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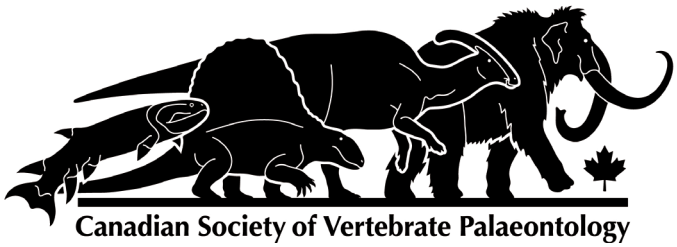
Meeting Logo Design: Many thanks to Brigid Christison for creating our 2022 CSVP logo!

Brigid explains her creative take on the design:

This year's CSVP logo is an embroidery of the holotype skull of *Parasaurolophus walkeri*, chosen coincidentally in honour of the 100th anniversary of the species being described. The majority of the piece is chain stitch, except for the leaves and skull sutures which are satin stitch. The main colour is ecru, or undyed, meant to mimic fresh bone tissue, and the chain stitching follows the contour directions of the different bones.

This is CSVP's first textile logo, a choice that might seem strange given the all-digital nature of the rest of the conference. Since moving to virtual platforms and physical separation, craft has become increasingly important as a tool for self-expression, mental health, and concentration. As our colleagues try new skills and share their creations, it's a reminder that we each have the capacity to learn and create in many different ways.



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10th Annual Meeting Canadian Society of Vertebrate Palaeontology

May 24–25, 2022

Online

Abstracts

Message from the Organizing Committee

Hello to all CSVP members in Canada and around the world:

We are now in year three of the pandemic. Given the uncertainty that still surrounded travel earlier in the year, CVSP chose to once again host the annual meeting remotely. Thanks to more than two years' worth of practice using Zoom, our meeting went smoothly through this platform. The success of the meeting highlighted the fact that even in the face of a lingering pandemic, our palaeontological community is resilient and continues to do impressive work. We were happy to see some research groups watch presentations together, a small step towards gathering fully in person next year!

The CSVP 2022 meeting was held on May 24–25th, following a keynote lecture by Nussaïbah Raja Schoob from the University of Erlangen-Nuremberg, Germany, highlighting the role of colonialism in palaeontology, and how we can address this and similar issues moving forward. This was a particularly illuminating talk for our members, given the society's recognition of our responsibility to address historical inequities here in Canada and in our field more generally, and our society's commitment to support Equity, Diversity, and Inclusion (EDI) initiatives, notably the new award available to members.

Although we all miss the joys of gathering in person, holding the CSVP meeting remotely in 2021 and 2022 offered an opportunity for higher student and international participation. During our AGM following this year's meeting, the CSVP decided that options for hybrid meetings will be explored for future meetings. We are grateful we could reconnect with each other while staying safe.

Your Virtual Organizing Committee,

Emily Bamforth
Kirstin Brink
Thomas Cullen
Thomas Dudgeon
Danielle Fraser
Greg Funston
Zoe Landry
Talia Lowi-Merri
Annie McIntosh
Jason Pardo
Mark Powers
Yan-yin Wang
Misha Whittingham

TABLE OF CONTENTS

Understanding the developmental mechanisms involved in the evolution of the unique skull–neck boundary region in lissamphibians

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The fossil record reveals a long history of morphological transformations throughout evolutionary time. Although these morphological transformations are captured in the fossil record, the developmental mechanisms underlying such transformations are less understood. Studying the underlying developmental mechanisms requires an integrative approach combining developmental and palaeontological data. This approach has been immensely fruitful in interpreting large scale evolutionary patterns. Unfortunately, the developmental mechanisms that drove many key morphological transformations, such as the apparent shift in the location of the skull–neck boundary, are not well understood. Developmental work completed in the twentieth century revealed that both amphibians and amniotes incorporate more somites, mesodermal building blocks of embryos, into the head than living agnathans, and it was thought that amphibians represented an intermediate condition between the two. More recent work synthesizing palaeontological, phylogenetic, and developmental data has clarified that the extant amphibian condition is instead a secondarily derived reduction from an ancestral condition that was likely more amniote-like. This derived condition has been hypothesized to be the product of an anterior shift in the location of the skull–neck boundary along the anterior–posterior axis relative to their fossil ancestors and other tetrapod lineages. Here, we aim to further understand the potential evolutionary mechanism that gave rise to the derived lissamphibian condition via the manipulation of Hox gene expression domains in amphibian model organisms *Ambystoma mexicanum* and *Xenopus laevis*. We applied exogenous retinoic acid and a retinoic acid inhibitor to embryos, which resulted in the translocation of the skull–neck boundary anteriorly and posteriorly, respectively. We demonstrated that homeotic transformations occurred via two methods of evaluation, the relative location of the hypoglossal nerve complex (cranial nerve twelve) to skeletal structures and cell-lineage tracing of somites. Significantly, anatomical details of the resulting phenotypes mimic skull–neck boundary morphologies observed in other tetrapod groups. This work suggests homeotic transformations and correlated genetic modifications may have played a role in the evolution of several aspects of the lissamphibian skull form.

A new, large specimen of *Prognathodon overtoni* (Squamata, Mosasauridae) from Grasslands National Park, Saskatchewan

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The Late Cretaceous mosasaur *Prognathodon* has a global distribution, with specimens found in Campanian and Maastrichtian marine deposits in Europe, New Zealand, North America and the Middle East (Schulp et al., 2008). With its large body size, blunted snout, and massively built jaws, the animal has earned the moniker '*T. rex* of the Sea'. Despite its size and robustness, *Prognathodon* is known primarily from fragmentary remains (Konishi et al., 2011). Exceptions to this include two articulated skeletons of *Prognathodon overtoni*, TMP 2007.034.0001 and TMP 2002.400.0001, recovered from the Campanian Bearpaw Formation (ca 74.5 Ma) of southern Alberta and described by Konishi et al. (2011). Until recently, this rare genus had not been reported from marine deposits of comparable age in Saskatchewan. Herein is described the first partial skull and post-crania of *Prognathodon overtoni* in Saskatchewan, a specimen which may prove to be the largest individual recovered in Canada.

The specimen was initially discovered by a local landowner in 2012 on land that would soon become part of the West Block of Grasslands National Park near Val Marie, SK. The deposits in the West Block are dominated by loosely consolidated, evaporite-rich, grey marine shales of the Bearpaw Formation (ca. 75-73 Ma), overlain in places by the deltaic deposits of the Eastend Formation. The landowner who made the initial discovery found several large fossils on the surface and contacted the Royal Saskatchewan Museum (RSM). The RSM investigated the discovery the following year but, under the conditions of the collection permit attained through Parks Canada at the time, could only collect material on the surface. During this initial collection, several vertebrae, dentary and maxilla fragments, ribs fragments, and paddle elements were recovered. The skull material was diagnostic enough to determine the specimen represented Saskatchewan's first *Prognathodon*, but a return to the site was not feasible for several years. A site check in 2020 revealed that more cranial material eroding onto the surface and a collection permit was obtained to excavate in 2021.

In September 2021, the RSM began excavating and almost immediately discovered two near-complete maxillae, an angular and subangular, partial dentary, and parts of the frontal, post-frontal, parietal, and quadrate. Three cervical vertebrae were also recovered. Of note to the excavators was the size of the teeth which, at an average length of 5 cm and circumference of 2 cm, were similar in size to those of *T. rex*.

When the specimen, RSKM P3194.1, was prepared and assembled, incorporating specimens collected in the earlier 2013 collection, the skull was measured to be 130 cm in length. This is considerably larger than the two Albertan specimens described by Konishi et al. (2011), which had lengths of between 80 and 90 cm. Extrapolating to body size, the animal is estimated to be 10 m in length, making it the largest *Prognathodon* found in Canada to date. Continued preparation of the cranial material, and further excavation of the West Block site are required to recover more information about this remarkable specimen.

This discovery may contribute to the understanding of *Prognathodon* paleoecology. Three other mosasaur species are found the Bearpaw Formation of Saskatchewan, including the smaller *Mosasaurus missouriensis* and *Plioplatycarpus* sp. and the larger *Tylosaurus saskatchewanensis* (Jiménez-Huidobro et al., 2018). These four genera shared the shallow marine eco-space, presumably exploiting different food sources and/or utilizing different life history traits. Understanding mosasaur niche partitioning, particularly among the two largest mosasaur species, may provide critical insight into the ecology of Cretaceous marine environments.

Figure 1. Right maxilla of RSKM P3194.1, a large specimen of *Proganthodon overtoni* from Grasslands National Park, SK.

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Redescription of the first mammoth tooth from the Québec-Labrador-Nunavut Peninsula and its implications for biogeography

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A heavily worn mammoth (*Mammuthus*) molar was discovered on Long Island, Nunavut in 1878. It is the only mammoth fossil from the Quebec-Labrador-Nunavut Peninsula. The specimen was originally identified as an upper premolar or molar stump of a Columbian mammoth (*Mammuthus columbi*) by Robert Bell in 1898. However, re-examination of the specimen's morphology helps classify the Long Island tooth instead as the stump of a last molar of a woolly mammoth (*Mammuthus primigenius*). The keel-shaped single root of the stump demonstrates it is a last molar and not a multiple-rooted premolar. This reclassification of tooth type puts the tooth's plate frequency and enamel thickness in the range of variation for a heavily worn woolly mammoth tooth and less

so for that of a Columbian mammoth tooth. Reconstructions of Long Island's grassland-like paleoenvironment, a habitat woolly mammoths were best adapted to, and a survey of other northeastern mammoth finds, most of which are woolly mammoths, provides additional circumstantial evidence that the tooth belonged to a woolly mammoth. In sum, this tooth extends the confirmed range of the woolly mammoths northward in eastern North America by several hundred kilometers. It also offers insights into the palaeoenvironmental range of this species. Ongoing palaeoclimatic and palaeofloral reconstructions of the region likely expand both the climatic and dietary tolerances of woolly mammoths. Finally, this large geographic range increase suggests the sparse Quaternary megafaunal record of the Quebec-Labrador-Nunavut Peninsula may hold more remains than previously thought over this poorly prospected region.

The Early Cretaceous Paja Formation biota in Colombia reveals an exuberant predator fossil record and a complex ecological network

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Few fossil assemblages have been used to reconstruct ecological networks of trophic interactions. Over deep time, they can be integrated with phylogenetic originations and extinctions to present larger-scale interpretations of ecological evolution. Here we present preliminary results on an ecological network for the marine Paja Formation fauna. The Paja Formation was deposited over 15 million years throughout a sequence spanning the Hauterivian through to the Aptian in central Colombia. The Early Cretaceous was a transitional period in Earth's history and of significant importance in terms of faunistic turnovers. This time represents the recovery of the end Jurassic mass extinction, high eustatic sea levels, and high global temperatures — all factors that are expected to facilitate high levels of phyletic radiations. The Paja Formation preserves a rich marine fauna and outcrops extensively around Villa de Leyva, Boyacá. This formation is subdivided into several units, including the highly fossiliferous *Arcillolitas abigarradas* member. This unit preserves several species of marine invertebrates and vertebrates. The invertebrate fauna consists of over one hundred species of ammonites and several bivalves and crabs. The vertebrate fauna includes massive short-necked plesiosaurs, large elasmosaurs, a teleosauroid crocodylomorph, several species of ichthyosaurs, several sea turtles, and at least four morphotypes of actinopterygian fish and one shark. The ecologically complexity of this palaeoecosystem hints at what this ecological network may look like. Several apex predators with ~10 m body lengths include the pliosaurs *Kronosaurus* (=*Monquirasarus*) and *Sachicasaurus* and a teleosaur. Mid-sized predators of > 4 m include the pliosaurs *Acostasaurus* and *Stenorhynchosaurus* and the ichthyosaur *Kyhytysuka*. Another trophic level can be constructed from the large-bodied but small headed elasmosaurs and stem sea turtles *Desmatochelys*, and *Leyvachelys*.

Although the Paja's biota is most famous for its large marine reptiles, little is really known about the broad ecological structure of the ecosystem. We are currently reconstructing an ecological network of the Paja Formation biota incorporating interactions between all described and undescribed taxa based on criteria such as body size, tooth guild, tooth size, jaw length, skull attributes, and postcranial attributes, which we consider as proxies for describing network linkages between species. These interactions inform us about the trophic functioning of the

system, including the predator-prey interactions, the potential resources needed to maintain apex predators, potential energy flow across the chain, and estimates of ecological complexity. Although the fishes are relatively poorly known, the complex network constructed from the ammonites suggests an equally impressive network of fishes. This exercise also reveals several potential confounding factors such as taphonomic and sampling biases. Our preliminary results reveal a complex Paja ecosystem network. We explore its utility to understand the resilience of marine ecosystems after mass extinctions (i.e., J/K mass extinction) and the stability of the emerging Paja ecosystem that has similarities to those that dominated the remainder of the Cretaceous marine systems for the next 50 million years.

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Of drones and dinosaurs: a new Geographic Information System for the Belly River Group of Dinosaur Provincial Park based on aerial orthomosaics

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One of the major challenges in studying the evolution of ancient ecosystems through the fossil record is obtaining a sufficiently high temporal resolution to reduce the impacts of time averaging on our interpretation of observed patterns in climate and/or biodiversity. The Campanian Belly River Group (BRG) outcropping in Dinosaur Provincial Park, Alberta, constitutes an ideal study system to fulfill this objective. This is due to a very high vertebrate diversity represented in its fossil record combined with sedimentological evidence of environmental change over a relatively well-constrained time interval. However, a sequence stratigraphic correlation for all of the Park's quarries has proved elusive thus far, largely because of an apparent lack of lateral continuity in several lithological units formed during cycles of channel cutting and filling. Here, we attempt this stratigraphic correlation not from the ground, but from the air.

We propose the creation of a Digital Elevation Model (DEM) and of orthomosaics of all 75 km2 of BRG outcrops in Dinosaur Provincial Park (DPP) to facilitate the detection of marker beds over longer distances than

what has previously been achieved. We have started to create this alternate map of DPP by capturing over 30,000 images with six multirotor survey drones covering approximately 6 km2 of contiguous outcrops during the 2021 field season. Various selections of these images were aligned by photogrammetry using Pix4Dmapper and Pix4Dmatic to create three-dimensional georeferenced point clouds of a section of DPP. The geolocation accuracy of the models was increased by marking ground control points with a GPS receiver in the field. These 3D models enabled the creation of DEMs, which in turn enabled the creation of orthomosaics in which the varying distances of the drones' cameras relative to the uneven terrain of the DPP badlands for each photograph were accounted for. Thus, vertical and horizontal distances on these new photographic maps were corrected for perspective. All GeoTIFF files were then visualized in QGIS, where the observation of DPP's geology and the identification of candidate marker beds has recently begun.

This image dataset is the most recent contribution to a new Geographic Information System (GIS) for DPP that also includes an updated database of all its fossil occurrences. A variety of challenges were encountered during the project, such as geolocation accuracy, taphonomic biases, the complexity of the BRG outcrops' sedimentary structure, logistical constraints in the field and computing power. However, we expect it to deliver significant outcomes for future geological and palaeoecological studies of this fossil locality. Firstly, the 2 cm2/pixel resolution of the latest obtained orthomosaic constitutes an upgrade on an earlier photomosaic currently deposited at the Royal Tyrrell Museum of Palaeontology, which reaches a resolution of 6 cm2/pixel. Secondly, a broader overview of the BRG's geology could reveal that the frequent channel downcutting observed throughout this stratigraphic interval interrupts hitherto undetected lithological units that are far more laterally continuous than previously thought. This could lead to a subdivision of the Dinosaur Park Formation into more temporally constrained members. Thirdly, it provides additional geological context to all the quarries whose previously estimated stratigraphic positions only accounted for an estimated height relative to the nearest recorded formational contacts. We therefore expect the results of this project to further constrain the stratigraphic position of each of DPP's known fossil quarries, to reduce uncertainties in the stratigraphic distributions of the vertebrate taxa from the DPP fossil record, and ultimately lay a more solid foundation for testing hypotheses of biotic turnover and climate change in this ancient terrestrial ecosystem.

Calvarial suture interdigitation suggests supracranial crests modified feeding mechanics in hadrosaurids (Ornithischia: Ornithopoda)

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Lambeosaurine hadrosaurs exhibited extreme modifications to the arrangement of the facial skeleton, where the premaxillae, nasals, and prefrontals were modified to form and support their iconic supracranial crests. This morphology contrasts starkly with their sister-group, Hadrosaurinae (=Saurolophinae) which possess the plesiomorphic skull condition and arrangement of bones. Although many studies have discussed anatomical differences between lambeosaurine and hadrosaurine skulls, in addition to lambeosaurine crest ontogeny, there is an absence of information detailing suture modification through ontogeny in hadrosaurids, where one might predict significant developmental changes due to the extreme cranial ontogeny in lambeosaurines. Suture morphology has

become an increasingly prevalent tool in the last few decades because of its close relationships with mechanical loading while feeding. Here, we contrast the morphology of interfrontal and frontoparietal sutures in lambeosaurines, hadrosaurines, and basal iguanodontians, to provide an ontogenetic and evolutionary context for suture interdigitation. We employed the suture sinuosity index and a windowed short-time Fourier transformation with a power spectrum density estimate, which together elucidate differences in suture sinuosity and morphology between the frontal and parietal bones in iguanodontians. We found that suture sinuosity clearly increases through ontogeny in iguanodontians, though this increase is far more extreme in lambeosaurines than hadrosaurines and basal iganodontians. No significant differences were found between hadrosaurines and basal iguanodontians. Similarly, lambeosaurines have more complex suture features than hadrosaurines and basal iguanodontians, while the latter two groups show no difference. Interestingly, suture complexity was not found to change significantly through ontogeny in any group. Taken together, these results suggest that the calvarial sutures of lambeosaurines are more interdigitated than other iguanodontians, and although suture sinuosity increased through ontogeny, overall suture morphology remained consistent. These ontogenetic and phylogenetic patterns in Iguanodontia strongly suggest that increased suture sinuosity observed in lambeosaurines coincides with supracranial crest development, indicating that the development of these crests may have significantly altered the distribution of mechanical stress through the skull while feeding.

Tyrannosaur forelimb reduction is not linked to large body size

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The peculiarly short forelimbs of tyrannosaurid theropods, including the famous *Tyrannosaurus rex*, have generated considerable debate and speculation about their functions and the causes of forelimb reduction. Emphasis is often placed on the negative relationship between the length of the forelimb and body size in theropods, and this allometric pattern has been historically linked with the short arms of tyrannosaurids. However, little is known about forelimb scaling through ontogeny or evolution in large-bodied tyrannosaurids, and even less is known about how forelimb length evolved in the broader Tyrannosauroidea, which includes small-bodied antecedents. Here, we evaluate forelimb scaling across Tyrannosauroidea, using one of the largest fossil theropod datasets to date (n = 279; 50 tyrannosauroids), to assess the link between body size and forelimb length in this group. We used bivariate regressions of each of the forelimb bones and femur to evaluate ontogenetic allometry at the genus level and among progressively more inclusive tyrannosauroid clades. We find divergent trends between early-branching tyrannosauroids and tyrannosaurids, which, surprisingly, each exhibit isometric patterns at both evolutionary and ontogenetic scales. Whereas basal tyrannosauroids retain the plesiomorphic scaling of other non-avian theropods, the short arms of tyrannosaurids result from a change in intercept, rather than growth coefficient—in effect, the arm became significantly shorter at all body sizes [df = 9.4534; t = 9.196; p <0.001]. We further show, using ancestral state estimation, that this transition was likely to have occurred in the Early

Cretaceous at small body sizes, during the myriad changes that established the tyrannosaurid bauplan. Among tyrannosaurid genera, negative forelimb allometry occurs only in the ulna of *Tarbosaurus* and the humerus of *Tyrannosaurus*, suggesting independent derivation of negative allometry in these two taxa. Nonetheless, these negative allometric trends cannot account for the short arms of these taxa, and instead represent variations on a theme established far earlier. Overall, these results refute the idea that short forelimbs in tyrannosaurids are linked to their large body sizes. Instead, our findings indicate that tyrannosaur forelimbs grew isometrically and were shortened at small body sizes in a restricted tyrannosaurid clade. This has ramifications for speculation on the causes and processes that led to forelimb shortening in tyrannosaurids.

Survey of metatarsal paleopathologies in Coelurosauria from the Dinosaur Park Formation

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By capturing moments in time in an animals life, and recording evidence of strain, wear, and tear, paleopathologies provide a unique window into the lifestyles of extinct animals. While these are well-reported among theropods, the bulk of the literature are case studies, and literature reviews. Few studies have investigated the rate of occurrence within particular taxa or assemblages, and even fewer on a specific morphological feature. In the Dinosaur Park Formation, four taxa (Caenagnathidae, Ornithomimidae, Troodontidae, Tyrannosauridae) exhibit the arctometatarsalian morphology associated with increased gracility, which will be compared with a non-arctometatarsalian taxon: Dromaeosauridae. In an opportunistic survey of the collections of the Royal Tyrrell Museum of Palaeontology (RTMP) and the University of Alberta Laboratory of Vertebrate Palaeontology (UALVP), all metatarsals that could be identified and sided were scored for the presence of pathology, location, and simple type (proliferative versus lytic). Preliminary descriptive statistics and two-way tests were utilized to examine significant deviations from overall occurrences that define different groups and/or morphologies. Several pathologies were observed in all groups, with tyrannosaurs having the highest occurrence rate followed by troodontids. All taxa except Caenagnathidae were most afflicted on metatarsal II. A wide range of pathologies were observed but they most commonly exhibited reactive growth concentrated in and around the distal ligament pits suggesting a stress-related origin. A few notable specimens were also documented with healed fractures and possible osteoarthritis. This study is the first multi-taxa opportunistic survey of pathology occurrence of a specific hindlimb element within an ecosystem, and the first to investigate the relationship between the arctometatarsalian structure and pathology occurrence.

Evidence of mosasaur migration in the Western Interior Seaway of Manitoba from isotopic studies of dentine

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Mosasaurs were dominant marine reptiles of the Late Cretaceous Western Interior Seaway (WIS) in North America and are notable for having teeth which effectively snagged and crushed prey. Previous oxygen isotopic work on mosasaur enamel in specimens from Alabama and Kansas has suggested that mosasaurs (like modern sea snakes) migrated weekly to bi-weekly from saltwater to freshwater, potentially for osmoregulation. The timing of these freshwater incursions was calculated using incremental growth markers in the dentine, called von Ebner lines (VEL), which are visible through the enamel on the external surface of the teeth. Normal VEL have consistent width, colour, and regularity in mosasaur teeth. However, some teeth when examined in cross section demonstrate abnormal VEL (darker colour, thicker in width and irregular in pattern). In this study, we wanted to determine if 1) a similar pattern of freshwater incursion could be observed in δ18O values of the dentine within mosasaurs originating in Manitoba, and 2) if the abnormal VEL could be correlated with freshwater incursions, suggesting a relationship between water chemistry and dentine development. To achieve our goal, we measured the oxygen isotopic composition of dentine along transects of sectioned teeth, using the in situ analytical capabilities of Secondary Ion Mass Spectrometry (SIMS). To minimize the potential effects of diagenesis, as is typical in dentine, the specimens were mapped using Electron Probe Microanalysis (EPMA) and Scanning Electron Microscopy (SEM) to identify areas of dentine devoid of visible tubule and crack infilling with rimming. Oxygen isotopic patterns in dentine suggest a potential migratory pattern similar to previously reported patterns in enamel. The potential migratory pattern follows a semi-regular δ18O pattern of sharp decreases paired with an increase in δ18O values. The periodicity reported in the Alabama and Kansas studies suggests bi-weekly to weekly osmoregulatory trips while the pattern identified within the dentine suggests a semi-monthly requirement for freshwater intake. However, these patterns do not correlate with abnormal VEL formation. The average values obtained through oxygen isotope analysis from the Manitoba mosasaurs are most similar to those of the Kansas specimens at ~17.1‰ and ~17.4‰, which is likely due to the animals living in similar open marine and/or nearshore environments in the central WIS. Future work will determine if the formation of abnormal VEL is due to other biological processes affecting tooth development or if they are simply the result of the fossilization process.

Preliminary marine biostratigraphy of the upper unit of the Pembina Member of the Pierre Shale in Manitoba

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The Pembina Member of the Upper Cretaceous Pierre Shale in Manitoba has provided Canada with a vast collection of marine reptile fossils since their first discovery in the province by C.M. Sternberg in 1934 (Graham 2009). Most of the specimens were collected during the 1970's and 1980's when the Pembina Member was

mined locally by Pembina Mountain Clays for the calcium bentonite deposits common throughout the lower portion of the member (Duda and Hatcher 2011). Many of these salvaged vertebrate marine reptile specimens are in museum collections across Canada today, representing a collection bias to the lower portion of the member (Nicholls 1988). In addition, due to the salvage nature of the fossil collection, important biostratigraphic data for the majority of these specimens has historically been absent from the academic record.

Previous collaborative field studies resulted in the establishment of four subgroups of the bentonite layers throughout the Pembina Member of the Pierre Shale in Manitoba: The Interlayered, or I Beds at the base of the Member; the L Beds; the four Quartet, or Q Beds, and finally the C Beds near the top of the section (Bamburak et al, 2013). The Q Beds are the thickest bentonite layers of the Pembina Member, and it was these four layers that Pembina Mountain Clays were industrially mining. As a result, the majority of the fossil vertebrates representing the Pembina Member of the Pierre Shale from Manitoba are biased to having been collected from the lower shale layers between the L and Q Beds specifically, thus leaving the upper C Beds of the uppermost Pembina Member understudied.

Recent field work in search of new un-mined Pembina Member exposures has resulted in the discovery of an in-situ outcrop of the uppermost Pembina Member of the Pierre Shale. Located in the upland region of the Pembina Mountain area of the Manitoba Escarpment, this site has provided the opportunity to begin detailed fossil collection of the upper unit of the Pembina Member to begin alleviation of the collection bias.

In the carbonaceous shale horizon immediately beneath the C2 bentonite layer are early indications of an abundant fossil bed including fossils from fish, mosasaur, plesiosaur, and squid taxa. The fish taxon *Cimolichthyes nepaholica* (specimen F2021-01A) comprises a solitary fragmented dentary. Approximately 1.5 metres to the north along the same plane, pelvic girdle fragments consisting of the pubis from a large sauropterygian reptile (P2021-01A) were identified. Continuing along northward in the same shale horizon, a partial teuthid squid gladius (SQ2021-01A) was identified, adding a large octopod to the megafaunal biodiversity. The matrix of SQ2021-01A provided additional fish and mosasaur fossils. A single mosasaur tooth and single *Enchodus* maxillary tooth were identified. The selenite encrusted preservation that is typical to fossils from the Pembina Member is also present in each of the specimens and limited classification to the family level for some of the specimens.

While representing only four taxa, these specimens comprise the first preliminary in-situ biostratigraphic record for the uppermost Pembina Member of the Pierre Shale in Manitoba. This evidence supports the shale layer below the C2 bentonite layer as a potential fossil abundant layer of the upper Pembina Member in Manitoba.

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Lower Cretaceous spinosaurid remains of La Rioja (Spain): preliminary results of the Cameros hindlimb

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Review of recent discoveries including new theropod material from the Iberian Peninsula shows that spinosaurids were more common and diverse than previously expected. Its diversity is composed of the recently described *Iberospinus and Vallibonavenatrix, Baryonyx*, and the probable spinosaurid, *Camarillasarus*. Nonetheless, to date spinosaurid skeletal remains have been mainly limited to isolated elements in the Iberian Peninsula.

Findings of spinosaurid remains from the Enciso Group (upper Barremian-lower Aptian) in Eastern Cameros Basin is becoming habitual, with growing interest in these sites for the study of this clade. Here, we describe an associated and nearly complete left hindlimb found in the Enciso Group, which was previously attributed to *Baryonyx*. This specimen was found at La Virgen del Villar-1 site (La Rioja province, Spain) and it consists of a left pubis, right ischium, both femora and tibiae, left fibula, astragalus, calcaneus, metatarsal III, two pedal phalanges and a hallux. Fragments of a neural arch and ribs have also been recovered, presumably from the same individual due to the lack of overlapping material and proximity of the remains at the site. The rounded cnemial crest of the tibia and the hourglass-shaped outline of metatarsal III suggest tetanuran affinities, based on previous phylogenies in early-branching tetanurans. Moreover, the fibular crest extends to the proximal end of the tibia as a low ridge, as in some early-branching tetanurans. In addition to these similarities, the medial epicondyle of the femur is rounded in shape and the medial fossa is shallow, as in Megalosauroidea. The orientation of the long axis of the medial condyle of the femur is posterolateral in distal view, but to a fairly lesser extent compared to *Baryonyx, Suchomimus* and FSAC-KK 11888. The ascending process of the astragalus is very high, similar to those in spinosaurids. All of these comparisons suggest phylogenetic affinities with Spinosauridae.

Preliminary evaluations suggest that this specimen cannot be attributed to any previously described spinosaurid with preserved pelvic and hindlimb elements; it differs from the other spinosaurid taxa in the shape of the pubic boot, the extension and position of proximal articular groove or the orientation of the medial condyle of the femur. Therefore, these remains are tentatively defined as a new taxon in the Iberian Peninsula.

Ecomorphological disparity of the palate and evolutionary paleoecology of early salamanders (Amphibia, Caudata)

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Among modern amphibians, salamanders (Caudata: Urodela) are often chosen as analogues when investigating the paleoecology of early tetrapods, including the potential ancestral group of modern amphibians, Temnospondyli by virtue of a more conservative body plan and more diversified life history strategies (e.g., neoteny, metamorphosis) than anurans and caecilians. Such comparisons, however, are undermined by an unclear evolutionary paleoecology of early salamanders. Most early salamanders, including almost all stem urodeles are exclusively neotenic and aquatic, and are likely subjected to preservational bias. Unlike neotenic taxa, modern metamorphosed species have their ecological preferences decoupled from life history strategy and are able to live in water, on land, or both. Our knowledge of the paleoecology of metamorphosed taxa is often hindered by insufficient taphonomic analyses on fossil horizons with salamander discoveries and by rare preservation of soft anatomical structures (e.g., gill, fin, labial fold) or stomach contents that are usually well-preserved in remains of neotenic taxa. The biggest constraining factor is that reliable ecological indicators have not yet been established from bony skeletons for early salamanders, especially considering that homoplasies are rampant in modern taxa. Our series of studies on the most primitive salamander clade Cryptobranchoidea (Pancryptobrancha and Panhynobia) found that the palate (vomer and parasphenoid) has high morphological disparity. Exploring the constraints on palate morphology and testing if they are ecologically informative in this clade would be helpful to advance our understanding on the evolutionary paleoecology of early salamanders.

Here we conducted statistical analyses on seven non-shape measurements mainly associated with the vomerine teeth and 2D landmark-based geometric morphometric analyses on the shape of the palate across 71 specimens in 36 stem and basal crown urodeles. Based on a time-calibrated cladogram we reveal that the morphospace of the palate is dominated by ecological types when impacts from asymmetry, allometry and phylogeny were sequentially counterbalanced. Five continuous and two categorical non-shape covariate measurements were also demonstrated as reliable ecological indicators for early salamanders by Mann Whitney U tests and Cochran-Mantel-Haenszel statistical tests. Evolutionary rates of the palate and ancestral states of both shape and non-shape variables were reconstructed for groups classified by ecological preferences, life history strategies and taxonomic affiliations. Our evolutionary rate analyses show that basal panhynobians evolves the fastest among all taxa, and the highest evolutionary rate in the palate is located at the sutural areas among the vomer, parasphenoid and orbitosphenoid, which corresponds to the same place enduring the highest stress during feeding as shown in previous biomechanical analyses. Stepwise evolutionary patterns at this sutural area were also identified for early salamanders, where the cultriform process of the parasphenoid is bilaterally widened with limited support from vomer and orbitosphenoid in primitive taxa. In derived taxa, the same process becomes bilaterally constricted and is dorsoventrally "thickened" due to increasing articulations with the vomer and an anteroventral process of the orbitosphenoid. The palate is heavily constrained by feeding mechanisms and balances these constraints with different phenotypic configurations. We show that palaeoecological disparities in early salamanders took place before the Middle Jurassic and that most ecological types in modern salamanders were achieved in the Early Cretaceous.

Our ancestral state reconstruction reveals that the earliest salamanders shared a biphasic ecological preference (aquatic larvae + terrestrial adults) with anurans and caecilians, and thus metamorphosis is significant not only in the morphospace expansion of the palate but also for the rise and diversification of modern amphibians.

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Taphonomy of a monodominant juvenile *Hypacrosaurus stebingeri* (Hadrosauridae: Lambeosaurinae) bonebed from the upper Campanian Oldman Formation at Devil's Coulee, southern Alberta, provides insight into age segregation in hadrosaurs

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Social behavior in young hadrosaurs has been a subject of debate. Some fossil evidence suggests that young hadrosaurs were segregated from older individuals, whereas other evidence, mainly from trackways, indicates they travelled in multigenerational herds with larger, potentially adult, individuals. Taphonomic study of a monodominant bonebed of juvenile *Hypacrosaurus stebingeri* individuals from the Upper Cretaceous (upper Campanian) Oldman Formation at Devil's Coulee in southern Alberta offers an opportunity to shed light on the behavior of young hadrosaurs. The bonebed preserves 174 disarticulated elements, representing both cranial (12%) and postcranial (88%) elements in a well-sorted, fine-grained sandstone. Based on the number of left fibulae and left radii, a minimum of four similar-sized individuals are preserved in the bonebed. The juvenile status of the individuals is inferred based on their small size relative to fully-grown adults and the unfused contact between the neural arches and the centra of the vertebrae. No bones from larger individuals are present in the bonebed. Light skeletal elements, such as vertebrae and phalanges, are under-represented in the bonebed (observed proportion of 70% vs expected proportion of 90%), while heavier skeletal elements, such as limb bones, are over-represented (observed proportion of 30% vs expected proportion of 10%, $\chi 2 = 13.86$, df = 2, p = 0.001). Other than compaction damage, the bones are largely pristine, with less than 20% of the elements exhibiting early stages of abrasion and about 10% exhibiting early stages of weathering. Most (~80%) of the abraded bones are light skeletal elements. Theropod tooth marks are uncommon, being observed on less than 2% of the bones. The consistent taphonomic signature among the skeletal elements indicate that the fossil assemblage was formed as a result of a single event and is not time-averaged. Hydraulic transport and sorting were limited, but sufficient for lighter bones to be preferentially washed away and slightly abraded. The hadrosaur carcasses were exposed for a short period of time shortly after death, causing decomposition, disarticulation, scavenging, and slight hydraulic transport and sorting to occur prior to burial. Based on the matrix encasing the bones, the similar size of the individuals preserved in the bonebed, and the uniformity of the taphonomic signatures of the bone assemblage,

we interpret the Devil's Coulee bonebed to represent a cohort of young *Hypacrosaurus stebingeri* individuals that died together in a single event. The individuals were buried in a river deposit after limited exposure and transport. As such, the Devil's Coulee bonebed supports the hypothesis that juvenile hadrosaurs were segregated from older conspecifics.

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Investigating the reliability of metapodials as taxonomic indicators for Beringian horses

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The metapodials of extinct horses have long been regarded as one of the most useful skeletal elements for assigning specimens to distinct species. However, recent research on both extant and extinct horses has revealed the possibility for plasticity in metapodial morphology, leading to variability within taxa. This calls into question the reliability of metapodials in species identification, particularly for species identified from fragmentary remains. Here, we use ten measurements of hindlimb metapodials from 137 specimens representing four Pleistocene horse species (*Equus lambei, E. scotti, E. verae*, and *Haringtonhippus francisci*) and 66 specimens without proper species identification (designated as *Equus* spp.) from eastern Beringia (present-day Yukon Territory) to test whether there are significant differences in metapodial morphology that supports the presence of multiple species. We then reconstructed the body masses for every specimen to assess the range in body size within each species and determine whether species differ significantly from one another in mean body mass. Our principal component analysis revealed that all metapodial measurements are highly autocorrelated, and that taxonomic groups are based largely on the overall size. Linear discriminant analysis successfully classified identified specimens by species 95% of the time and reclassified the unidentified *Equus* spp. specimens to one of the four species. As expected, many of the smaller specimens were assigned to *E. lambei*, while the largest specimens were identified as *E. verae*. We also found that mean body mass differed significantly among most, but not all, named species. Specifically, mean body mass did not differ between *E. lambei* and *H. francisci* specimens, and between *E. scotti* and the *Equus* spp. group, suggesting a gradation of size in Beringian horses. We suggest that metapodial measurements are unreliable taxonomic indicators for Beringian horses, given the effect of size on taxonomic grouping, the continuous variation in body mass, and the known plasticity in metapodial morphology in modern *Equus*. We thus recommend future studies use more reliable indicators of taxonomy, such as palaeogenomics, to identify late Pleistocene horse species.

An overview of *Edmontosaurus* from the Frenchman Formation: implications for body size variation

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The Late Cretaceous (Maastrichtian) Frenchman Formation of Saskatchewan preserves the last few million years of the Cretaceous period, leading up to the K-Pg mass extinction. In the contemporary Hell Creek Formation of the northern USA, the hadrosaurid *Edmontosaurus annectens* is relatively common. However, hadrosaur fossils are rare in Saskatchewan, represented largely by disarticulated and isolated remains with few cranial elements. Here, we provide an overview of the available hadrosaurid material from the Frenchman Formation and discuss the potential implications that these specimens have on adult body size variation in *E. annectens*. Interestingly, many *Edmontosaurus* specimens from Saskatchewan appear to have a similar, small body size and were originally considered to represent a smaller species of *Edmontosaurus* endemic to the Frenchman Formation (*E. saskatchewanensis*). These specimens were recently reclassified as *E. annectens* after the holotype (CMN 8509) was suggested to be a subadult of this species. Recent work involving histology and scale types in Saskatchewan hadrosaurs has confirmed that one of the small-bodied specimens represents an adult *Edmontosaurus*. It is possible that CMN 8509 and other small specimens from the province also represent small-bodied adults. The presence of much larger specimens and cranial characteristics of a partial skull clearly indicates that typical exemplars of *E. annectens* are present in the formation. The presence of both large and small adult individuals suggests that significant variation in adult body size occurs within *E. annectens*. By histologically studying the age of the smaller specimens from the Frenchman Formation, we can determine if other specimens from the formation also exhibit small adult body sizes. In the future, expanding the scope to specimens from other formations may help confirm if this variation represents a widespread characteristic of *Edmontosaurus*, or something more localized occurring within the *E. annectens* population from the Frenchman Formation.

Whose tooth is this tooth? An exceptionally large crocodyliform caniniform crown from the Maastrichtian Frenchman Formation of south-central Saskatchewan, Canada

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Crocodyliforms were a common component of the latest Cretaceous floodplain ecosystem in north-central United States and southwestern Canada. *Borealosuchus* and *Brachychampsa* are the best represented taxa, known from numerous specimens, some of which are complete. "Thoracosauridae", a group of gavialoid-like crocodyliforms are extremely rare from this region of North America during the latest Cretaceous to early Paleocene, only represented by a few fragmentary individuals in the Hell Creek Formation, possibly due to preferences for coastal habitats. Here we report an unusually large tooth crown collected from a microsite in the Frenchman Formation of Grasslands National Park's East Block in southwest Saskatchewan. Its near conical form, presence of longitudinal striations, and a smooth carina preserved on the lateral-medial axis of the tooth suggest a crocodyliform. The specimen was compared to the large caninform crowns of contemporary *Borealosuchus* and *Brachychampsa* species from other Hell Creek and Frenchman Formation localities, as well those from 'thoracosaurs' and other gavialoid-like crocodyliforms found elsewhere in North America. This specimen surpasses the size of the caninform teeth belonging to the two previously recognized taxa. Additionally, the crown height is much greater than it is basal width and shows a well-developed carina and distinct fine striations on the preserved enamel. This combination of features closely resemble the teeth of 'thoracosaurs', however in the absence of cranial material we refrain from formally referring the tooth to any specific clade. The discovery of this strange tooth sparks discussion about the range of these elusive animals and their implications relating to the extent of the receding interior seaway in Canada prior to the K-Pg extinction.

‘Raking illumination’: shedding light on the utility of feeding structures as indicators of relatedness

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The skeletal fossil record is extremely variable across Pachycormiformes, due primarily to the cline of reduced ossification for increasing adult body size in pachycormid taxa. The smallest specimens tend to preserve completely with full ossification of vertebral centra and scales, whereas the largest rarely preserve more than a few isolated components, with no scales or vertebrae. The considerably expanded (~100+ character) version of the dataset that has been used in a variety of iterations throughout the past decade is notably skewed, with over 75% of the characters based in the skull and almost 8% of the dataset consisting of dental characters in a group that contains a significant tribe of often edentulous suspension-feeders. In order to examine the possible influence of this weighting, the dataset was run both with and without dental characters and the resulting phylogenetic hypotheses generated were then compared. The removal of the dental characters caused a significant change to the phylogenetic positions of the macropredatory genera *Protosphyraena* and *Australopachycormus* moving them into the suspension-feeding group from their previous position as the last Cretaceous representatives of a carnivorous tribe. This placement is consistent with other postcranial similarities between those two taxa and the suspension-feeders. Although this result indicates that carnivory appeared independently in these two predatory pachycormid genera, this is likely to be a more parsimonious explanation than invoking convergence in multiple regions of the skeleton in order to explain the similarities between those two taxa and the ecologically distinct suspension-feeders. This demonstrates the possible consequences of weighting to specific regions of the skeleton within a group with such differential skeletal preservation.

INTRODUCTION

Pachycormids are extinct Mesozoic actinopterygians that are consistently placed near the holostean-teleostean transition and feature the first definitive large suspension-feeding vertebrates. Whereas many suspension-feeding diets are inferred from the fossil record based primarily on a lack of dentition (e.g., Coatham et al. 2020), the evidence for suspension-feeding pachycormids is solidly based on preserved feeding structures, specifically the presence of gill rakers in the branchial basket that are both numerous and ornamented. Gill rakers are branchial structures attached to the gill arches of osteichthyans and selachians that function to protect the soft tissue of the respiratory gill filaments from damage. Although subject to proliferation and ornamentation amongst suspension-feeders, they are not limited to representatives with such diets, being ubiquitous structures in osteichthyans. Both gill raker presence and form can be hard to assess, as in most fossil osteichthyans (i.e., < 1 m standard length = SL) they are both small and delicate. In pachycormids, which demonstrate a cline of reduced skeletal ossification with increasing adult body size for a taxon, the likelihood of these structures preserving is an additional challenge to their potential utility.

Lambers' (1992) pachycormid phylogenetic hypothesis was the first to note gill rakers in the group, featuring a character for the presence of gill raker 'needle teeth', which he scored as being present in two of the eleven pachycormid taxa in his matrix. However, both of these taxa were large (>1 m SL), with no gill rakers being known, whether with or without 'needle teeth', for any of the other pachycormid taxa in the matrix. As gill rakers could rarely be identified in many fossil taxa and the literature on contemporary osteichthyans was replete with examples of environmentally-driven raker plasticity (see Liston 2013 and references therein), Liston (2007) suggested that gill rakers had little utility as a character for cladistic analysis and proposed that the character might therefore skew phylogenetic hypotheses for pachycormids, testing the effect on the results of excluding the character from the existing 16 character dataset for the group.

In 2010, Friedman et al. significantly expanded Lambers' dataset, basing the expansion in large part on that of Hurley et al. (2007), incorporating 15 pachycormid taxa with 93 characters, 69 (74.2%) of which were cranial, nine (9.7%) of those being specifically dental. Subsequently, Friedman (2012) revised the dataset and despite the variable preservation across the group, 77% of the 121 characters are cranial, of which nine deal with tooth absence/presence. Although modestly expanded by Schumacher et al. (2016) to 127 characters, the relevant proportions (99 cranial, 77.9% and ten dental, 7.9%) are broadly unchanged.

Outside of considerations of preservation due to size, two major tribes have previously been identified within pachycormids, suspension-feeders and macropredators (Liston and Friedman 2012), the former group having gill rakers rather than teeth as their primary feeding structure. However, within a dataset that relies heavily on cranial characters, the dental characters, having little utility in suspension-feeders that are often edentulous, constitute almost 8% of the dataset. Characters from gill rakers were considered to be a poor potential source of data by Liston (2013) with one character scored for only two taxa in Lambers' 31 character 11 taxon matrix of the group, but removal of the character had little effect on the results from that dataset (Liston 2007). In the same way that gill rakers were of limited use across the entire group, only being detectable in large suspension-feeders, so teeth are of little utility in the suspension-feeders. Furthermore, the suspension-feeders tend to be larger and therefore less well-ossified, with less preservation of post-cranial material, and cranial material with unfused margins often significantly damaged, thus disguising their full extent, form and articulation as well as suturing, compromising their utility for scoring general skull characters.

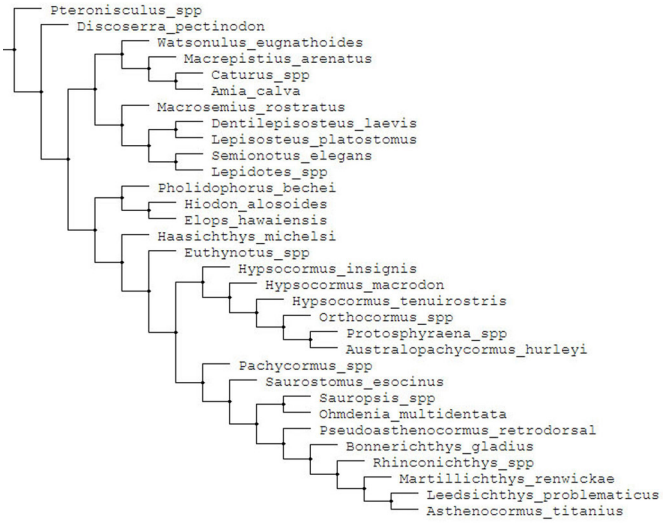

Figure 1. Strict consensus tree derived from 132 character 32 taxon dataset. Note classic topographic split between carnivorous and suspension-feeding tribes (Liston & Friedman 2012).

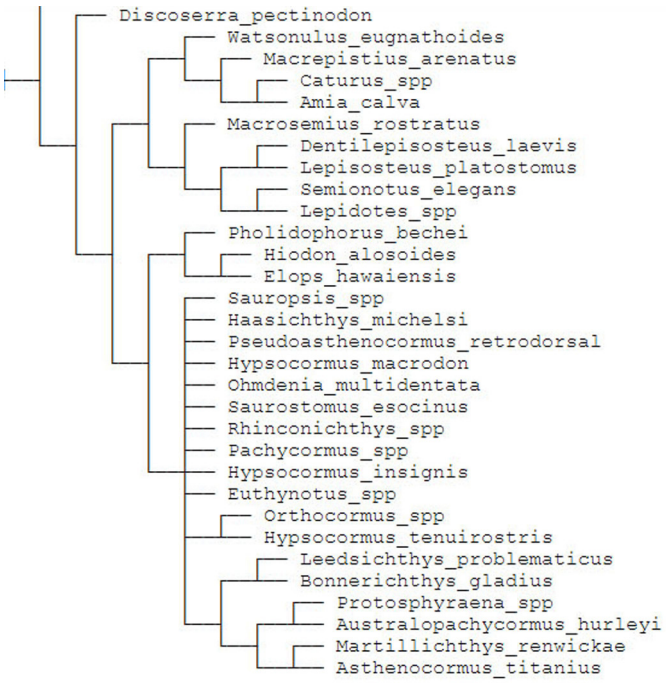

Figure 2. Strict consensus tree with ten dental characters removed (122 character, 32 taxon dataset). Note topographic shift of *Australopachycormus* and *Protosphyraena* into the suspension-feeding clade.

The dataset of Friedman et al. (2010) was already flagged as problematic due to the high percentage of unknown characters present (Arratia and Schultze 2013), to the extent that there were only three characters that distinguished the Late Cretaceous predator *Protosphyraena* from the Late Jurassic predator *Orthocormus*. This was equal to the three characters that distinguished *Protosphyraena* from the Late Cretaceous suspension-feeder *Bonnerichthys*, (formerly misidentified as a species of *Protosphyraena*, Friedman et al. 2010), implying that they were equally related, despite being the crown member for the two extreme groupings within pachycormids of predatory carnivores and suspension-feeders. However, the further issue of the potential skewing of the data due to characters for taxa not being mutually present for assessment across the whole group is also worth considering. As such, it is worthwhile reviewing characters that have previously been selected for analysis of interrelationships within the group, to ensure that their potentially variable presence as characters (in whatever state) has not introduced significant biases.

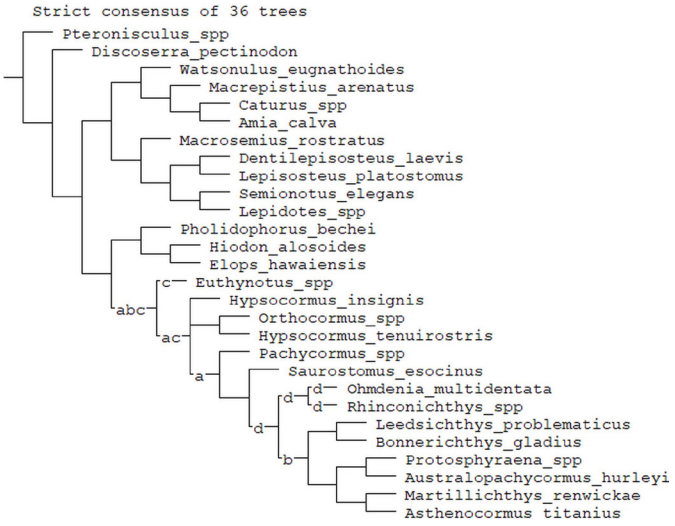

Figure 3. Reduced consensus tree generated by using the prunnelsen command in TNT, with four taxa excluded (122 characters, 28 taxa) Legend of excluded taxa:- a: *Hypsocormus 'macrodon'*, b: *Pseudoasthenocormus retrodorsalis*; c: *Haasichthys michelsi*; d: *Sauropsis* spp.

METHODS

The full dataset (132 characters, 32 taxa) based on the Schumacher et al. (2016) iteration of the expanded Friedman et al. (2010) dataset was run in TNT. Additionally, an exploratory analysis was conducted after removing all 10 dental characters.

RESULTS

The topology of the strict consensus tree based on the analysis of the full dataset conforms to the widely-accepted picture of the suspension-feeding tribe adjacent to a carnivorous cohort (Fig. 1). With the dental characters removed, the strict consensus of the 36 most parsimonious trees (Fig. 2) depicts *Protosphyraena* and *Australopachycormus* as a clade at the crown of the suspension-feeders and as the sister group of the suspension-feeders *Martillichthys* and *Asthenocormus*. Given the low resolution of this tree, a reduced strict consensus of these MPTs was then generated using the prunnelsen command in TNT, removing the four unstable taxa (28-31)

Figure 4. Left maxilla of *Leedsichthys* (GLAHM V3363, 695 mm long) with a perfectly smooth and intact ventral surface. Scalebar = 50 mm.

Figure 5. Left maxilla of *Leedsichthys* (PETMG F.174/10,004, 1047 mm long), with five peg-like crushing teeth orientated near the apex of the jaw line. Scalebar = 50 mm.

Hypsocormus '*macrodon*', *Pseudoasthenocormus retrodorsalis*, *Haasichthys michelsi* and *Sauropsis* spp. to show the strict consensus tree that results without them (Fig. 3).

DISCUSSION

Although the use of gill rakers for cladistic analysis was called into question by Liston (2013), given the environmental plasticity of their occurrence in contemporary osteichthyans and the difficulty of examining them in fossil forms, the experimental omission of the character from the dataset did not significantly affect the phylogenetic results (Liston 2007). That said, considering the increase from two to nine pachycormid taxa for which the gill raker form is known in the intervening years, there might be a more significant difference were that analysis to be rerun. In contrast, the omission of the dental characters here produces a significant shift for the Cretaceous carnivorous pachycormids into the heart of the suspension-feeding clade. Furthermore, this new position, effectively recovering the Cretaceous genera of *Protosphyraena* and *Australopachycormus* as secondarily carnivorous predators, requires less invocation of convergence to explain similarities in pectoral fin, pelvic fin and gill raker characteristics between *Protosphyraena* and *Bonnerichthys*.

This is far from the first indication of dental data performing poorly in reconstructing other phylogenies (Sansom et al. 2017). In the case of pachycormids, one reason for this might be due to plasticity of teeth reflecting intraspecific dietary variability. Clupeiformes arise some 15 million years later than Pachycormiformes (Toarcian, Early Jurassic) close to the holostean-teleostean transition, but feature a similar dietary range from predatory carnivores to suspension-feeders. Svetovidov (1964) pointed out the variability of teeth development in clupeids, particularly noting the absence of teeth in large specimens of *Caspialosa caspia*, despite their presence in young and smaller individuals. More recently, a large sample of *Alosa caspia* and *Alosa immaculata* from the Ponto-Caspian basin (Vernygora et al. 2018; Vernygora 2020) exhibited a similar pattern (pers. obs. OVV) with distinct ecomorphs in highly structured populations, the varied timing of spawning and overwintering largely determining the development of feeding structures, whether gill rakers or teeth. This reflects a pattern by which potentially derived dental characters can be subsumed within a suite of ecomorphotypes, which would be challenging to distinguish accurately from the fossil record.

There is some evidence of similar plasticity in pachycormids. The large suspension-feeder *Leedsichthys* is known from approximately 70 specimens worldwide (Liston 2010), from which only two maxillae have ever been

recorded. The first is part of the specimen GLAHM V3363 (left maxilla, 695 mm long; Fig. 4) with a perfectly smooth and intact ventral surface. The second is PETMG F.174/10,004 (left maxilla, 1047 mm long, FIG. 5) (Vivacity 2016), with five peg-like crushing teeth orientated near the apex of the jaw line, consistent with the iliophagous behaviour previously discussed (Liston 2010). This could indicate similar environmental plasticity for dentition to that described for contemporary clupeids.

Given the extensive collapse of the previously resolved tree, it is unclear whether these results are more of a reflection of the degree to which the dental characters hold together the pachycormid phylogeny, rather than an indication of underlying signal previously swamped by a plastic dental noise, it is worth noting that the topographic shift for *Australopachycormus* and *Protosphyraena* is consistent with the latter taxon sharing characters with the suspension-feeder *Bonnerichthys* (Liston and Maltese 2022), namely elongate pelvic fins located immediately rear of the pectoral fins; pectoral rays terminating on leading edge rather than trailing edge (Liston et al. 2019); lack of ossified vertebral centra; lack of caudal segmentation; presence of skull boss; and scale and gill raker pattern. The topographic shift therefore renders it unnecessary for convergence to be invoked in these varied areas of the skeleton.

CONCLUSIONS

Although the results from this experiment may not necessarily mean that *Protosphyraena* and *Australopachycormus* were secondarily carnivorous, it is worth noting that in groups that cross ecomorphotypes, there is a very real risk of overweighting with characters that are not universally applicable across a given group.

ACKNOWLEDGEMENTS

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If trees could talk: the palaeoenvironmental implications of a Late Cretaceous inclusion-bearing amber deposit in Southern Saskatchewan

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Amber preserves an exceptional record of small, soft-bodied organisms that are underrepresented in the fossil record, and original chemical signals from the environment in which it was produced. This unique window into the past allows palaeontologists to gain detailed information about the ecology and evolution of ancient amber-producing forests and their inhabitants. Our group recently discovered an inclusion-bearing amber deposit in the Big Muddy Badlands of Saskatchewan, dated to the Late Maastrichtian (67.04 ± 0.16 Ma), which represents the last known diverse insect assemblage prior to the K-Pg mass extinction and offers new insights

into the palaeoenvironment of Southern Saskatchewan. The stratigraphy of the sampled area suggests that one million years before the K-Pg extinction event, the Big Muddy Badlands were a subtropical swamp. Comparisons between the Fourier-transform infrared (FTIR) absorption spectrum of Big Muddy amber and extant tree resin suggest that the amber-producing source tree for the deposit likely belonged to the Cupressaceae (conifer) family. The hydrogen stable isotope ratios (δ2H = -285.7‰ ± 18.6‰) in the amber, which indicate the water source accessed by the amber-producing trees, suggest that the swamp was located a moderate distance from remnants of the Western Interior Seaway (the δ2H values are comparable to modern Atlantic Canada). These results agree well with other palaeoenvironmental proxies, such as fossil leaves, but the use of amber has the distinct advantage of only requiring a fraction of the sample size (i.e., only eight 5 mm amber pieces were required for the reported FTIR and isotope analyses). The specific ecological requirements of the insects captured in Big Muddy amber and the vertebrates (e.g., turtles and crocodiles) found near the amber site allow us to further resolve the palaeoenvironment. Amber is a valuable tool for developing insights into environmental and geographic changes through time, and, due to its prevalence in Canadian Cretaceous and Palaeogene sediments, provides more opportunities for spatial and temporal comparisons.

Avian sternum morphology outperforms skeletal proportions in predicting locomotory ecology of *Ichthyornis* (Avialae: Ornithurae)

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The avian skeleton is uniquely adapted to a variety of locomotor ecologies, with skeletal form often correlating with ecological function. Functional morphological traits, especially in elements of the pectoral and pelvic girdles, provide informative correlates of locomotion in Neornithes. Distinct morphologies are associated with certain locomotory styles, such as soaring, continuous flapping, and foot-propelled diving. The fossil bird *Ichthyornis* (Avialae: Ornithurae), found in Late Cretaceous shallow-water marine sediments of North America, has been hypothesized to be a volant seabird, similar to modern terns or gulls. While certain skeletal features of *Ichthyornis* have been noted to resemble diving bird adaptations, rigorous quantitative analyses of the locomotory abilities of *Ichthyornis* have yet to be performed. Here, we provide the first comprehensive morphometric analysis of *Ichthyornis* to test hypotheses on its locomotory ecology. We performed a 3D geometric morphometric analysis on the sternum, as well as a linear morphometric analysis of measurements across the entire skeleton of *Ichthyornis* and a broad phylogenetic scope of ecologically diverse Neornithine taxa. Locomotory variables associated with morphology were identified using a Procrustes distance-based phylogenetic generalized least squares, and locomotory abilities present in *Ichthyornis* were estimated using a phylogenetic flexible discriminant analysis. We find strong support for *Ichthyornis* being both a soarer and foot-propelled underwater diver, as indicated by its sternal morphology, similar to the extant darter (*Anhinga anhinga*: Suliformes). We also find that the ster-

num alone provides much greater predictive power for locomotory mode than overall skeletal proportions. Our study presents the first detailed statistical analysis of the locomotory ecology of *Ichthyornis*, allowing us to more accurately reconstruct the ecosystems in which these fossils have been found. Further, we reveal the power and importance of avian sternal morphology in predicting locomotory ecology in fossil birds, which is invaluable to reconstructing the origin and evolution of flight across the dinosaur-bird transition.

New embryos from the Upper Cretaceous of China help polarize reproductive strategy in duck-billed dinosaurs

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Dinosaurs eggs and embryos are generally rare, but the Upper Cretaceous (?Maastrichtian) Hekou Formation of China preserves them in abundance. Recently, a clutch of subspherical eggs was found in these strata, and two eggs made available for examination. The eggs are referrable to the oofamily Spheroolithidae and are among the smallest (660 mL) and thinnest-shelled (0.3–0.4 mm) known for this oofamily. The preserved embryos are attributable to the superfamily Hadrosauroidea on account of the large jugal contact of the maxilla that faces strongly laterally, and the deltopectoral crest of humerus that is wide relative to the minimum width of humeral shaft. The embryos do not, however, belong to the family Hadrosauridae because they lack a well-defined ectopterygoid ridge of the maxilla, and a pointed distal corner of the deltopectoral crest. The squamosal is distinctive in having a tall, blunt postorbital process, reminiscent of the condition seen in the hadrosauroids *Levnesovia transoxiana*, *Tanius sinensis*, and *Nanningosaurus dashiensis*, suggesting possible affinities. The embryos fill little more than half the egg, so were presumably several developmental stages away from hatching. Even so, the small size of the eggs suggests that the neonates would have been correspondingly small. Neonates of the non-hadrosaurid hadrosauroid *Telmatosaurus transsylvanicus* are likewise quite small and possess poorly formed epiphyses of the limb bones. This indicates that small hatchling size and altriciality (underdevelopment at time of hatching) are likely primitive for Hadrosauridae, and that the large size and precocial nature of lambeosaurine neonates are derived.

A late-surviving brachylophosaurin (Ornithischia: Hadrosauridae) from the Dinosaur Park Formation of Dinosaur Provincial Park, Alberta

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Brachylophosaurin hadrosaurs are well-documented in the lower part of the Belly River Group (Foremost and Oldman formations) of Alberta and similar-aged units in the western United States, but until now have not been identified from the slightly younger Dinosaur Park Formation, despite extensive prospecting and abundant hadrosaur material. Evans et al. (2009) described a large, unusual hadrosaur braincase (CMN 52845) from the Dinosaur Park Formation of Dinosaur Provincial Park, and tentatively assigned it to "cf. *Parasaurolophus* sp." However, as noted, CMN 52845 has some characters that are unusual for *Parasaurolophus*, but occur in *Brachylophosaurus*, including the incorporation of the entire length of the dorsal surface of the frontals into the frontal platform, and the surface of the frontal platform with straight, relatively widely spaced ridges. Detailed comparisons to subsequently collected parasaurolophin braincase material supports the exclusion of CMN 52845 from this clade. Instead, CMN 52845 shares previously unrecognized similarities with the large brachylophosaurin braincase MOR 720 (Freedman Fowler and Horner 2015; McDonald et al. 2021) from the Judith River Formation of Montana, including the posterior projection of the platform supporting the crest being formed entirely by the frontals, and substantially (>50 mm) overhanging the parietal and dorsotemporal fenestrae; the latter character was originally considered uniquely shared by CMN 52845 and *Parasaurolophus*. Although referred in the literature to *Brachylophosaurus canadensis*, MOR 720 was collected relatively high in the Judith River Formation, and along with CMN 52845, may belong to a new brachylophosaurin taxon that stratigraphically succeeds *B. canadensis*. The identification of a brachylophosaurin in the well-sampled Dinosaur Park Formation is the first addition in 100 years to the tribe-level diversity of Hadrosauridae in this formation. Its apparent rarity may reflect a different habitat preference from other hadrosaurs.

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Amber inclusions associated with the Danek Bonebed (Upper Cretaceous, Horseshoe Canyon Formation), and efforts to place museum collections into a stratigraphic context

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Museum collections of Canadian Cretaceous amber provide a valuable supplement to the palaeoecological information available from vertebrate bonebeds and other fossil-rich intervals. Amber allows us to identify which trees were producing resin in ancient ecosystems (through resin chemistry), the ecological and climatic conditions experienced by these trees (through resin stable isotopes), and rare glimpses of small and soft-bodied organisms in a terrestrial setting (through inclusions trapped in fossil tree resin). However, much of the material has been collected with minimal or no stratigraphic information. In order to reconstruct the stratigraphic context of the museum specimens, it is necessary to characterize as many in-situ amber deposits as possible. Here, we will examine new inclusions and chemical data obtained from the Whitemud Creek amber site. This material is directly associated with the Danek Bonebed in Edmonton (Horseshoe Canyon Formation, Royal Tyrrell Museum Collection), providing additional paleoecological and paleoclimatic information relevant to the Danek site. Whitemud Creek amber contains inclusions such as a ceratopogonid midge (Diptera), mite (Acari), wood with cellular preservation, insect feces, and fungal resting stages (sclerotia), which provide ecological information. Fourier-transform Infrared Spectroscopy of the amber permits chemical comparisons between modern resins and the amber deposit, indicating a source tree within the Cupressaceae. Meanwhile, stable isotopic compositions of carbon and hydrogen support the connection to the Danek Bonebed and suggest that precipitation experienced multiple rainouts before reaching the Whitemud area. We will also examine a new outcrop near Rolling Hills, Alberta (Taber Coal Zone, Foremost Formation). This material stratigraphically anchors the largest and most diverse insect assemblage prior to the end-Cretaceous extinction event (Grassy Lake amber, Royal Tyrrell Museum Collection). Similarities in terms of diversity and abundance of inclusions, resin chemistry, and stable isotope compositions all support this stratigraphic and faunal connection. Aside from their faunal contents and their paleoecological and paleoclimatic information, amber deposits in the Late Cretaceous of western Canada allow us to track larger palaeogeographic trends, such as the influence of the Western Interior Seaway. With sufficient sampling, amber deposits may also provide an alternative source for information about the composition of ancient atmospheres or ecological disturbances.

Comparative body size distributions of Pleistocene and Modern Canadian Wolves (*Canis lupus*)

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During the Pleistocene of Beringia (~40,000 – 11,700 ybp), competition for prey with several extinct large carnivores (e.g., *Arctodus simus* and *Panthera atrox*) may have resulted in the evolution of the Pleistocene Beringian wolf ecotype. Relative to their modern counterparts, Pleistocene Beringian wolves evolved robust jaws, wide carnassial teeth, and short, wide snouts, presumably to enhance bite forces and enable enhanced carcass utilization. However, body mass is also an important correlate of carnivoran ecology, influencing potential prey sizes and enabling niche partitioning. Given the drastically different competitive landscape, Pleistocene Beringian wolves may have been i) larger than their modern-day counterparts, allowing them to compete for food resources with other, now extinct large carnivores or ii) smaller than their modern counterparts due to a competition-driven preference for small-bodied prey. We selected 32 specimens of Pleistocene grey wolves from the Yukon in the collections at the Canadian Museum of Nature (CMN) and the Yukon Government Paleontology Program. A total of 106 specimens of modern grey wolves with recorded body masses were selected from the CMN and other collections across Canada. To estimate body masses for the Pleistocene wolves, we used linear regressions of the m1 and P4 length and width against the body masses of extant carnivorans. We then compared the body mass distributions of modern and Pleistocene wolves using Kolmogorov-Smirnov tests. We found no significant differences ($p > 0.05$) in the body mass distributions between the modern and Pleistocene gray wolves, which suggests three possible explanations, i) there were no ecological differences between the Pleistocene Beringian and modern gray wolves, ii) any ecological difference that did exist did not lead to noticeable differences in body mass, or iii) there were ecological differences but the measurements and tests we performed did not detect them. We favour the second explanation, given our previous stable isotopic work that showed a shift from a diet comprising primarily horse during the Pleistocene to one comprising large cervids today. We therefore suggest that wolves remained large ungulate specialists, which did not necessitate measurable shifts in body mass.

A new Late Cretaceous leptoceratopsid specimen from the Oldman Formation (Campanian) of Alberta, Canada

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Leptoceratopsid ceratopsians are poorly represented in the Upper Cretaceous fossil record of the Western Interior of North America. In Alberta (Canada) specimens are rare in the Santonian and Campanian, with complete skeletons of *Leptoceratops* only becoming common relative to other ceratopsian remains in the Maastrichtian. As such, their early evolutionary history in North America is poorly understood. The description of TMP 2011.053.0027, an isolated right leptoceratopsid frontal from the lower unit of the Oldman Formation (~76 Ma), helps to fill in a significant time gap in the leptoceratopsid record in Alberta between the occurrence of TMP 1987.089.0008 (~75.05 Ma; referred to *Prenoceratops*) and the oldest known leptoceratopsid, *Gryphoceratops*, from the Santonian Milk River Formation (~83.5 Ma). TMP 2011.053.0027 has key characters confirming its referral to Leptoceratopsidae (i.e., a large caudolateral process and the relatively deep frontal depression), but a phylogenetic analysis failed to resolve its placement within Ceratopsia beyond Neoceratopsia indet. due to the specimen only having a limited number (2) of phylogenetically-informative characters. Re-examination of these characters in all available leptoceratopsid frontals from Alberta and Montana confirms that the shape of the transverse ridge demarcating the anterior margin of the frontal depression is highly variable (ranging from straight to deeply curved) and, thus, cannot be used to distinguish *Prenoceratops* from *Cerasinops*, the latter only known from the Two Medicine Formation of Montana. This is confirmed by the description and analysis of a new frontal (ROMVP66302.1) from the holotype *Prenoceratops* bonebed in the Two Medicine Formation of Montana.

TMP 2011.053.0027 is tentatively referred to *Cerasinops* based on the time equivalency of their quarries, which are both older than the locality of the *Prenoceratops* bonebed. The previous referral of TMP 1987.089.0008 from the upper unit of the Oldman Formation to *Prenoceratops* sp. is not supported by the diagnostic characters available on the specimen and it may be better referred to *Unescoceratops* sp., also based on the closer time equivalences of their respective localities than either has to the *Prenoceratops* bonebed.

Along with *Gryphoceratops* from the Santonian, TMP 2011.053.0027 helps to establish the presence of leptoceratopsids as a currently enigmatic member of the mid-Late Cretaceous dinosaur biota of Alberta. The shape of TMP 2011.053.0027 also allows us to infer that the typical leptoceratopsid skull roof morphology and the relatively deep frontal depression was well-established within the clade by the mid-Late Cretaceous.

Vascular preservation in *Tyrannosaurus rex* from the Frenchman Formation

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The Frenchman Formation dates to the Late Cretaceous (67–66 Ma) and it outcrops across much of southern Saskatchewan. It provides information on dinosaurs in their final evolutionary stage before the K-Pg mass extinction event. The Frenchman Formation has produced numerous *Tyrannosaurus* specimens of various sizes and ages, including the largest *T. rex* specimen by estimated weight, nicknamed Scotty (RSM P2523.8). Soft tissue preservation is rare in the fossil record, and claims of their discovery have long been controversial. Soft, pliable blood vessel structures have been reported in dinosaurs, mainly recorded through the work under the leadership of Mary Schweitzer using destructive bone dissolution. Here, we have used a suite of advanced synchrotron and lab-based experimental techniques (Computed Tomography, X-Ray Fluorescence Spectroscopy and Mapping, X-Ray Absorption Near Edge Structure, Scanning Electron Microscopy) on a rib bone section from Scotty to resolve and chemically analyze a vast blood vessel network. The chemical composition of the vessels reveals a strong iron (III) signature in the form of goethite. While this iron presence might not be original to the blood vessel, it may be a key diagenetic factor that allowed the structures to be preserved. The rib features a large fracture in the process of mending situated at the region of the found vessels, caused either by injury or pathology. We hypothesize this could contribute to the extensive remodeling of the rib bone which necessitated the increase in vascular activity. To confirm this hypothesis, future studies involving other dinosaur specimens with pathologies are planned. Healed injuries may provide better targets for the investigation of soft tissue preservation in dinosaurs.

An undescribed DPF outcrop in west-central Saskatchewan reveals the paleocoastline of the Western Interior Seaway

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Since the 1990s, the small town of Herschel in West-Central Saskatchewan has been known for its marine fossils from the Late Cretaceous Bearpaw Formation. These deposits have yielded several plesiosaurs, sharks, and ammonites. In the past 30 years, pieces of these aquatic giants surface occasionally on the Western slope of the "Coalmine Ravine", but most of the excitement has subsided along with the sporadic visits from paleontologists. In 2014, a team from McGill prospected the eastern slope of the ravine and discovered a thin outcrop of the Dinosaur Park Formation (DPF) wedged between a regression-transgression cycle of the Western Interior

Seaway's coastline. The team discovered poorly preserved remains of a large adult ceratopsid dinosaur. Within meters of the specimen, a partial, articulated plesiosaur was recovered downsection in the underlying Bearpaw Formation and ammonites upsection in the overlying Bearpaw Formation. The depositional environment of the DPF is interpreted to be a barrier island or on-shore lagoon. Although the DPF outcrops extensively in Alberta and parts of western Saskatchewan, the northeastern extreme identified at Herschel presents a novel depositional environment for this formation.

This research into this Coalmine Ravine quarry can contribute to the natural heritage of Saskatchewan while attracting both scientists and nature educators to the region. The community of Herschel, as with many small prairie communities, is made of brilliant, determined multi-taskers: farmers who work day and night, innovative entrepreneurs attracting visitors from across the province, and volunteers of all ages who are passionate about conserving the cultural heritage of the prairies. They have all earned our respect despite the vast differences in our worldviews. Our work with this new dinosaur fossil will be integrated with the local interpretive center. We wish to help them draw attention to the unique terrestrial and marine palaeontological heritage of their region called "Ancient Echoes" which is slowly being swept up into large-scale industrial farming projects. One of their main concerns is preserving and continuing to build knowledge of the indigenous sacred sites in the area without the support of sustainable tourism. The union of paleontology and indigenous heritage is challenging in the context of this small community but offers a unique temporal perspective for the interpretive center.

Phylogeny and historical biogeography of Cenozoic (66 ma – present) ursids

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Ursids (i.e., bears) have a modern geographic range that spans multiple continents and climate zones. While the distribution of modern bears is relatively well understood, the conditions, specifically in a historical biogeography context, that led to their current distributions are not. The phylogeny of ursids is also generally incomplete with few taxa outside of modern subfamilies (i.e., Ursinae) included. Using a collection of published source trees and a backbone taxonomic tree, we generated twenty dated supertrees based on European and North American land mammal ages that include all extant and fossil species. We then use BioGeoBEARS to infer the historical biogeography of ursids using the phylogeny along with fossil and modern occurrence data provided by the Paleobiology Database (PBDB). To estimate the roles of climate change and plate tectonics in the global interchange of ursids, the BioGeoBEARS tree was aligned with significant events such as climate change events and land bridge timings. The BAYAREALike+j model, one that does not allow for range evolution at cladogenesis but does allow for founder events, was the best fit model. Biogeographic stochastic mapping, a form of ancestral character estimation, showed that the greatest degree of biotic interchange occurred between Europe and Asia followed by Europe and North America. These findings reinforce the importance of Bering Land Bridge in ursid evolution but, surprisingly, suggest that the North Atlantic Land Bridge provided an important route of interchange for ursids until ~9 Ma.

Tooth replacement in snakes: synapomorphy or chaos?

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Serpentes (snakes) is the most diverse clade of lizards with nearly 4000 living species. Many species have highly kinetic maxillary, mandibular and palatal bones related to uniquely modified feeding styles with specializations for both large and small gapes. Many large-gape snakes possess highly recurved teeth that help hold prey, as well as slide their jaws over prey during food ingestion. Scolecophidian snakes (small-gape snakes) have a highly modified feeding apparatus reducing the number and size of their teeth. However, the degree and consistency of tooth recurvature observed in snakes is not observed in other lizards and is considered a uniting feature of Serpentes. Early investigations of tooth replacement in snakes demonstrated the teeth developed in soft tissue epithelia adjacent to the functional teeth. It was suggested that the crowns began development in an orientation parallel with the jawbones and changed in orientation as they moved to a functional position. Surveys of alcohol, and freezer preserved specimens corroborated this pattern. "Horizontal tooth replacement" became a synapomorphy of Serpentes in addition to tooth crown recurvature. Horizontal tooth replacement, however, has not been quantified for statistical significance, nor observed in vivo via X-ray or CT scanning. This creates uncertainty around the validity of the synapomorphy as it may be a consequence of both the tooth crown recurvature and postmortem effects on soft tissues housing replacement crowns. This has major implications for fossil taxa as taphonomy may create misleading conditions supporting erroneous referral to major clades defined by untested primary homology statements. Using micro-CT scanners, thawed snake heads from frozen specimens housed at the University of Alberta and Museum of Comparative Zoology, Harvard University, were scanned to examine their jaws and teeth. Representatives were selected from most major clades within Serpentes to incorporate any taxonomic variation. Functional and replacement crowns from each tooth family (functional tooth position and all associated replacement crowns) were segmented and their orientation to the jaw was measured. Crown angles were examined for patterns and significant changes in tooth crown angles throughout development into a functional tooth. Patterns were compared across different jaw elements and between taxa for variation within individuals, and between species. In the absence of in vivo specimens, a pattern of tooth replacement is observed in which crowns begin development at near identical orientations to functional crowns, then proceed through a "horizontal" position late in development, prior to attachment. Crown angles show high variation between jaw elements and taxa demonstrating no clear rule or order to replacement crown orientation through development. Without a consistent pattern of crown orientation across all specimens and taxa, the validity of "horizontal tooth replacement" as a synapomorphy for Serpentes is here refuted. We propose an alternative pattern of tooth replacement in which the soft tissue epithelia constricts the expansion of the teeth as they become larger, altering their orientation to a more horizontal position prior to attachment to an alveolus. Effects of post-mortem alterations to the epithelium on tooth crown orientation remains to be tested.

The genetic signaling necessary for the development of jaws arose in jawless stem-gnathostomes

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A review of the state of the nasal and hypophyseal ducts in stem gnathostomes, proposing a new model for the nasal and hypophyseal duct in Osteostraci based on recent and new osteostracan species and discuss the ancestral state in stem-gnathostomes based on ancestral character reconstruction. The buccohypophyseal duct is an unassuming feature of the early gnathostome (jawed vertebrate) head that was necessary for the development of the gnathostome face and the evolution of jaws (Khonsari et al. 2013). Gnathostomes have a pair of nasal capsules and separation of the hypophyseal duct from the nasal duct. Primitively, the hypophyseal duct of gnathostomes extends ventrally to the oral cavity (a buccohypophyseal duct) instead of dorsally to the nasal capsule. In contrast, lampreys and hagfish, the only extant agnathans (jawless vertebrates), have a single, median nasal capsule and a hypophyseal duct that extends to the nasal capsule followed by a duct that connects the nasal capsule to the dorsal or terminal end of the head (nasohypophyseal duct; Oisi et al. 2013). The differences in morphology are a direct result of differences in gene expression associated with development of the brain, face, and jaws (Retaux and Kano 2010). The conditions of most extinct agnathan groups are not well known except for Galeaspida who, despite having a single median nasal opening, have a gnathostome condition (buccohypophyseal duct with separation of nasal capsule and hypophyseal duct (Gai et al. 2011). However, most phylogenies place Osteostraci between Galeaspida and Gnathostomes, a position that has complicated interpretations of buccohypophyseal evolution because osteostracans superficially resemble the condition in lampreys. Recent study of the anatomy of the nasal and hypophyseal ducts in osteostracans shows a more complex condition that is analogous with lampreys, rather than homologous. A prior study proposed a possible separation of the nasal and hypophyseal ducts in osteostracans, but was unable to verify the condition in other taxa (Scott and Wilson 2015). Additional examination of previous specimens and a currently undescribed basal osteostracan shows osteostracans have internal divisions between the nasal and hypophyseal ducts, at least in taxa with a constriction between the nasal and hypophyseal regions of the nasohypophyseal opening. Reconstruction of the ancestral character state with this updated model for the nasal and hypophyseal duct supports separation of the hypophyseal duct and the nasal capsule deep within vertebrate evolution and therefore at least some of developmental pathway necessary for the appearance of jaws was already in place within the jawless stem gnathostomes.

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Cranial anatomy of a juvenile *Edmontosaurus regalis* (Lambe, 1917), with comments on ontogeny and biogeography

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Edmontosaurus regalis is an abundant and widespread hadrosaur taxon in Alberta during the upper Campanian. Despite its prevalence, juvenile cranial elements of *E. regalis* are poorly known. A newly collected specimen from the Horseshoe Canyon Formation, UALVP 60425 (nicknamed "Gary"), represents a small (skull length ~ 50 cm) hadrosaurine that preserves a partial skull. UALVP 60425 can be referred to Edmontosaurini based on the presence of a postorbital fossa, as well as anteroposteriorly long frontals that both lack the dorsally-oriented nasal contact seen in crested hadrosaurs, and contribute more to the orbital margin than in Kritosaurins. Despite its small size and presumed ontogenetic immaturity, UALVP 60425 can be further assigned to *E. regalis* on provenance, as well as a horizontal shelf on the postorbital process of the jugal. The deep postorbital fossa of *E. regalis* begins formation only in late-stage juveniles, and a ventral deflection of the anterior dentary of young *Edmontosaurus* is greatly reduced through ontogeny. UALVP 60425 is nearly identical to juveniles of the Alaskan Prince Creek hadrosaurine ("*Ugrunaaluk kuukpikensis*"), though both show consistent anatomical differences in the maxilla, lacrimal, jugal, and postorbitals with comparatively-sized *E. annectens*. The Alaskan hadrosaurine is therefore referred to *E. regalis* in the absence of adult hadrosaurine cranial material from the Prince Creek Formation. Ontogenetically late development of the postorbital fossa accompanies changes in the visual fields, suggesting behavioural shifts later in life history.

Ontogenetic variation of nuchal musculature size on the frill of the ceratopsian *Centrosaurus apertus*

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One of the defining characters of ceratopsid dinosaurs is the posteriorly expanded parietosquamosal frill. Fossae are present on the ventral side of the frill and have been interpreted as sites for nuchal muscle attachment, but little is known about how these fossae changed through ontogeny and what this might have meant for the de-

velopment of the nuchal musculature. In this study, using parietosquamosal frill specimens of *Centrosaurus apertus* (representing a partial ontogenetic series) from the Canadian Museum of Nature, Royal Ontario Museum, University of Alberta, Royal Tyrrell Museum of Palaeontology, and a previously published model of ceratopsid nuchal musculature (based on the extant phylogenetic bracket), we identify fossae on the parietal, squamosal, and occiput as sites for nuchal muscle attachment. Reconstructions of these muscle attachments across the ontogenetic growth trajectory show associated changes in the nuchal musculature: younger specimens display poorly defined muscle insertions that become deeper, larger, and more oval with age. We hypothesize that since it is well-established that the ceratopsid cranial frill grew with positive allometry relative to body mass, so too did the nuchal muscles. This is based on the prediction that greater head and neck movements became more important with age in *C. apertus*, likely as a means of more effectively wielding the fully developed frill in adulthood. Bivariate regressions of muscle attachment area vs. frill area of eight specimens (including the smallest known individual) tentatively reject the hypothesis of positive allometry of muscle growth and reveal isometry for each muscle investigated; however, because the ceratopsid frill is known to scale with positive allometry relative to body mass, it is likely that the nuchal musculature did, as well. The large confidence intervals bounding the regression lines indicate that more data are needed to more reliably establish our observed trends.

Dimetrodon jaw models bite harder than previous estimates

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The most renowned predator of the Early Permian, *Dimetrodon*, evolved as members of a novel, amniote-dominated terrestrial landscape. Reconstruction of the early synapsid jaw borrows differing influence from a transitioning stem amniote musculature towards what would eventually develop into the powerful masticatory complex used by extant mammals. Since the last of these reconstructions, seminal works in the subfield of biomechanics have revolutionized our understanding of the feeding apparatus and muscle reconstructions. In this study, we use a virtual skull of *Dimetrodon incisivus* constructed from CT (Computed Tomography) scanning to create three competing models (reptilian, rhynchocephalian, and mammalian) of the early synapsid feeding apparatus to compare their effective cumulative output. 3D muscles are built to spatial limitations and areas of attachments on the virtual skull to determine physiological cross-sectional area and inform individual force values. Multi-body dynamics analysis determines bilateral muscle system output as experienced on prominent heterodont teeth. A 'reptilian' style of musculature returned the highest force in our models, peaking at 4000 N. General taxon bite force estimates based on body size and skull height underestimate the bite force of *Dimetrodon*. A modification of the traditional dry skull method used in reptiles comparatively underestimates the values returned from our muscle reconstructions except in the rhynchocephalian attachment style. A higher bite force experienced on the caniniform teeth of *Dimetrodon* furthers their role as apex predators of the Permian. This informs our understanding of the primary factors informing stem-mammalian feeding complexes and supports a dietary shift towards the emerging large-bodied herbivores for the first time in the fossil record.

Functional stasis of mammalian communities across the Paleocene-Eocene Thermal Maximum

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The Paleocene-Eocene transition in North America was marked by a rapid global warming event, with mean annual temperatures rising by 5° to 8°C (Paleocene-Eocene Thermal Maximum; ~56 Ma) that followed an abrupt carbon isotope excursion lasting 120 thousand years or less. The Paleocene-Eocene Thermal Maximum (PETM) saw a significant shift in the composition of North American floral communities as well as expansion of the perissodactyl, artiodactyl, and primate distributions into North America from Eurasia, which correlated with significant body size change. However, a previous study found little to no change in the phylogenetic and functional components of North American mammal diversity throughout the PETM. This study did not, however, include data on the extrinsic environment or mammalian traits relating to diet and locomotion. In this follow-up study, we assembled a database of 121 fossil mammal species from the Bighorn Basin, Wyoming which included body sizes, inferred diets, and limb postures alongside a database of 40 palynofloral localities as proxies for environment. For each mammal species, we determined their environmental preferences based on the microfloral assemblages with which they most co-occurred. For each North American Land Mammal Age (NALMA), we then calculated mean difference in traits and environmental preference. We found little to no change in trait dispersion across the PETM, aligning with previous work. We found that species occurring during the PETM showed higher dispersion in environmental preference, suggesting that mammal species more finely partitioned the available environmental space or had broader climatic niches than previously anticipated. These results indicate the persistence of a stable mammalian functional community structure despite considerable taxonomic turnover as well as a decoupling of Eltonian (morphological) and Grinnellian (environmental) niche occupation.

A new predatory actinopterygian from Blue Beach, Nova Scotia

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The Early Carboniferous represents a fundamental shift in vertebrate faunal composition (i.e., from predominant placoderms and non-tetrapod sarcopterygians to predominant actinopterygians, chondrichthyans,

and tetrapods) and ocean ecology (i.e., reorganization of nekton). Tournaisian-aged strata from Blue Beach and Walton, Nova Scotia capture this moment and have yielded a diverse fauna of actinopterygians and other vertebrates. Indeed, even partial fossils from these localities preserve critical evidence allowing tests of hypotheses on faunal and ecological change. For example, a hypothesis that Early Carboniferous actinopterygians are homogeneous and restricted in body plan was recently countered by the oldest deep-bodied actinopterygian (recovered from Walton), which evinces post-cranial disparity, a new body plan, and a new locomotory mode.

Here, we report an actinopterygian mandible preserved in 3D, representing a new genus and species. This mandible is elongated, gracile, arches anterodorsally, and bears a primary dentition of heterodont fangs. Actinopterygian identity is established by the characteristic ornamentation, dentition, and overall mandible construction (the dentary forms most of its posterior margin) observed in the specimen. Mandible length, curvature, and fang morphology combine to produce a functionally differentiated dentition with distinct regions for prey capture and prey processing. Comparison with modern actinopterygians places this taxon as a back-fanged macrodont, distinguishing it from front-fanged macrodont actinopterygians of the Late Devonian. This earliest known instance of back-fanged macrodonty in actinopterygians provides further evidence (along with, e.g., the Walton deep-bodied actinopterygian) of actinopterygian morphological and functional differentiation post-Devonian, implies experimentation in feeding strategy, and refines our understanding of the Devonian-Carboniferous transition.

New findings from the transition period between the Jurassic and Cretaceous: the earliest feathers of Jehol biota

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The Jurassic Yanliao Biota and Cretaceous Jehol biota of Northeastern China, which have yielded numerous feathered non-avian dinosaurs and early birds, are significant for studying avialan origin and evolution. Due to volcanic activity and depositional environment changes caused by the craton destruction of North China, there is a 30 Ma gap from the Late Jurassic to Early Cretaceous. The interval has thus yielded few terrestrial vertebrate fossil discoveries, which hampers our understanding of the feature of the fauna. Here we report two isolated feather specimens from the oldest sedimentary strata of Jehol Biota dating back to 134 Ma, the Dabeigou Formation of Luanping Basin in north Hebei Province, China. SEM examination reveals both feather specimens preserved as carbon traces. Morphological analysis demonstrates that one feather is the typical pennaceous contour feather capable of such functions as protection, thermo-regulation, and aerodynamics, while the other resembles the simply branched primary feather of non-avian theropod. These two feathers were discovered close to the horizon of Peipiaosteus, the earliest vertebrate recorded from the Jehol biota, and represent the oldest feathered theropods (including birds) among Jehol group to date. This discovery suggests that the local terrestrial vertebrates quickly adapted to the climate changes caused by geological tectonic movements at the very beginning of the Early Cretaceous, then established a complex ecosystem with multiple trophic levels, bringing in the dawn of the flourishing Jehol biota.

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A new orientalosuchine (Crocodylia, Alligatoroidea) from the Upper Cretaceous of China and its implications for the relationships of Orientalosuchina

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In recent years, there have been several fossil reptiles discovered in the Upper Cretaceous red beds in Municipality of Ganzhou City (MGC), the southern part (Gannan) of Jiangxi Province. Most were exposed by the construction activities associated with local infrastructure development in some districts of MGC. Up to the present, the reptile fossils excavated include a few dinosaur species (Xu and Han 2010; Wang et al. 2013; Wei et al. 2013; Lü et al. 2013a, 2013b, 2014, 2015, 2016, 2017; Xing et al. 2020a), two lizards (Mo et al. 2010, 2012), two turtles (Tong and Mo 2010), and dinosaur eggs, including those with embryos (Sato et al. 2005; Cheng et al. 2008; Xing et al. 2020b, 2021). In addition to the vertebrate fossils mentioned above, there is a crocodylian reptile, *Jiangxisuchus nankangensis* described by Li et al. in 2019, which was soon assigned to the Orientalosuchina by Massonne et al. (2019) and later further confirmed by Shan et al. (2021).

In 2021, a new fossil crocodylian was excavated from the Upper Cretaceous of MGC. The fossil locality is situated at Shahe Town of Zhanggong District, about 2 km northeast to the Ganzhou Railway Station or about 50 km northeast to the quarry of *Jiangxisuchus nankangensis* in Nankang District. The new crocodylian is represented by a well-preserved skull and some postcranial elements. It is the fifth alligatoroid known from southeastern China in addition to *Jiangxisuchus nankangensis*, *Protoalligator huiningensis* Wang et al., 2016 (= *Eoalligator huiningensis* Young, 1982), *Dongnanosuchus hsui* Shan et al., 2021, and *Eoalligator chunyii* Young, 1964. The new alligatoroid differs from all others mainly in the skull morphology. The most striking of the differences include: (1) the short and broad appearance of the skull, (2) the skull table is abnormally short, less than half its width, (3) the single parietal is excluded from the occipital ridge posteriorly, (4) the postdentary part of the mandible is much deeper than the anterior part dorsoventrally, (5) the splenial is excluded from the mandibular symphysis, and (6) the external mandibular fenestra is small and nearly vertical in orientation. Our preliminary study suggests that the new alligatoroid can be phylogenetically nested into the Orientalosuchina. Within the Orientalosuchina, the new orientalosuchine may further form a sub-group with other four genera from China and Vietnam. The discovery of the new orientalosuchine not only illustrates the diversity of the local crocodylian fauna but also provides a chance to test the hypotheses made by previous studies on the early history of alligatoroid crocodylians, particularly the origin of the Orientalosuchina and the dispersal route that the latter alligatoroid clades used to move between continents.

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A new tooth mark classification system

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Tooth marks (sometimes referred to as bite marks) are produced when one or more teeth damage, and/or penetrate the bone of a living or recently deceased vertebrate. Bony elements bearing tooth marks are observed not only in modern settings, but also in the fossil record. Such features contain a wealth of information and an array of tooth mark producers have been proposed ranging from fish, to mammals, to dinosaurs. Although numerous studies have reported on observed tooth marks and provided possible interpretations of the head and jaw movements that might have produced them, the lack of consistent terminology has hindered comparisons among tooth-marked specimens, both modern and extinct. Here we present a new, more quantitative classification scheme that can be applied to bones bearing tooth marks. Unlike those proposed previously , the new scheme not only provides clear, definable boundaries between categories based on tooth mark proportions, but also includes methodology to assess mark orientation relative to the long axes of the mark-bearing bone. Marks are first broadly categorized as 'elongate' or 'non-elongate', based on whether they are ≥4 times longer than wide. If depth information is available, marks can be further subdivided into shallower 'scrapes' or 'dents', or deeper 'scours' or 'punctures', depending on whether the width of the mark is <2 times the depth. Once a tooth mark has been categorized in this fundamental sense, descriptive modifiers relating to serration features and curvature can be added. Using photographs, simple geometric relationships, and rose diagrams, it is also possible to assess patterns in mark orientations relative to the bone long axes to gain information on defleshing behaviours and assess the relative orientations (parallel, subparallel or oblique to one another) of the marks observed on each element even if the marks are on opposite sides. The classification scheme proposed here should aid future researchers in compiling and comparing tooth mark data, not only within the field of palaeontology but with respect to extant animals as well.

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