman Formation (Upper Maastrichtian), Saskatchewan, Canada

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In 1973, Dale Russell collected a small, partial ornithischian skeleton from the Frenchman Formation (upper Maastrichtian) of what would become Grasslands National Park, Saskatchewan, Canada. The specimen primarily consists of the pelvic and hindlimb elements, and a series of ten caudal vertebrae. It was eventually reported in the literature as belonging to a juvenile *Thescelosaurus*. Our re-examination of the skeleton has instead revealed it to be a juvenile pachycephalosaurid. This identification is based on such characteristic features as a sigmoidal

dorsal margin of the ilium, the near exclusion of the pubis from the acetabulum, and a prominent medial process of the iliac blade. The juvenile status of the specimen is attested by the lack of neurocentral fusion within the vertebral column. Histological analysis of the tibia demonstrates a fibrous bone texture and absence of annuli, further supporting the young age of the individual (probably less than a year). This new skeleton is therefore significant as Canada's second most complete pachycephalosaur skeleton, and as among the world's youngest known pachycephalosaurids. Because both juvenile and postcranial material is rare in this taxon, this specimen provides a unique opportunity to broaden the understanding of the evolutionary relationships, functional morphology, and ontogeny of these otherwise poorly understood animals.

### Vertebrate faunal assemblage of the Upper Cretaceous Lagerstätte-type deposits of the Apulian Platform, Southern Italy

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During the 1970s and 1980s, several excavations conducted across the Salento Peninsula (Puglia, Southern Italy) resulted in a large number of well-preserved and important fossil specimens that today are housed in several Italian institutions. Despite the high potential of these fossil sites to produce more quality specimens, little additional collecting has been conducted in the area since the original fieldwork investigations.

The majority of vertebrate fossils from these Salento Peninsula localities are fish. High taxonomic diversity representing several different families has been described so far, though a large amount of material still remains undescribed. Moreover, recent examination of the previously described fish material shows that at least some of the taxa should be re-analysed and their relationships reassessed. The first marine reptile from the area was reported in 2018: a new species of dolichosaur (Pythonomorpha, Squamata) from near the town of Nardò, with mineralized skin and muscles preserved in association with the skeleton.

The exceptional quality of preservation of the fossils from Nardò prompted the undertaking of a new fieldwork project. Thanks to collaboration with the local prehistoric museum (Museo della Preistoria di Nardò) and cultural heritage authority (Soprintendenza Archeologia, Belle Arti e Paesaggio delle Provincie di Lecce, Brindisi e Taranto), an inactive stone quarry was identified as a suitable site for new fieldwork.

The rocks exposed in the quarry consist of platy limestones, often dolomitized, that are part of the informal geological unit 'Calcari di Melissano' (Cenomanian–Maastrichtian), which was deposited in a shallower portion of the inner lagoon of the Apulian Carbonate Platform. The age of the Nardò limestones is considered to be upper Campanian–lower Maastrichtian based on nannofossils, however, the new stratigraphic data we gathered will certainly help refine this record and establish a more accurate age for the fossil-rich layers.

In terms of fossil finds, our recent excavation resulted in the recovery of almost 40 new specimens, including ray-finned fishes, remains of a probable soft-shelled turtle, lizard fragments, echinoids, crustaceans, and coprolites. Moreover, amongst the undescribed material collected during past excavations, we recognized an almost complete hard-shelled turtle, an articulated limb of a semi-aquatic turtle, and a partial vertebral column and forelimb of a small halisaurine mosasaur.

The ray-finned fish fauna previously reported from Nardò consists of a wide array of teleosts, including dercetids (elongate Aulopiformes), a syngnathiform (a pipefish relative), several clupeiforms (herring-like fish), and other taxa that are commonly found in shallow marine deposits of the Eastern Tethys. The perciforms previously reported from the site should be revaluated, as they are likely better placed with more basal acanthomorph lineages. The new collections from our recent fieldwork include material belonging to a probable ichthyodectiform or osteoglossiform, clupeomorphs, a dercetid, and an aipichthyoid.

These deposits clearly possess all the characteristics of a fossil Lagerstätte, both for the high quality of preservation and abundance of fossils. Lagerstätte-type deposits represent rare windows into life in the past, making their discovery and conservation of paramount importance. Deposits yielding fossils of such exceptional quality of preservation from the final stages of the Cretaceous are extremely rare at a global scale. Critically, new data from the limestones of Nardò will enhance our understanding of the state of marine ecosystems and faunas of the Mediterranean realm a few million years before one of the biggest extinction events in the history of life on Earth.

## Examination of maxillae morphology within eudromaeosaurian dromaeosaurids using computed tomography and the implications for phylogenetic interpretation

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Eudromaeosauria is the most diverse clade within the family Dromaeosauridae and is known throughout the Cretaceous across Laurasia. Dromaeosaurid evolution, especially in terms of osteology, remains relevant in paleontological research because dromaeosaurids shared a more recent common ancestor with modern birds than most other non-avian dinosaur clades. The maxilla of eudromaeosaurians is preserved relatively commonly with several eudromaeosaurian species having been diagnosed almost exclusively by the maxilla. Diagnosing species from limited material can bias phylogenetic analyses via overweighting of particular elements. *Acheroraptor* and *Atrociraptor* are two examples of dromaeosaurids described primarily by their maxilla and given their geological age, these taxa are important datapoints in understanding dromaeosaurid evolution during the Late Cretaceous. *Acheroraptor*, however, is distorted from taphonomic processes which may affect ratio measurements of various maxillary anatomical features that have been used to define its phylogenetic relationship, and *Atrociraptor* has only been described based on the anterolateral sections of the maxilla due to its delicate nature and incomplete preparation. Crushing and distortion has also caused a restricted view of the maxilla in *Deinonychus* and the relationship with surrounding elements, leading to conflicting reconstructions of its skull anatomy. These factors introduce additional biases as some morphological features (e.g., length of the anterior ramus, fenestra shape,

etc.) are easily affected by postmortem damage. As a result, taphonomic and diagenetic processes, as well as incomplete preparation, in turn can cause potential misinterpretations of morphology, which in turn, can cause potential errors in anatomical and phylogenetic interpretations.

Computed tomography (CT) scans were taken of the three North American taxa (*Acheroraptor, Atrociraptor*, and *Deinonychus*) to review previous anatomical interpretations. All specimens are thought to be mature, however, comparative material does not exist to confirm this assessment. Retrodeformation was performed on *Acheroraptor* (ROM 63777) using DragonFly and Mesh Mixer to segment and then align displaced fragments along lines of fracture for consistent comparisons. These three dromaeosaurids were then compared to the CT scans of *Saurornitholestes*, *Tsaagan*, and *Velociraptor* with focus on anatomical features common but variable among eudromaeosaurians, and the topological relationships between the maxilla and surrounding bones. Tooth replacement was observed when possible and patterns of replacement were comparable to previously reported patterns in other theropod dinosaurs.

The close relationship between *Atrociraptor* and *Saurornitholestes* is supported by shared characters (maxillary fenestra nested within accessory antorbital fossa, a tall anterior ramus, etc.). However, our analysis demonstrates that once the specimen of *Acheroraptor* underwent retro-deformation, the elongate anterior ramus which contributed to the placement of *Acheroraptor* in Velociraptorinae was far less pronounced than that of velociraptorines, and numerous features of the maxillary sinus system were shared with members of Saurornitholestinae (i.e., morphology of the maxillary fenestra, position of the maxillary fenestra relative to promaxillary fenestra, long and slender ascending ramus, two distinct chambers of the maxillary sinus system). In further contrast to previous studies, the maxilla of *Deinonychus* also has mosaic characters (e.g., maxillary fenestra opening laterodorsally, a tall anterior ramus) documented in Asian and North American taxa respectively. CT scan is a useful methodology for character constructions for fossil specimens subjected to taphonomic distortions and/or incomplete preparation. Ratio-based characters conflict with discrete characters describing homologous structures, and more likely represent analogous characteristics indicative of convergence.

## Confirmation of dire wolf from Medicine Hat, Alberta using geometric morphometrics

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The banks of the South Saskatchewan River near Medicine Hat, Alberta preserve nine fossiliferous strata of late Pleistocene age, from which over 1,200 vertebrate fossils were collected by C.S. Churcher and A. MacS. Stalker in the 1960s and early 1970s. Recent work on these deposits have confirmed the presence of iconic large Rancholabrean taxa, such as the sabre-toothed cat *Smilodon fatalis* and the American lion *Panthera atrox*. The biogeographic implications of these occurrences suggest that the complete Rancholabrean carnivore guild extended further north than previously known. In 1970, C.S. Churcher collected a right dentary that, based on its large size and morphology, he identified as belonging to the dire wolf *Canis dirus*. The dentary is missing much of

the ramus and incisor arcade, and retains most of C1, the root of P1, partial P2, and P4. The preserved teeth are heavily worn and the alveoli for M1 are partially infilled by pathological bone growth, indicating that the tooth was lost, and healing occurred before death. Heavy wear and tooth loss suggest that the specimen belonged to an old adult individual but have also obliterated dental characters that could confirm its taxonomic assignment. The overall size and robusticity of the specimen are consistent with an identification of *C. dirus*, but this may simply be due to allometric shape change associated with a large body size. Thus, the taxonomic identity of the Medicine Hat specimen cannot be ascertained based on qualitative morphological characters alone.

Previous work established that two-dimensional geometric morphometrics may be used to differentiate the dentaries of dire wolves from modern and Pleistocene Beringian grey wolves *C. lupus*. To test the taxonomic identity of the Medicine Hat dentary we applied a 2D geometric morphometric analysis using a previously published dataset, which was modified to remove landmarks that are missing in the specimen. After modifications, the dataset contained 12 landmarks for 315 dire wolves, 28 fossil Beringian wolves, and 35 modern grey wolf specimens. We performed a Principal Component Analysis (PCA) to visualize the morphological variation between known *C. dirus* and *C. lupus* specimens as well as the unknown specimen. Additionally, we performed a group affinity test by calculating the typicality probability of the Medicine Hat specimen belonging to each group based on its distance from the group means, using the first five PC axes of shape.

The PCA identified 20 principal components axes of morphological variation, showing the Medicine Hat dentary clustering with the dire wolves along PC 2, which explains ~15% of morphological variation, and is correlated with dorsoventral breadth of the mandible. The group affinity test produced a probability of 0.738 that the Medicine Hat specimen belongs within *C. dirus*, and much lower probabilities that it would belong in either of the other groups. Mahalanobis distances between *C. dirus* and *fossil C. lupus* and modern *C. lupus* are 3.71 and 4.97, respectively. Meanwhile, the Mahalanobis distance between fossil and modern *C. lupus* is 3.66. These results suggest that, in addition to other large Rancholabrean carnivores, dire wolves were present in Alberta, thus expanding their known range into the Pleistocene of Canada.

## Reassessment of *Coronosaurus brinkmani* from the Oldman Formation (Campanian) of southern Alberta

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*Coronosaurus brinkmani* is a centrosaurine ceratopsian typically recovered as the sister taxon to *Centrosaurus apertus* in the tribe Centrosaurini; indeed, it was originally described as a species of *Centrosaurus* (Ryan and Russell, 2005). To date, all material attributable to the taxon comes from two localities in the Comrey sandstone unit of the Oldman Formation (Campanian) of southern Alberta. The holotype comes from a monodominant bonebed (BB 138) in Dinosaur Provincial Park with additional referred material coming from the centrosaurine dominated Milk River Ridge bonebed (MRRBB) approximately 180 km to the SW near the village of Warner, Alberta.

*Coronosaurus brinkmani* is diagnosed by several cranial characters known from multiple specimens from BB 138: adult-sized postorbital horncores project laterally and are circumferentially inflated with an axial length: basal length ratio of typically <2:1; epiparietal (EP) locus 2 hosts a large, rosette-like process formed by numer-

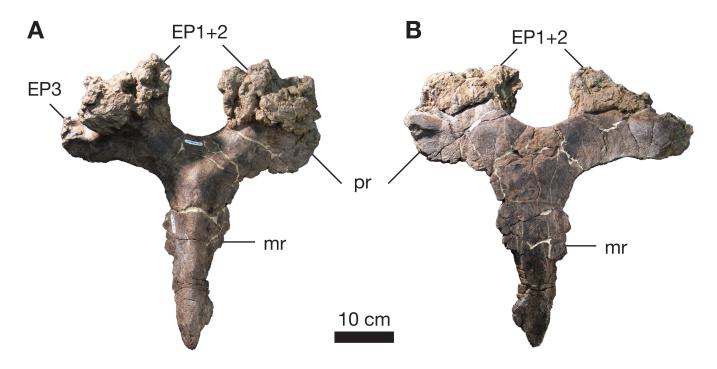
ous, variably developed, short, spine-like dermal ossifications that can extend onto the dorsal surface of EP1; and, EP3 developed as a short, dorsolaterally-oriented, tongue-like hook or tapered spike. The majority of the BB 138 specimens are of putative adult size, although numerous subadult-sized elements chart, in part, the ontogenetic trajectories of postorbital and the epiparietal morphologies.

The material from MRRBB is more fragmentary than elements from BB 138 and, while examples of all of the key cranial features are represented, there are no complete, unbroken posterior parietal rami. The best preserved parietal (TMP 1999.082.0001; Fig. 1), and other catalogued partial specimens from the MRRBB, do not exhibit EP1 and EP 2 morphologies identical to those seen on parietal specimens from BB 138. None of them have a distinctive procurved EP1 or rosette-like EP2 shape. Instead, the EP1 and EP2 loci of the ramus are dominated by a single dorsally-positioned, sponge-like, bony mass. These structures were originally inferred to be the coalesced EP1 and EP2 processes that had been the taphonomically modified (eroded) prior to fossilization. However, if is the case, it should be noted that none of the BB 138 parietals exhibit the degree of EP1 and EP2 coalescence seen on the MRRBB parietals.

Despite the smaller sample size, the MRRBB parietal ornamentation appears to also have other novel features not present on the BB 138 specimens. These include; 1, adult-sized postorbital horncores tending to be longer; 2, the palpebral contact with the postorbital in subadults is longer relative to horncore height; and, 3, the posterior margin of the parietal midline is V-shaped rather than the shallow U-shape seen on BB 138 parietals (and *Centrosaurus apertus*); as a consequence of the latter feature, the EP1s are in closer proximity to each other than those on parietals from BB 138. The MRRBB parietals also have one additional, possibly apomorphic, character not observed on any specimen from BB 138; the posterior margin of each epiparietal extends onto the ventral surface of the parietal. Whether these features are simply characters yet to be observed on other *Coronosaurus brinkmani* specimens from BB 138, or whether they are indicative of another new Albertan centrosaurine ceratopsid remains to be determined with the recovery of additional ceratopsid material from the Western Interior of North America.

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**Figure 1.** Best preserved parietal from MRRBB (TMP 1999.082.0001): A, dorsal view; B, ventral view. Abbreviations: EP, epiparietal; mr, midline ramus; pr, posterior ramus.

### Pliocene fish fauna from Gona, Ethiopia

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Late Cenozoic fossiliferous sites in the Afar Depression of Ethiopia are well known for the discovery of the hominids *Australopithecus afarensis* ("Lucy"), and *Ardipithicus ramidus*, as well as several species of *Homo*. While much work has concentrated on the hominids and their associated mammalian faunas and environments, little is known of the fossil fishes associated with these sites. However, fish remains can be particularly important to determine hydrographic connections between areas, and aid in reconstructing the biogeography of the total fauna.

The Afar Depression is the northern point of the East African Rift Valley. This is the area where three tectonic plates meet and are pulling apart – the Red Sea, Gulf of Aden and East African Rift. The fish remains we report here are from Gona, west of Hadar, but are part of the fluvio-lacustrine sedimentary sequences of the western margin of the Afar Depression. Gona is one of a number of areas along the Awash River that sample fluvio-lacustrine environments of the Busidima and Hadar formations. These formations cover approximately three million years of sediments, and are well known for the earliest human stone tools. The fossil fishes from Gona are from several different sites; the majority of the material is from early Pliocene sites, which contain the greatest diversity of fish taxa. There are at least four different genera of fish represented, each in its own family, two different catfishes (Clariidae and Bagridae), a minnow (Cyprinidae), and a cichlid (Cichlidae). These fishes allow us to reconstruct potential migration routes that would have been used not only by fish, but other vertebrates including hominids.

## Abundant juvenile plesiosaur fossils from an upper Campanian marine reptile bonebed in Saskatchewan, Canada

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A micro- to macrovertebrate bonebed from the Upper Cretaceous (Campanian) Dinosaur Park–Bearpaw transition of west-central Saskatchewan is dominated by marine reptile fossils, particularly isolated plesiosaur elements. Marine reptile bonebeds are relatively rare in the fossil record, and this site near Herschel, Saskatchewan is particularly noteworthy due to the abundance of juvenile plesiosaur material. Juvenile skeletal elements are recognized by incomplete ossification and lack of fusion between developmentally separate regions of bones, e.g., vertebral centra bearing facets for neural arches, isolated transverse processes with articular rather than broken surfaces, undifferentiated articular surfaces on propodials, and endochondral bone cores separated from cortical bone sheaths. Dozens of vertebral fossils and more than 20 propodial specimens exhibit these indications of skeletal immaturity. While some of the juvenile plesiosaur fossils are too poorly ossified, or too incomplete to allow for taxonomic identification beyond Plesiosauria, certain specimens are diagnostic of Elasmosauridae and Polycotylidae, which parallels the identifications of adult plesiosaur material from the bonebed. The skeletal elements from osteologically immature individuals, particularly the propodials, exhibit a range of sizes and degrees of ossification. This developmental spectrum could offer support for differing hypotheses about the use of the region by the plesiosaurs that inhabited it. If plesiosaurs lived in social groups, the presence of subadult fossils could indicate that individuals remained with a "pod" throughout their lifespan and that pod returned to the same birthing grounds year after year. Conversely, it is possible that the juvenile plesiosaurs remained in this shallow, lagoonal system as they grew before venturing into the open ocean upon reaching skeletal maturity. Regardless of any social system employed by plesiosaurs, this site can be added to the list of shallow water localities hypothesized to serve as marine reptile birthing grounds or refuges for young individuals. Similar concentrations of juvenile material have been reported from Australia, Antarctica, New Zealand, and elsewhere in Canada. These fossils sites were deposited in highly productive marine environments – the high nutrient load being attributed to the cold water at high latitudes or the terrestrial input in estuaries – so the abundance of juvenile material from this site further supports the interpretation of a lagoonal depositional environment for the Herschel bonebed.

### The BC Megafauna Project at the Royal British Columbia Museum: sampling collections for isotopic analysis and radiocarbon dating

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There are few published instances of ice age megafauna in British Columbia, particularly mammoths (*Mammuthus* sp.), when compared to bordering Yukon, Alberta, and Washington State. Due to the scattered nature of these remains across museums and private collections, there are also few radiocarbon dates and isotopic work on BC mammoths. As a result, no synthesis of the quantity or quality of these remains in repositories available for study has occurred, limiting our knowledge of not only western North American mammoths, but also the ecosystems they inhabited. Further, it is hoped new radiocarbon dates will shed light on whether megafauna dates correspond to early physical evidence of humans in the province.

Last summer, the BC Megafauna Project travelled to BC museums to sample ice age megafauna such as bear, bison, caribou, elk, muskox, mastodon, and mammoths for stable isotope analysis and radiocarbon dating. Across museums, mammoths are the best represented, and the bulk of the specimens sampled are housed at the provincial repository, the Royal BC Museum. Forty-five megafaunal specimens from its collections were selected for sampling. All were processed for collagen at the Simon Fraser University Archaeology Isotope Lab, of these, a full thirty retained sufficient collagen and twenty-eight had good carbon/nitrogen collagen results and were sent for radiocarbon dating.

Greater Victoria appears to be a hot spot for megafauna, with many of the sampled specimens found locally. Preliminary isotope values show marked difference from the high nitrogen values seen in Yukon mammoths with lower values common across Vancouver Island. At one Victoria locality, four mammoths had a spread of ~5–9  $\delta$ 15N. Paired with dating, we will determine how separated these nitrogen values are by time, and if other dates can contribute to glacial refugia discussion during the late Pleistocene on Vancouver Island.

## The first record of the hadrosaur *Probrachylophosaurus* in the Foremost Formation, representing the oldest occurrence of a brachylophosaurin in Alberta

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The Belly River Group of Alberta is noted for its abundant fossil record preserving the diverse Campanian palaeocommunities of Alberta. The uppermost Dinosaur Park Formation has the best documented dinosaur assemblages, with the sequentially underlying Oldman and Foremost formations being relatively under-represented in fossils. This is unfortunate because the upper Foremost Formation preserves the first post-Santonian terrestrial sediments following the regression of the Western Interior Seaway (Niobrara Cycle) in the southern part of the province. This severely limits our ability to develop hypotheses regarding the origin and diversification of well-known clades from the upper portion of the Belly River Group.

We report here the first description of the brachylophosaurin hadrosaurid *Probrachylophosaurus* sp. indet from the Foremost Formation. This material represents the first hadrosaurid diagnostic to the genus level from the formation and oldest occurrence of Brachylophosaurini in Alberta. Although all available hadrosaur skeletal material from the formation was examined (mostly isolated elements; no diagnostically informative cranial elements), two specimens were determined to be potentially phylogenetically informative: CMN 58592, a partial skeleton including the right ilium, ischia, pubis, and femur, and TMP 1983.180.0001. The latter specimen was originally considered to be an associated skeleton, but the presence of multiple elements from different size classes indicates that the material is from a bonebed. A third partial skeleton, CMN 9951 (associated left hind limb including femur, tibia, fibula and a partial pes) does not have features diagnostic above the level of family and so was excluded from the analysis. All this material was collected from the upper portion of the Foremost Formation below the Marker A coal zone of the Taber Coal Zone that caps the formation.

Phylogenetic analyses using both PAUP 4.0b10 and TNT 1.1 yielded identical strict consensus tree topologies, including a well-supported Brachylophosaurini. The clade comprising the OTU represented by CMN 58592 plus the OTU represented by TMP 1983.180.0001 was the sister clade to *Probrachylophosaurus*. The clade [CMN 58592 + TMP 1983.180.0001] is supported by six ambiguous characters and one unambiguous character (the angle between the anterior dentary and its contact with the predentary). The CMN 58592 and TMP 1983.180.0001 OTUs are each supported by different unambiguous characters: a completely enclosed obturator process foramen and the dentary-predentary angle, respectively. However, as both of these features are known to change ontogenetically in hadrosaurs, we consider the CMN 58592 and TMP 1983.180.0001 OTUs to be indistinguishable from each other and *Probrachylophosaurus*.

The *Probrachylophosaurus* sp. indet. material described here occupies an intermediate stratigraphic position between other Campanian brachylophosaurini hadrosaurids. Below it is *Acristavus gagslarsoni* (~81 Ma) from the Two Medicine and Wahweap formations of Montana and Utah, while the holotype and only know specimen of *Probrachylophosaurus bergei* (79.5 to 79.2 Ma) is stratigraphically younger, occurring only a few meters above the Marker A coal zone in the equivalent beds of the Judith River Formation just across the border in Montana (Freedman Fowler and Horner 2015).

Although North American brachylophosaurins are confined to the Campanian, the presence of the brachylophosaurin, *Wulagasaurus dongi*, from the Maastrichtian Yuliangze Formation (approximately 69 Ma) of China, suggests that this taxon may be a Late Cretaceous immigrant back to Asia (Godefroit et al. 2008). If this is the

case, then there is a significant gap in the brachylophosaurin fossil record that can only be reconciled by the discovery of new material.

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### Phylogenetic relationships of the herring superorder Clupeomorpha (Teleostei) with implications for key trait evolution within the group

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The Clupeomorpha is a group of teleost fishes that includes over 500 living and fossil species traditionally divided into the extant order Clupeiformes (herrings and allies) and the extinct order Ellimmichthyiformes (double armoured herrings). Members of this group have a worldwide distribution and occur in marine, freshwater, and brackish environments, with some representatives of the group undertaking seasonal migrations between marine and fresh waters. Such ecological diversity and plasticity may account for the evolutionary success of these fishes that have a fossil record of over 130 million years. Additionally, clupeomorphs are commercially significant fish, contributing almost a quarter of the total world fisheries catch.

Despite their abundance and economic importance, clupeomorphs remain surprisingly poorly known with little understanding of their evolutionary history. Morphological studies of the Clupeomorpha were conducted over 30 years ago and did not fully resolve evolutionary relationships, nor were they performed using current methods of cladistic analyses. The most recent classifications on the other hand are based on molecular data which prevent fossil members from informing phylogenetic relationships in these studies.

Here, I present the first comprehensive cladistic analysis of the Clupeomorpha including representatives of all major extant and extinct lineages at the species level. The data matrix constructed for this study integrates morphological and molecular data with the morphological character list thoroughly revised and updated based on the previously published studies and personal observations of the specimens. I analyse the newly constructed data set using multiple phylogenetic inference methods (equal and implied weights maximum parsimony, Bayesian inference) to address questions of monophyly of the traditionally recognized clupeomorph lineages. I also provide a time-calibrated phylogeny with the estimated divergence times that points out some key events in the evolutionary history of the group.

Results of our phylogenetic analysis indicate considerable congruence of the phylogenetic signals in the morphological and molecular data sets. Unexpectedly, most analyses do not recover the extinct ellimmichtyiforms as a sister group to the Clupeiformes, but rather as a sister clade to the herring family Clupeidae. The denticle herring (Denticipitidae) is consistently recovered as the earliest clupeomorph lineage followed by anchovies (Engraulidae), and long-fin herrings (Pristigasteridae). The recovered evolutionary relationships among the clupeomorph lineages provide new insight into the trait evolution within the group, such as the cranial sensory system and body scute armour.

## The diverse faunal assemblage of the *Acheroraptor temertyorum* holotype locality from the Hell Creek Formation of Montana, USA

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Our understanding of the ecology and evolution of ancient ecosystems is based on the holistic study of productive fossil localities. One of these localities is the Acheroraptor temertyorum holotype locality (AHL) from the Upper Cretaceous Hell Creek Formation of Montana. Several scientifically important fossils already known in the literature have originated from this locality. Acheroraptor temertyorum (Evans et al. 2013) was the first significant dromaeosaurid cranial material from the Maastrichtian of North America. The AHL has also produced the ontogenetically youngest known Pachycephalosaurus wyomingensis cranial material (Goodwin and Evans 2016). Here we add to the scientific value of this latest-Cretaceous palaeocommunity by updating the stratigraphic placement of the AHL and reporting new macrofossil and microfossil material. Our revised stratigraphy and palynological samples place the AHL within the lower half of Hell Creek Formation, rather than the upper Hell Creek Formation originally reported. New macrofossil material includes three manual phalanges and one claw representing the first known postcranial material of A. temertyorum. The pachycephalosaurid Sphaerotholus buchholtzae is represented by two fronto-parietals and three squamosals, the caenagnathid Anzu wyliei is represented by a dentary, and the crocodilian Borealosuchus sternbergii is represented by the posterior portion of the skull. The surface collected microfossil assemblage of the AHL contains at least 17 species representing Chondrichthyes (Myledaphus pustulosus), Actinopterygii (Acipenseridae, Lepisosteidae, Holostean A, and Amiidae), Lissamphibia (Scapherpeton sp. and Anura indet.), Testudines (Baenidae, Chelydridae, Adocidae, and Basilemys sp.), and Dinosauria (Hadrosauridae, Ceratopsidae, Tyrannosauridae, Oviraptorosauria, Dromaeosauridae, and Troodontidae). The presence of salinity-intolerant lissamphibians and the absence of sharks indicate the AHL assemblage preserves a non-marine environment. The AHL continues to contribute important material for enriching our understanding of latest-Cretaceous palaeobiology.

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# Variation or evolution? Assessing the significance and validity of *Styracosaurus ovatus* within Eucentrosaura (Ceratopsidae: Centrosaurinae)

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Ceratopsids are among the most ubiquitous dinosaur taxa from the Late Cretaceous terrestrial formations of the Western Interior of North America, comprising two subfamilies, Chasmosaurinae and Centrosaurinae. The Campanian Two Medicine Formation of northwestern Montana has produced numerous remains of centrosaurine dinosaurs, representing four taxa: Styracosaurus ovatus, Einiosaurus procurvicornis, Achelousaurus horneri, and a new, unpublished taxon. A recent study (Holmes et al. 2020) proposed that the type specimen of Styracosaurus ovatus (USNM 11869) falls within the range of variation of Styracosaurus albertensis, and is therefore a junior synonym of S. albertensis. However, the study by Holmes et al. (2020) includes a survey of individual character states that overlap between S. ovatus and S. albertensis, and infers a broad range of possible morphologies for the diagnostic parietal ornamentation of a single centrosaurine taxon. While our study agrees that the generic name 'Rubeosaurus' is unnecessary, we retain S. ovatus as a valid taxon. USNM 11869 was collected from the uppermost Two Medicine Formation of Montana from the Landslide Butte area, and while the precise stratigraphic location of USNM 11869 is unknown, this region of Two Medicine Formation exposure preserves radiometric dates about 800,000 years younger than the upper temporal range for Styracosaurus albertensis (Fowler, 2017). Holmes et al. (2020) identified exceptions to the typical diagnosis of S. albertensis (e.g., lack of P1 is an exception to the typical condition of S. albertensis), which match the morphology of USNM 11869 for individual characters, but nonetheless remain outliers compared to specimens like the holotype of S. albertensis. In contrast, features such as the lack of P1 processes are the typical condition in the eucentrosaurans of the younger strata of the uppermost Two Medicine Formation, rather than the exception, and other character states such as degree of elongation of the P5 and P4 processes follow a strongly stratigraphic trend, demonstrated in our present study. This indicates that evolutionary change may be responsible for these differences between specimens of S. albertensis and the type specimen of S. ovatus, rather than variation within a single species. In order for S. ovatus and S. albertensis to be considered one taxon, this taxon must express both large P1 processes and completely absent P1 processes, large and hook-like P2 processes and diminutive P2 processes, and fully-elongate P5 processes and minimally elongate P5 processes. Additionally, factors such as ontogeny and stratigraphic placement have not yet been accounted for in each specimen included in the assessment of S. albertensis variation, leaving ambiguity to the cause of the apparent pattern of wide morphological variation. Variation within a single taxon would most meaningfully be invoked within a contemporaneous breeding population when temporal change is not a factor, and when controlling for other affecting factors such as ontogeny. Alternatively, our study demonstrates that through the stratigraphic record of the Two Medicine Formation, eucentrosaurans progressively reduce the degree of elongation of P5 and P4, and lack P1 processes; therefore, because S. ovatus comes from younger strata than S. albertensis and likewise appears to follow the trend of P1 elimination and P5 length reduction, we entertain a second working hypothesis and consider the *S. ovatus* morphology reflective of evolutionary change rather than variation within *S. albertensis*, and we retain *S. ovatus* as valid.

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### A differentiation of soft tissues based on enthesis associated collagen fiber arrangement at the bone surface with implications for paleontological soft tissue reconstructions

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In the absence of direct preservation, the evaluation of a fossil organism's soft tissue anatomy can be a daunting task. Studies that aim to evaluate fossil soft tissues often must rely on clear osteological correlates, such as muscle scarring and minute striations on the bone surface. These osteological correlates are formed at the site of attachment of soft tissue to bone, called entheses. The evaluation of these correlates is often coupled with the use of an extant phylogenetic bracket in order to constrain speculation. However, even in large-bodied, adult organisms there is a large volume of soft tissues that do not leave clear osteological correlates. Furthermore, some fossil taxa are so phylogenetically removed from their extant bracketing taxa that it calls into question whether there is a reasonable comparison to be made. We have shown that with the use of scanning electron microscopy it is possible to identify areas of soft tissue attachment on the bone surface in the absence of osteological correlates that are visible with the naked eye. There is also differentiation between soft tissue type (muscle, tendon, cartilage, aponeurosis) in the presence of, or manner in which collagen fibers are incorporated into the bone tissue at entheses. At cartilaginous entheses these collagen fibers are not incorporated into bone tissue, leaving the surface relatively smooth but with small, organized hummocky structures. Areas of direct muscle attachment are generally planar, but with occasional spider-like projections where the collagen fibers have been incorporated into bone tissue. Tendinous entheses are areas where long string-like collagen fibers have been incorporated into bone tissue, usually within concave impressions on the bone surface. These areas are generally more organized than other entheses. Lastly, aponeurotic entheses are large areas of thick, high density, disorganized collagen fibers. All four categories of entheses have been observed through broad taxonomic sampling using extant organisms, though the same signal is also seen in three-dimensionally preserved fossil specimens. Based on this qualitative differentiation of enthesis categories, a database of over 2000 images were generated in order to train a custom image recognition artificial intelligence program. This allows for the quantitative assessment of the difference and morphological distance between these attachment site types.

### Ontogenetic niche shifts in hadrosaurids of the Late Cretaceous of North America

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Most research on hadrosaurid ontogeny has focused on the development of cranial ornamentation, but few studies have considered the dietary implications of growth. In modern ecosystems, size differences facilitate resource partitioning both between and within species. Many extant reptiles that experience long growth trajectories undergo ontogenetic niche shifts (ONSs) wherein different ontogenetic stages occupy different ecological niches. These niche shifts are typically facilitated by differences in size, and are accompanied by allometric growth within the skull. Given that hadrosaurids experienced long growth trajectories, it is likely that they also underwent ONSs.

We investigated skull allometry among hadrosaurids using 12 linear measurements known to correlate with feeding ecology in living vertebrate taxa. We also applied a univariate measure of beak shape, and traditional methods for dental microwear analysis. Our results show that juvenile hadrosaurids differed from adults in their possession of relatively shorter, less ventrally depressed rostra, and squatter occiputs. The shorter occiputs of juveniles suggest that they did not require sharp backward/upward movements of the head to sever vegetation. Instead, the young may have subsisted on softer vegetation that required little effort to pluck. The shorter, smaller rostra of juveniles would have made them more selective than their adult counterparts, making it easier for juveniles to feed on this softer vegetation. Dental microwear analysis yields no statistical differences in relative pit/scratch counts (likely as a result of small sample sizes). However, a comparison of scratch distributions reveals greater variability in juvenile scratch orientation. This may indicate that juvenile skulls were more kinetic than those of adults, possibly due to the presence of more cartilage and/or lack of sutural fusion in juvenile skulls.

Our results suggest that juveniles were better equipped to pluck soft, low-growing vegetation while adults were able to access vegetation of various mechanical resistances growing at various different levels, but more data are needed. This study is one of few to assess the dietary implications of growth in dinosaurs and may have important implications for the structuring of dinosaur communities with juvenile hadrosaurids being potentially key competitors for small-bodied ornithischian taxa.

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