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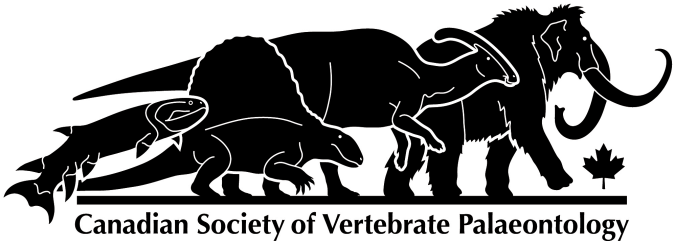

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Abstracts

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A Mississippian-aged embolomerous early tetrapod from Point Edward, Nova Scotia, Canada

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Embolomerous anthracosaurs (or more commonly, embolomeres) are large, predatory tetrapods that lived from the Early Carboniferous to the Early Permian. Embolomeres are recognized in the fossil record by their circular, bipartite vertebrae, and have been historically classified as stem amniotes, although recent researchers have challenged their position as crown tetrapods (e.g., Pardo et al. 2017). In spite of the group's phylogenetic uncertainty, embolomeres provide an important osteological record of a relatively long-lived Carboniferous tetrapod lineage, with their earliest record occurring during the period referred to as 'Romer's Gap' – a 20-million year interval spanning much of the Mississippian that is characterized by a seemingly depauperate tetrapod fossil record.

Here we report an embolomerous tetrapod originally collected in 1915 by W. A. Bell in the Point Edward Formation, currently housed in the Canadian Museum of Nature (CMN 10015). Holmes (1984) briefly noted the material, but a formal description and phylogenetic analysis are lacking and constitute the aim of the current study. The specimen consists of disarticulated remains, including a well-preserved left lower jaw, a fragmented skull roof, vertebral elements, as well as rib fragments and limb bones. The material represents at least three individuals. A phylogenetic analysis was conducted using the matrix of Klembara et al. (2014) and run in the program PAUP 4.0. We were able to code CMN 10015 for 28 characters. Two most parsimonious trees were recovered, each with a tree length of 615 steps. The strict consensus tree depicts a polytomy between the Point Edward embolomere, *Proterogyrinus* and a clade containing *Archeria* and *Pholiderpeton*. The clade is united by the following character transformations: the position of the midpoint of the anteroposterior orbit diameter, from closer to the posterior end of the skill to at the mid-length of the skull (2 to 1); the presence of a point-like prefrontal contact, rather than a broad contact; the absence of the prefrontal-jugal suture (0 to 1); the presence of a rectangular postorbital process of the jugal with a bluntly terminated posterior end (1 to 0); and the presence of a shagreen texture on the posterior plate of the parasphenoid behind the cultriform process (0 to 1), rather than a smooth condition (3 to 0). However, it should be noted CMN 10015 was only coded for the first of these characters.

The overall similarity between CMN 10015 and the well-known embolomere *Proterogyrinus*, as well as the unresolved phylogenetic position of CMN 10015 relative to *Proterogyrinus*, suggests these may be the same taxon. However, CMN 10015 differs from *Proterogyrinus* in that both pleurocentra and intercentra are complete dorsally. Either way , CMN 10015 represents a new taxon for the Point Edward Formation that, when considered within a paleoecological context, increases the known diversity of this aquatic assemblage that already includes an embolomerous jaw Romer (1963) tentatively attributed to *Pholiderpeton betonense*, as well as additional undescribed embolomere material along with *Gyracanthus* fin spines, and other various fish remains.

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Evidence for gender identification in *Pteranodon*, a Late Cretaceous pterosaur from the Niobrara Formation of Kansas

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Testing for sexual dimorphism or being able to identify gender in the fossil record is difficult as many of the useful secondary sexual characters are believed to be related to soft tissues or behaviours (including vocalization) that are rarely preserved. However, osteological indicators have proven to be useful in some modern taxa (e.g., absolute size in many mature birds, and the crests of some casque-headed lizards (Corytophanidae) such as *Basiliscus*). Recent examination of the dinosaur fossil record suggests that previous identifications of sexual dimorphism are equivocal, at best. However, work on the well-sampled Late Cretaceous pterosaur, *Pteranodon*, indicate that the length of some postcranial elements of adult-sized individuals fall into discrete bimodal size ranges, with the larger purported to be male and the smaller to be female. These gender assignments are supported by consistently larger cranial crests observed in the larger morph, which were interpreted as secondary sexual characteristics resulting from sexual selection in males. Additionally, significantly larger pelvic canals were observed in the smaller morph, which was suggested to allow for the passage of eggs in females.

These conclusions were tested by examining two previously undescribed, complete pterosaur wings recovered from the Niobrara Formation of Kansas. Selected elements of these specimens were photographed and measured, and compared to the published criteria for assigning gender in *Pteranodon*. The larger wing (CMN 8167) was confirmed to be correctly assigned to *Pteranodon longiceps*, and its measured elements fell well within the "male" size range for this taxon. The second specimen (CMN 8168) was originally referred to *Pteranodon*, but has since been assigned to *Nyctosaurus gracilis*; this analysis confirms this assignment based primarily on characters of the manus. It is currently unknown whether size is a reliable indicator of gender in *Nyctosaurus*, and thus, the sex of this specimen remains unknown.

An enigmatic tetrapod from Five Points, Ohio (Upper Carboniferous), further supports aïstopod placement among the tetrapod stem group

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A specimen from the newly available collection of cannel coals from Five Points, Ohio (Westphalian D, Pennsylvanian) in the collections of the Carnegie Museum, previously identified as an embolomere by the late Don Baird, is revealed to be part of the largest aïstopod skull known. The specimen had been previously prepared by removing the infilling bone and kaolinite and latex peels produced, from which specimen drawings were made. We also constructed a virtual cast of the specimen by scanning each half in a micro-CT scanner, and infilling the empty space using Amira 5.

The specimen preserves the postorbital skull roof and most of the braincase, which permits close comparison to the recently described braincases of *Lethiscus* and *Coloraderpeton*. The skull roof, and particular the articulation between the posterolateral process of the parietal with the tabular, and locality identify the specimen as belonging to the genus *Oestocephalus*. The parasphenoid closely compares with other described aïstopods by having an anteriorly restricted basal plate, which exposes the well-ossified basioccipital with notochordal occipital cotyle, in ventral view. The cultriform process is narrow, non-denticulate, and sharply keeled. Two large descending flanges of the parietals wall the braincase laterally in this region laterally. An open bucohypophyseal canal may be present at the junction of the basal plate and cultriform process, although this area has several fractures making this identification tentative. Large fenestra vestibulae are seen in lateral view, above and slightly rostral to two ossifications of the basioccipital. These structures, previously described as basal tubera, are massive and appear to end in an articular facet. Considering the lack of parasphenoid contribution to these structures, we suggest these may represent the point of articulation with the first pharyngeobranchial. Collectively, these features support a recently published phylogenetic analysis that places aïstopods deep on the tetrapod stem rather than in the crown, challenging lepospondyl monophyly but resolving extended ghost lineages in early tetrapod evolution.

New absolute paleoclimate estimates from Dinosaur Provincial Park, Alberta (Campanian, Late Cretaceous): Preliminary results based on a new fossil leaf assemblage

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Dinosaur Provincial Park in southern Alberta contains one of the world's best-preserved and most complete Late Cretaceous terrestrial paleoecosystems. Designated as a UNESCO World Heritage Site due to its global paleontological significance, Dinosaur Provincial Park contains forty-five dinosaur species, as well as numerous other vertebrate and invertebrate taxa (Currie and Koppelhus 2006). The rocks at Dinosaur Provincial Park record a coastal floodplain environment undergoing a major period of climatic change (Eberth and Brinkman 1997; Eberth et al. 2005), while the abundance of microvertebrate sites has also allowed for broader studies of vertebrate biodiversity through time (i.e., Brinkman 1990). Additionally, new dinosaur species from Dinosaur Provincial Park are being discovered every year (i.e., Ryan et al. 2010; Holmes et al. 2011; Farke et al. 2011).

While the relative paleoclimate of the Dinosaur Provincial Park ecosystems has been studied in detail (i.e., Eberth et al. 2005), there are few absolute paleoclimate estimates available. Relative paleoclimate change can be assessed using, for example, changes in palynology, paleofloral assemblages and paleosols over time. These studies are critical for establishing the regional paleoclimate framework through which changes in paleobiodiversity can potentially be addressed. Conversely, absolute paleoclimate estimates, such as those attained through stable isotope geochemistry, provide a precise numerical value for paleoclimate proxies. These values can provide a better comparison with today's climates, determining, for example, if a climate would be classified as subtropical or warm-temperate in today's criteria, and if there would have been seasonal frost. Plant macrofossils (leaves) have an advantage as paleoclimate proxies, as they constitute a direct biological link to the paleoenvironments that they provide climate estimates for. When preserved in association with fossil vertebrate assemblages, fossil plant data provides invaluable information about local abiotic factors influencing paleoecosystems at the time of deposition. In this study, we used the Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe 1993; Spicer 2006), which utilizes the physiognomy of fossil dicotyledonous angiosperm leaves to generate an estimate of mean annual temperature (MAT) based on modern flora. One of the benefits of the CLAMP program is that it is ataxonomic (it can be used even if the leaves are unidentifiable), and it is robust against missing data (i.e. incomplete leaves).

Included in this study were approximately one hundred fossil leaves collected from one paleofloral site in Dinosaur Provincial Park during the summer of 2017. This diverse assemblage of leaves represents one of the best fossil leaf collections from Dinosaur Provincial Park, containing 16 distinct leaf morphotypes. All of the morphotypes were from angiosperm plants, with the exception of two *Ginkgo* species. Several of the more common morphotypes, such as the *Plantanus*-like, *Betula*-like and *Salix*-like morphotypes are reasonably well-known in the Late Cretaceous of Canada (Aulenback 2009; Bamforth et al. 2014), while other morphotypes were rare or unknown. Although more research and more specimens are required, it is possible that Dinosaur Provincial Park contained a relatively unique paleoflora.

Our preliminary CLAMP analysis indicates that mean annual temperature at the time the fossil leaves were living was 13.8°C (± 2.0), with a cold month mean temperature of 7.6°C (± 3.3) and a warm month mean temperature of 21.7°C (± 3.1). According to the Köppen Climate Classification System (Köppen 1936; Esssenwager 2001), this places Dinosaur Provincial Park within a 'mesothermal' environment classification, defined as a climate in which the temperature during the coldest month is less than 13°C. Subtropical climates (a subdivision of mesothermal climates) are characterized by a temperature range of 6-13°C during the coldest month, and an

average temperature greater than 22°C during the warmest month. With a cold month mean temperature of 5.1°C, the paleoenvironment of Dinosaur Provincial Park falls just within this range.

At this preliminary stage, the assemblage appears to lack morphotypes associated with evergreen angiosperms, unlike paleofloral sites of similar age in the United States (McIver et al. 2002). This suggests that the north-south ecotone suggested by McIver et al. (2002) to have been present in the Maastrichtian of central Canada was established as early as the Campanian. Insights such as these could provide critical, and hitherto unknown, insights about the climate in DPP, and about the abiotic drivers that shaped its biodiversity.

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Endocast reconstructions and comparisons between *Cricosaurus* sp. and *Stolokrosuchus lapparenti*

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Crocodylomorpha encompass a wide range of ecological niches that have spanned from the Late Triassic to the modern era. While modern crocodilians share very similar ecological roles to each other, they do not do justice to the long ancestry of the lineage. As the superorder has been so diverse, differences in brain structure between species and lineages is only to be expected. The endocasts of two species of extinct members of Crocodylomorpha have been reconstructed and examined. The two species that were reconstructed were *Cricosaurus* sp., a member of the marine group Metriorhynchidae, and *Stolokrosuchus lapparenti*, a member of Neosuchia that lived a terrestrial or semi-aquatic life in a fresh-water environment. The endocasts were then compared to each other, followed by comparing each of them with the contemporary *Crocodylus johnstoni* and the extinct *Pholidosaurus meyeri*. The species were chosen as we have excellent reconstructions of the endocasts of modern crocodilians for comparison while the extinct species was chosen due to the similar niche it filled to modern crocodilians, but evolved from a separate branch within Neosuchia. Current results show that the endocast of *Cricosaurus* sp. appears to be radically different from the endocasts of other members of Crocodylomorpha, though this may be an artifact of the lower resolution of the CT scans. Due to the poor quality of the scan, in particular the cerebrum, it is difficult to say whether the large differences are due to ecological influences or is a matter of phylogeny. By comparison, the endocast of *Stolokrosuchus lapparenti* has more in common in terms of endocast structure and the contacts between nerves and the endocast with more derived members of Crocodylomorpha. Smaller olfactory bulbs can likely be correlated with its ecology as a probable mud-sifter, relying on the specialized snout tip for detecting prey rather than smell (Larsson & Gado 2000). It is difficult to say what the function of the abnormal pneumatics present within the skull of *Stolokrosuchus lapparenti* was at the given time, though it may simply be a product of being a derived species from basal Neosuchia.

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Tooth development time and the evolution of heterodont dentitions

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Patterning of the vertebrate dentition is an extensively studied topic in the fields of palaeontology and developmental biology. It is well known that animals with continuous tooth replacement (polyphyodonty) replace their teeth in distinct waves around the mouth, the timing of which is predictable over long time periods. The slowing of tooth replacement in the synapsid lineage has been posited as one of the key mechanisms in the evolution of diphyodont (one replacement), heterodont dentitions from polyphyodont, homodont ancestors. As most studies on the patterning and timing of polyphyodonty have focused on homodont animals, the relationship between tooth size and shape and wave replacement patterns is unknown. In this study, we reanalyze historical x-ray data of polyphyodont heterodont reptiles [*Dracaena* (n=2), *Varanus* (n=3), *Teius* (n=2), and *Alligator* (n=2)] collected monthly for up to two years by Gord Edmund of the Royal Ontario Museum in the 1960s. The timing of tooth development versus tooth replacement can be determined by scoring the presence/absence of functional and developing teeth over the course of the data collection period. Results in all animals show normal, predictable wave replacement patterns in the dentition. In *Teius*, which has teeth with shape differences but are similarly sized, the timing of tooth development and tooth replacement is tightly correlated. However, in the heterodont reptiles with pronounced differences in tooth size, the developmental time is different between teeth: smaller teeth take one or two months to develop before eruption, while larger teeth take up to five months. The results of this study in reptilian model organisms suggest that larger, more complex teeth take more time to develop than smaller, simple teeth in the same jaw. Therefore, the slowing of tooth replacement over evolutionary time is likely a key mechanism in the development of heterodont dentitions.

Nano-CT scans reveal the morphology of a Weberian apparatus in the earliest-known, articulated otophysan (Teleostei: Ostariophysi) from the late Maastrichtian Scollard Formation of Alberta

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Teleost fishes are an important element of non-marine aquatic communities of the Late Cretaceous of North America, but understanding their diversity and distribution has been challenging because they are strongly sensitive to taphonomic conditions. Although they are well represented by isolated elements preserved in vertebrate microfossil localities, articulated specimens in these fluvial-dominated systems are rare. Some taxa have been named on the basis of isolated tooth bearing elements (Estes 1964, 1969; Wilson et al. 1992) although it was recognized in these studies that the diversity of teleosts was underestimated because a large number of distinctive elements were present that could not be placed in established taxonomic groups. In an attempt to obtain a more complete understanding of the diversity and distribution of teleost fishes in the non-marine communities of North America, a morphotype approach has been used to supplement formal taxonomic studies (Brinkman and Neuman 2002, Neuman and Brinkman 2005, Brinkman et al. 2013, and Brinkman et al. 2014). Morphologically distinctive centra and tooth-bearing elements that could not be identified but were judged to be from taxonomically distinct kinds of fishes, rather than a result of variation within a taxon, were given alpha-numeric designations and treated as operational taxonomic units in the faunal analyses. Comparison with recent fishes allowed some of the morphotypes to be attributed to higher taxonomic categories (e.g., Newbrey et al. 2009), but many remain of uncertain relationships.

The discovery of a locality with complete articulated specimens of small teleosts in the late Maastrichtian Scollard Formation of Alberta presents an exceptional opportunity to identify some of the previously recognized morphotypes. Dentaries and tooth-bearing elements can often be clearly seen in the prepared specimens, but precaudal centra are generally obscured by ribs. In an attempt to overcome this limit, a specimen of particular interest was scanned with a nano-CT machine (Xradia), based in the The Cell Imaging and Analysis Network facility of McGill University. Based on general body form as seen when first discovered, this fish was tentatively identified as an ostariophysan. Features of the anterior-most vertebrae obtained through these nano-CT scans further indicate that a Weberian complex is present, refining the identification of this fish as an otophysan. These data also provide details on the morphology of the individual centra that allow the re-interpretation of isolated centra as representing otophysan fishes, which had previously been tentatively identified as ostariophysans by Brinkman et al. (2017). Based on the stratigraphic and geographic distribution of these isolated centra, this group of fishes first appeared in North America in the Turonian and are primarily southern in their distribution during the Cretaceous.

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

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The East African early Miocene is important as it was a period of taxonomic and morphological diversity among early fossil apes and monkeys (Primates: Catarhini), which exceeded their living counterparts. In order to fully understand and appreciate this diversity they must be placed into environmental context.

Traditionally, Miocene environments in East Africa have been reconstructed as dense tropical forests composed of C3 plants and likely would have been represented as a continuous stands of evergreen trees and closed interlocking crowns (Verdcourt 1963; Andrews and Van Couvering 1975). These environments were interpreted to remain stable until the middle Miocene (16-11 Ma) when global temperatures fluctuated and the continued development of the East African Rift System resulted in uplift that altered climatic regimes in Africa (Andrews and Couvering 1975; Zachos et al. 2001). This instability would have caused the break up of forest canopies and result in mixed forest, woodland and grassland environments. To date, fossil remains indicate that the earliest C3 grasslands appear in Fort Ternan, Kenya in the middle Miocene (14 Ma) and C4 grasses appeared in Kenya by 15.3 Ma but did not become a dominant feature in African environments until the late Pliocene (Retallack 1992; Cerling et al. 1997). However, emerging isotopic evidence from Ugandan fossil sites of Napak (20 Ma), Moroto (21 Ma) and Kenyan fossil sites of Rusinga Island (20-18 Ma) and Tinderet (20 Ma) indicate open canopy forests, forest mosaics and woodland environments to be present throughout the early Miocene (Kingston et al. 2009, 2011; Garrett et al. 2015; Arney et al. 2017).

This study builds on preliminary research by analyzing stable carbon isotopes of mammalian tooth enamel collected from Kalodirr and Moruorot, Kenya. Kalodirr and Moruorot are two fossil localities situated in the Turkana Basin of northern Kenya and represent the latest early Miocene (17.5-16.8 Ma) (Boschetto 1998). The goal of this project is not only to give environmental context to the fauna of these sites, but also investigate whether or not the environments of East Africa began opening before the middle Miocene.

We analyzed the stable carbon isotopes from 98 specimens belonging to 8 large bodied herbivorous mammalian families. Specimens were bulk sampled and run through an isotope mass spectrometer at the University of Florida. Environmental proxies were taken from modern African environments according to data collected by Cerling and Harris (1999) and Cerling et al. (2011). These environmental proxies were adjusted to pre-industrial atmospheric carbon levels.

Preliminary analysis of the isotope signatures from Kalodirr and Moruorot suggest a mosaic of C3 vegetation too irradiated to indicate a closed canopy forest environment and are more similar to values found in open canopy forests or woodlands. These values could indicate two environmental conclusions: (1) an open canopy forest or woodland with highly irradiated values, or (2) an open canopy forest or woodland environment with some indication of C4 components. These values demonstrate that the environmental history of East Africa was more dynamic than previously described and that the forest canopies were opening before the middle Miocene.

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A remarkably well-preserved elasmosaurid (Sauropterygia: Plesiosauria) specimen from the Upper Cretaceous (Campanian) Dinosaur Park Formation of southern Alberta

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Plesiosaurs are a bizarre and globally distributed group of aquatic reptiles that lived from Late Triassic to Late Cretaceous time. While most plesiosaur remains have been derived from marine deposits, they are also known sparingly from non-marine units such as the fluvial to estuarine sediments of the Dinosaur Park Formation (DPF) of southern Alberta. These sediments formed part of the western coastal plain of Laramidia, draining eastwards into the Western Interior Seaway, and have yielded a stratigraphically extensive collection of elasmosaurid specimens. However, most specimens collected over the past 120 years are fragmentary and non-diagnostic. This study reports on a specimen (TMP 2009.037.0068) recently collected from the upper DPF of southernmost Alberta, and which represents the most complete elasmosaurid yet known from this formation.

TMP 2009.037.0068 is a well-preserved partial skeleton, consisting of most of the trunk region and a partial forelimb, as well as the base of the neck and anterior half of the tail. This skeleton was found in a disarticulated state, within a carbonaceous, brackish to marginal marine sandstone bed just above a coal seam. This coal seam represents the base of the Lethbridge Coal Zone, which forms the uppermost 15 metres of the DPF. Other DPF specimens with overlapping anatomy are morphologically similar to TMP 2009.037.0068, but vary in size and likely ontogenetic stage, as suggested by the differing degree to which their external features are developed. This morphological similarity, especially amongst postcranial elements considered to be the most diagnostic in plesiosaurs (e.g., forelimb and girdle elements), suggests that at least some of these specimens represent the same taxon.

Study of TMP 2009.037.0068 suggests that this individual was not fully osteologically mature at the time of death. This preliminary age assessment is supported by the presence of open neurocentral sutures in most of the vertebrae and by the relatively smooth surfaces of most elements, which typically become more rugose with age. However, a comparison between this specimen and some other morphologically similar DPF specimens, whose elements are only slightly larger and exhibit ontogenetically more advanced features, suggests that TMP 2009.037.0068 was approaching full osteological maturity.

TMP 2009.037.0068 is estimated to have had a total body length of between four and five metres, which is unusually small given its presumed near-adult status. However, its diminutive size is consistent with other DPF specimens, the largest of which are markedly smaller than most Late Cretaceous marine elasmosaurids from marine units (e.g., *Albertonectes*, *Elasmosaurus*, *Styxosaurus*, *Terminonatator*). This suggests that elasmosaurids inhabiting the fluvial to estuarine deposits of the DPF may have had greater constraints on body size than those inhabiting deeper marine settings, and may represent an example of niche partitioning within a predominantly marine group of extinct tetrapods.

Comparison of creodont and carnivoran dental morphology from the Calf Creek Local Fauna (late Eocene) of Saskatchewan

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Carnivora (including bears, cats, and dogs) is a monophyletic order of placental mammals possessing two pairs of carnassial teeth. Carnassials function as self-sharpening blades that enable slicing during mastication. Creodonta is an extinct, possibly polyphyletic order of carnivorous mammals which emerged around the same time as Carnivora, but went extinct globally during the Miocene. Unlike carnivorans, creodonts often possessed more than two pairs of carnassials, which have likely evolved convergently. Competition with carnivorans has been proposed as a driver for creodont extinction, potentially exacerbated by late Paleogene and Neogene climate change. Using tooth shape metrics (orientation patch count and Dirichlet normal energy) and estimates of body mass, we test for similarities in morphospace occupation amongst coeval creodonts and carnivorans. Our study is the first to explicitly compare Carnivora and Creodonta only from a single faunal assemblage (the late Eocene Calf Creek locality, Saskatchewan). Using Principal Component Analysis, we find apparent niche partitioning amongst carnivorans that are primarily associated with differences in tooth shape. The two creodonts, *Hyaenodon horridus* and *Hemipsalodon grandis*, share characteristics of their tooth shape with their carnivoran counterparts but diverge greatly in body mass. Based on the modern correlation of prey size with carnivoran body size, we suggest that, at the Calf Creek, competition among carnivorans and creodonts was unlikely. Construction of niche overlap for creodonts and carnivorans at a larger number of localities will allows us to definitively put the competition hypothesis to rest.

Chalicotheres from the Potwar Plateau, Pakistan

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The Chalicotheriidae (Perissodactyla, Mammalia) are an unusual group of clawed herbivores that achieve a nearly global distribution during the Miocene. In the well-calibrated and highly fossiliferous Siwaliks sequence (Potwar Plateau, northern Pakistan), chalicotheres are represented by a single species, *Anisodon salinus* (Forster Cooper 1922; Colbert 1935; Pickford 1982). As part of a larger project documenting the systematics and paleoecology of Siwalik mammals, we conducted a thorough re-assessment of this material, the results of which are reported here.

Two main questions regarding the Siwalik chalicothere have been: (1) the proper generic attribution for this taxon; and (2) whether the material includes more than one species. In a comprehensive phylogenetic analysis, Anquetin et al. (2007) resurrected the genus *Anisodon* for some species. They did not specifically include the Siwalik chalicothere in their analysis, but subsequent authors have suggested that using the generic diagnoses developed by Anquetin and colleagues (2007), it should also be moved to *Anisodon* (e.g., Semprebon et al. 2011; Fahlke et al. 2013). Chalicothere fossils have been reported from Siwaliks fossil localities ranging in age from 15 to 7 Ma. This would make *A. salinus* among the longest surviving mammalian species documented on the Potwar Plateau (Flynn et al. 1995), but perhaps more than one taxon is represented.

We re-analyzed all available material of the Siwalik chalicothere from the Harvard-Geological Survey of Pakistan collections housed at Harvard University, in addition to older collections from the Yale Peabody Museum, American Museum of Natural History, and Natural History Museum, London. The material is restricted to mandibles, maxillae, isolated teeth, and elements of the manus and pes, which are extremely distinctive in chalicotheriines. We photographed and measured the material, and coded the Siwalik chalicothere dental material for characters from two recent phylogenetic analyses (Anquetin et al. 2007; Fahlke et al. 2013).

Our results clearly confirm that the Siwalik chalicothere should be placed in the genus *Anisodon*. The presence of a wide postfosette and mesiodistally oriented metastyle on M3, and features of the mandible including the lack of a retromolar space and expanded mandibular angle resemble *Anisodon* and not *Chalicotherium*. We also find that *A. salinus* is a relatively basal member of the anisodont clade, lacking the strong brevirostry seen in more derived anisodonts.

Surprisingly, we document for the first time a second chalicothere taxon in the Potwar Plateau collections. One lower molar is far too large to belong in *A. salinus* and represents a schizotheriine similar to *Ancylotherium*, which had not previously been documented in this faunal province. Furthermore, we see some evidence for morphological variation within *A. salinus*. There are two morphs in some postcranial elements, as well as in upper premolar morphology (see also Pickford 1982). This provides tantalizing, but inconclusive, evidence to suggest that there may be a second taxon of chalicotheriine lurking in the material attributed to *A. salinus*. There is no obvious stratigraphic or geographic patterning to this variation, however, and a definitive answer to this question must await the discovery of further material.

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Stable isotopic characterization of extant and Cretaceous coastal floodplain forest ecosystems

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Stable isotopic analyses have been used to test a wide range of ecological and physiological questions pertaining to extant and Cenozoic vertebrate groups, but application of these methods to considerably more ancient ecosystems has been more controversial due to concerns of diagenetic alteration. As well, relatively few extant stable isotope ecology studies have been performed on forest floodplain communities, creating a potentially problematic lack of comparative data as Mesozoic systems are often dinosaur-dominated, mixed forest and fluvial environments with considerable marine input, and lack C4 plant components. Despite these potential concerns, previous stable isotope studies of dinosaurs have suggested niche partitioning based on habitat preferences in large herbivorous dinosaur taxa, and have also hypothesized that dinosaur diet-tissue trophic discrimination factors (TDFs) were greater than those found in most extant vertebrate groups, possibly related to some unique aspect of their physiology. In order to test these hypotheses, C and O stable isotope measurements were taken from specimens collected in a vertebrate microfossil bonebed from the Oldman Formation of Alberta. These sites allow for relatively fine-scale spatial and temporal resolution, facilitating ecological analysis in the Late Cretaceous vertebrate fossil record. This dataset represents the most taxonomically comprehensive Cretaceous stable isotope study of a single site performed to date, with 16 taxa analyzed from a wide range of dinosaurs and other vertebrates. In order to establish an isotopic baseline of a coastal floodplain forest ecosystem for comparison, similar isotopic analyses were performed on an extant analogue sample of 20 vertebrate taxa from the Atchafalaya River Basin of Louisiana.

Broad overlap exists in carbon and oxygen distributions between taxa in the fossil dataset, particularly among those in similar ecological roles, though some differentiation is detectable in carbon signal between terrestrial and aquatic taxa. This pattern was also seen in the isotopic results from the Louisiana extant dataset. The presence of original aragonite in fossil mollusc shells sampled alongside the Cretaceous vertebrate specimens, and close clustering of analyzed vertebrate material with their respective taxa, suggests that diagenetic overprinting, if present, is relatively negligible. The relative isotopic distributions of ecological guilds (based on comparisons with observational natural history data) and taxonomic groups present in both samples (e.g., holostean fish, crocodilians, metatherian mammals) were also similar, providing further support for the integrity of the Cretaceous stable isotope dataset. Within the Cretaceous sample, no distinct niche partitioning was detected isotopically between large herbivorous dinosaur taxa. Similarly, all five analyzed theropod taxa were found to have broadly similar isotopic

distributions consistent with being generalist/mixed-feeding faunivores, despite more divergent/specialized diets being previously hypothesized for some of the sampled species (e.g., *Troodon* and *Richardoestesia*). The hypothesis that large magnitude TDFs explain higher than expected stable carbon values previously found in dinosaurs is refuted, as similarly enriched values are found in all sampled vertebrate groups, suggesting instead that they are related to changes in local isotopic baseline and are not a feature of dinosaur physiology. The cause of this shift in baseline may be related to differences in atmospheric carbon, as well as the taxonomic composition of the local plant community and coastally-influenced osmotic stress on plant tissues. The broad isotopic overlap between taxa in both the extant and Cretaceous datasets suggest a high degree of resource mixing and terrestrial-aquatic interchange in coastal floodplain forest ecosystems. One explanation for the lack of detection of distinct ecological niches/guilds from the stable isotope data is that whatever niche partitioning exists may not be detectable using carbon or oxygen isotopes. Alternatively, it may be that in coastal floodplain forests there is a high degree of terrestrial-aquatic connectivity/mixing in resource use and a lack of ecological saturation in terms of niche-occupation, resulting in a greater selection for ecological generalists rather than specialists in these systems.

Dragons or flying squirrels: modeling the potential for powered flight versus gliding in the bizarre theropod *Yi qi*

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Flight is a locomotory strategy that has evolved over 30 times independently across vertebrates. Powered flight, a subset of this, is much more restrictive evolving only three times, in pterosaurs, bats and paravian theropods. Only in this last group do we have enough of a dataset that we can look at major questions such as what is sufficient to allow flight and even if it evolved more than once within the group. This last question became more tangible with the discovery of the bizarre membranous winged theropod *Yi qi* (Xu et al. 2015) which appears to be a derived theropod that built a wing in a completely different way from the traditional feathered theropod model. Here, using methods derived from extant avians on flight potential as well as modeling methods to generate estimates of force production and take off ability (Burgers and Chiappe 1999, Dececchi et al. 2016), I examine if *Yi* could employ powered flight, and if so from where. Using various mass and wing area permutations I show that while *Yi* was within the range of flight possible taxa, powered flight was unlikely and ground based take off was almost impossible. I find that it is much more parsimonious to reconstruct *Yi* as a glider and thus not an independent and unique means of obtaining powered flight in theropods. This finding helps inform us on the minimal requirements we should expect to see in powered flyers as well as illustrate how gliders and flapping based locomotion using non-avian theropods differ morphologically and ecologically. My finding reinforces the idea that in the Late Jurassic and Early Cretaceous small derived theropods were diversifying morphometrically, ecologically and behaviourally. It also raises questions as to what drivers during this period facilitated multiple lineages to independently to begin to explore aerial niches for the first time.

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Earliest occurrence of the extant bowfin subfamily Amiinae (Amiiformes, Amiidae) in the fossil record in the mid-Cretaceous Cedar Mountain Formation, Utah, U.S.A.

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We report diagnostic, albeit fragmentary, material representing the earliest known appearance of the only extant bowfin subfamily, the Amiinae, from the Mussentuchit Member of the Cedar Mountain Formation, in central Utah, U. S. A. The remains occur at the Early–Late Cretaceous boundary, having been dated to the latest Albian–earliest Cenomanian by Cifelli et al. (1997), with a mean $^{40}Ar/^{39}Ar$ radiometric age of 98.39 ± 0.07 Ma. This predates the former oldest record of the Amiinae, from the middle member of the overlying Cenomanian Dakota Formation of Utah (Brinkman et al. 2013), and includes cranial material, complementing our previous knowledge of the anatomy of early amiines. It additionally demonstrates that the Late Cretaceous aspect of the fauna noted by Cifelli et al. (1999) is also reflected in its freshwater component.

Recovered specimens include a well-preserved dentary in articulation with a fragmentary articular, and isolated centra and teeth, all of which can be reliably identified, and represent an amiine of essentially modern morphology. This material was found alongside another amiid centrum of a different morphology, similar to isolated centra previously described by Brinkman et al. (2013). This indicates that at least two different bowfin taxa were present at the time of deposition. A fragmentary tooth plate bearing blunt teeth, and isolated, similarly blunt styliform teeth were also recovered, and may represent amiid material as well, although these could alternatively represent semionotiform or pycnodontiform material.

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The internal cranial anatomy of *Champsosaurus lindoei* (Diapsida: Choristodera) and its functional implications

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Champsosaurus lindoei was a small, gharial-like reptile that lived during the Late Cretaceous in what is now Alberta and Saskatchewan. Although these animals are well represented in the fossil record, little is known about their internal cranial anatomy (e.g., brain endocast, inner ear) often due to poor preservation of their delicate skulls. Yet clarification of these structures promises to inform reconstructions of the animal's elusive life habits. Our research describes the internal cranial anatomy of *C. lindoei* using high-resolution computed tomography (CT) scanning of a well-preserved skull (CMN 8920) housed at the Canadian Museum of Nature (Ottawa). Between the small size of the skull (27.6 cm) and incomplete fusion of the parietals and frontals, the skull is interpreted as having belonged to an immature individual. The resulting CT data were visualized and segmented using Amira v.5 software to produce a three-dimensional model of the skull, and virtual endocasts of the brain and inner ear. Preliminary findings demonstrate that the opening between the brain endocast and inner ear is substantial, suggesting that the medial wall of the auditory capsule was cartilaginous in CMN 8920. Additionally, the fossa for the pars inferior is unusually large compared to other reptilian taxa such as gharials. On the basis of the canal that carried cranial nerve IX (glossopharyngeal nerve), which exits through the posterior wall of the auditory capsule, it is interpreted that the large fossa also housed the pharyngotympanic sinus in addition to the pars inferior. The inferred size and position of the pharyngotympanic sinuses suggests that the right and left middle ears of *C. lindoei* were acoustically coupled, a feature seen in many species of modern reptiles. The three semicircular canals are approximately orthogonal, and roughly circular in outline. The lateral semicircular canal is angled anteroventrally relative to the long axis of the skull, a trait not seen in modern crocodilians. The strongly curved semicircular canals suggest that *C. lindoei* was sensitive to angular movement of the head in each major axis of motion, supporting previous hypotheses that champsosaurs were agile when in the water. The angle of the lateral semicircular canals suggests that *C. lindoei* may have habitually angled its head anterodorsally when floating in water, consistent with the terminal location of the nares on the rostrum.

First record of Miocene-aged mammals from Grasslands National Park, Saskatchewan

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The Wood Mountain Formation (Miocene) extends across ~160 km of southern Saskatchewan from the east to west. In some locations, Wood Mountain deposits are thin, in others they reach a maximum thickness of 31 m and are characterized by loosely consolidated or unconsolidated gravels and sands. The Wood Mountain Formation unconformably overlies the Paleocene Ravenscrag Formation or Late Cretaceous Whitemud or Frenchman deposits. In Grasslands National Park (GNP), Wood Mountain deposits are confined to the north-western-most region of the East Block. In 2017, we identified two new fossil-bearing exposures of Wood Mountain Formation in GNP. The deposits are < 1m thick and typical of the Wood Mountain Formation, comprised of unconsolidated gravels and sands overlying the buff (mid Paleocene) facies of the Ravenscrag Formation. The fossils consist primarily of teeth and some post-crania. We report the occurrence of *Merychippus* sp., *Archaeohippus* sp., *Merycodus* sp., ?*Ticholeptus* sp., and Carnivora indet. *Merychippus* is, by far, the most common vertebrate fossil. The presence of low-crowned and high-crowned ungulate taxa is suggestive of a woodland savannah, as in previous palaeoenvironmental reconstructions. We collected matrix from the two new Wood Mountain sites in GNP for screen washing and expect to find small mammals, including rodents and lagomorphs. Continued work on Wood Mountain vertebrates will expand our knowledge of the Canadian Miocene and clarify whether these relatively high latitude faunas were similar to their lower-latitude counterparts.

The first record of dinosaur eggshell from the Horseshoe Canyon Formation (Maastrichtian) of Alberta, Canada

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Eggs and eggshell are generally rare in the Upper Cretaceous rocks of Alberta, despite being relatively abundant nearby in Montana. Palaeontologists and other people have been prospecting the Horseshoe Canyon Formation for more than a 130 years, but eggshell fragments have only just been recovered. The fragments are unornamented with angusticanaliculate pores and three structural layers. Numerous features support their referral to *Prismatoolithus levis*, and they confirm the presence of a bird-like external layer in this ootaxon. The fragments, which likely belonged to *Albertavenator curriei*, are from a site with abundant troodontid teeth and perinate material from hadrosaurs, ceratopsians, and theropods. The discovery of eggshell challenges the notion that the Horseshoe Canyon Formation is too heavily sideritized to preserve eggshell.

Unusual dentition in the first unequivocal tylosaurine mosasaur (Squamata: Mosasauridae) from above 60°N paleolatitude

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Mosasaurs were large aquatic lizards that lived during the Late Cretaceous (c. 100–66 Ma), the largest growing up to 13 m long. Of six subfamilies we recognize today, four are known to have been hydropedal, or flipper-bearing, either predominantly (Mosasaurinae) or exclusively (Tylosaurinae, Plioplatecarpinae, and Halisaurinae). These hydropedal mosasaurs exhibited a bifurcate vertical tailfin and many attained a body length of 5 m or more. They were cosmopolitan apex predators, and their remains occur on every continent, including Antarctica. In the Northern Hemisphere, the challenges of paleontological fieldwork in high latitudes have biased mosasaur collections such that a majority of mosasaur fossils are found within 0º–60ºN paleolatitude, and plioplatecarpine mosasaurs are the only mosasaurs yet confirmed to have existed in paleolatitudes higher than 60ºN. However, this does not mean that fossils of other mosasaurs are necessarily lacking at such latitudes. Herein, we report on the northernmost occurrence of a tylosaurine mosasaur from near Grande Prairie in Alberta, Canada (c. 85–80 Ma). Recovered from 65ºN paleolatitude, this material (TMP2014.011.0001) is assignable to Tylosaurinae by exhibiting the following suite of characters: cylindrical rostrum; broadly parallel-sided premaxillo-maxillary sutures; and overall homodonty. We further refer this material to *Tylosaurus* based on the premaxilla lacking a dorsal midsagittal ridge. Unexpectedly, TMP2014.011.0001 exhibits widely spaced, high-aspect-ratio teeth, a juvenile condition, despite its sub-adult or adult age based on the estimated body length of 5.9 m. This study suggests the presence of a rich Cretaceous boreal marine community that sustained apex predators as large as non-juvenile tylosaurines.

A new Dinosaur Park Formation (Campanian, Late Cretaceous) microvertebrate locality from southwest Saskatchewan

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The Dinosaur Park Formation has been well-studied in Alberta for decades, particularly in Dinosaur Provincial Park, a UNESCO World Heritage Site, from which the formation gets its name. Although deposits from the same time period have been known in Saskatchewan for nearly as long, it was not until this year (2018) that the Dinosaur Park Formation was described in the province (see Gilbert et al. 2018). Outcrops of the Dinosaur Park Formation are far less common and extensive in Saskatchewan when compared to Alberta but are rich in vertebrate fossils. Studying the floras and faunas of the Dinosaur Park Formation in both provinces can allow for important studies of spatial beta diversity trends, particularly in relation to proximity

to the paleocoastline as a biodiversity driver. Herein, we describe a new Dinosaur Park Formation locality in Saskatchewan known as Woodpile Coulee.

The site is located in the extreme southwest corner of the province on the southern flank of the Cypress Hills. Outcrops are recorded along two or three small creeks adjacent to the United States/Canada boundary and the Alberta border (Township 27, range 1). The best exposures in this region occur at Woodpile Coulee, where the entirety of the Belly River Group is exposed in roughly inclined strata (dipping ~40º to the south) associated with a Pleistocene thrust structure. Furnival (1946) studied the region and correlated the beds with the Judith River Formation of Montana. In the region, the Dinosaur Park Formation consists of coal dominated muds, silts, and fine-grained sands highly influenced by small-scale transgressive-regressive cycles. The microsite is situated very near the Bearpaw-Dinsosaur Park Formation contact in a silty mudstone dominated by gastropods and bivalves.

The Woodpile Coulee microsite contains at least 36 different paleospecies. Fossils were first collected in the late 1980s and early 1990s by the Royal Saskatchewan Museum, which currently curates the collection at the T. rex Discovery Centre in Eastend, SK. One subsequent collection was made in 2014, which included a bulk sample of the fossil-producing layer. The paleocommunity recovered from the Woodpile Coulee microsite is somewhat unusual in Saskatchewan, containing several taxa that are rare or unknown elsewhere in the province. Among the dinosaur species present are nodosaurs (possibly *Edmontonia* sp. and/or *Panoplosaurus* sp.), represented only by their distinct teeth, which are known from only one other site (Gilbert et al. 2018). Several teeth from a pachycephalosaur, suggested to be *Stegoceras* sp., have also been recorded, making it the first occurrence of this genus in Saskatchewan. At least one hadrosaur and one ceratopsian are known from the site, as well as a small hypsolophodont suggested to be *Thescelosaurus* sp. Tyrannosaurids are present, in addition to several small theropods, including *Troodon* sp. Crocodile material, attributed to the genus *Leidyosuchus* sp., and champsosaur material is fairly common. There are at least two families of turtles, including baenids and trionychids, as well as a broad diversity of fish from several different orders, including at least five teleost taxa. Teeth from the ray *Myledaphus* are also well represented.

Intriguingly, the fauna at Woodpile Coulee shares an interesting characteristic with the only other Dinosaur Park Formation assemblage found in Saskatchewan (see Gilbert et al. 2018). The microsite contains a diverse assemblage of both chondrichtians and amphibians. As the sharks present are marine species, and as amphibians are generally known to be intolerant of salinity, the presence of an abundance and diversity of both groups suggests mixing of two different environments. The single occurrence of an ammonite fragment reinforces that the site was deposited under marine influence, while the presence of salamanders, frogs and mammals reinforces the idea of mixing from a terrestrial environment.

The Woodpile Coulee site is unique both in terms of biodiversity and depositional environment. Future studies of this locality will provide important insights into our current understanding of the Dinosaur Park Formation in Saskatchewan, and will lead to very interesting and significant discoveries.

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A monstersaurian lizard frontal from the Wapiti Formation (Campanian) of central-western Alberta

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The Upper Cretaceous terrestrial deposits of the Wapiti Formation in central-western Alberta continue to provide novel insights into the diversity of Mesozoic vertebrates. The newly discovered DC Bonebed, inferred to represent a channel deposit, preserves an abundance of well-preserved, isolated elements from a diverse assemblage of small to medium-sized vertebrates. Among the specimens recently recovered is an isolated right frontal of a lizard referable to the anguimorph clade Monstersauria, which includes the extant Gila monster and beaded lizards (*Heloderma* spp.) alongside various extinct Mesozoic and Cenozoic species. This bone is essentially complete, including an intact interfrontal suture (indicating paired, unfused frontals) and the presence of mound-like, pitted osteoderms on the dorsal surface of the frontal, which are autapomorphies of Monstersauria. Although taxonomically indeterminate at the species level, osteoderms on the dorsal surface are comparable to those found on the skull bones of *Paraderma*, *Labrodioctes* and *Primaderma*, Cretaceous North American monstersaurs characterized by polygonal-shaped osteoderms and a pitted surface. The Wapiti taxon could belong to any of the previously mentioned genera, though it is unlikely to pertain to the much older *Primaderma* (Albian-Cenomanian). Furthermore, we cannot reject the possibility of this specimen pertaining to *Palaeosaniwa* due to lack of comparative material. The specimen from the Wapiti appears to represent an adult individual of comparable size (skull length = ~130 mm) to the Late Cretaceous monstersaur *Estesia mongoliensis* from Mongolia (skull length = 150 mm in the holotype), and potentially one of the largest monstersaurs known so far from the Late Cretaceous of North America. Whereas most lizard material from North America is highly fragmentary, this specimen is the most complete Cretaceous lizard frontal to have been reported in Alberta. This discovery significantly increases the known latitudinal range of monstersaur lizards during the Late Cretaceous and supports the systematic importance of the Wapiti Formation.

A diverse assemblage of Campanian turtles (Testudines) from northern Alberta

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Turtles were common terrestrial vertebrates in the Late Cretaceous of North America with an extensive fossil record. Previous work has suggested that their range was climate-mediated and that central Alberta represented the northernmost extent of their range during the Campanian-Maastrichtian, with the exact biogeographic boundary depending on fluctuations of global temperature through time. However, this understanding is based on sparse fossil evidence from areas north of the typical fossil-producing regions of southern Alberta. Previously recorded specimens from northern Alberta have been restricted to a small number of isolated shell fragments.

Here, we report on a diverse northern turtle assemblage from the Campanian Wapiti Formation in the region of Grande Prairie, including the skull of the northernmost baenid turtle ever recovered. Specimens are distributed among six different localities representative of different stratigraphic levels in the Wapiti Formation, and are penecontemporaneous with the well-known deposits and faunas from both the Dinosaur Park and Bearpaw formations of central and southern Alberta.

The baenid skull shares many features with *Plesiobaena antiqua* and *Gamerabaena sonsalla*, such as a short preorbital region, a jugal excluded from the orbital margin by a small dorsal flange of the maxilla, and lacking a contribution of the opisthotic to the stapedial foramen. A phylogenetic analysis based on a previously published phylogenetic matrix suggests this specimen is most closely related to *Plesiobaena*, *Gamerabaena*, eubaenines, and the shell taxon *Scabremys ornata*.

This assemblage allows us to examine Cretaceous turtles in detail for the first time near the limit of their northern range and has important implications for studying the biogeography of North American terrestrial turtles as well as gaining a better understanding of the poorly understood Cretaceous terrestrial vertebrate assemblages of northern Alberta. The relative diversity and abundance of a climate-sensitive vertebrate group in a near palaeo-Arctic (i.e., close to 66°N) setting also raises new questions about our understanding of terrestrial climates in the latest Cretaceous of northern North America.

Adaptations to durophagy in a new species of *Globidens* (Squamata: Mosasauridae) from the Late Cretaceous of Morocco

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Mosasaurs are giant marine squamates that roamed the world's oceans during the last 25 million years of the Cretaceous period. As apex predators in marine ecosystems, most were adapted to ambush or pursuit predation. Whereas tooth morphology and preserved gut contents have revealed that mosasaurs were probably generalists, the spherical crushing teeth and robust skulls of *Globidens* show that at least one specialized group consumed hard-shelled prey. Despite being the most recognized of the durophagous mosasaurs, *Globidens* was until recently known from partial and crushed skulls from the Santonian to Campanian of North America, as well as isolated teeth from younger Maastrichtian deposits in northern Africa. In contrast to their unique dental anatomy, surprisingly little is known about the cranial and postcranial anatomy of these rare mosasaurines.

Here we describe a new species of *Globidens* from the Maastrichtian phosphate deposits of Morocco based on a well-preserved, disarticulated cranial and partial postcranial skeleton. This new species is distinguished from the contemporaneous *Globidens phosphaticus* from Morocco and Angola by the presence of laterally compressed crushing teeth, a shorter tooth row along a straight dentary, and a lack of accessory vertebral articulations (zygosphenes and zygantra) on the cervical vertebrae. Moreover, the larger size and advanced ontogenetic stage of this specimen, as revealed by rib histology, suggest that the anatomical differences with *G. phosphaticus* could not be due to ontogenetic variation.

Skeletal reconstruction of this new species reveals an oddly proportioned skull, with a total skull length approaching a meter, but the dentaries measuring less than 40 cm. Whereas most mosasaurs have proportionally much longer and more slender jaws, this new taxon consumed prey with slow, crushing bites. The relatively undistorted cranial elements in this new specimen also reveal that the skull of *Globidens*, unlike that of modern shell-crushing lizards, was akinetic, exhibiting no movement between the skull bones during feeding. Unique to this new species and to *Globidens phosphaticus*, the teeth were attached to the jaws by a system of ligaments that would have dissipated the compressive forces of feeding, instead of being fused to the jaws as they are in most other lizards. The skull was also reinforced at the attachment sites for the jaw adductor musculature. As a result, it has the proportionally largest coronoid of any mosasaurine and a dorsally vaulted temporal arcade into which the jaw adductor musculature was inserted. Lastly, histological analysis of a cervical rib revealed the first evidence of osteosclerotic-like bone compactness in a mosasaurid, which we interpret as a buoyancy compensation mechanism for feeding on bottom-dwelling prey. These features highlight a higher degree of specialization in globidensines than previously recognized and add to a growing diversity of durophagous mosasaurs from the Tethyan region during the Maastrichtian.

Cranial and braincase morphology of diplocaulids

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Diplocaulids are iconic early tetrapods ranging from the Late Carboniferous to Middle Permian, classically placed within the taxonomic group Nectridea. A defining feature od the diplocaulids are distinct extensions of the posterior tabular elements of the skull into tabular horns. Diplocaulid dermal skulls are highly morphologically variable and therefore difficult to compare with other nectridean groups and with early tetrapods more generally, as well as with each other. This is made worse by the fact that the best known diplocaulids, *Diplocaulus* and *Diploceraspis*, are highly derived members of the group showing extreme morphology of the skull. This high degree of variability has made robust phylogenetic analysis difficult in the past, however investigations into mammalian and caecilian braincases show that the braincase is conserved across closely related taxonomic groups. To characterize diplocaulid cranial morphology we have used microscopic x-ray computed tomography (μCT) scans to study the skulls of short-horned diplocaulids from the Early Permian of Kansas, including *Ductilodon pruitti* and an undescribed broad-skulled form from the Speiser Shale (Council Grove Group) of Kansas.

Initial comparisons between the type specimen of *Ductilodon* and the broad-skulled form show differences in the shape and size of the parasphenoid with a thinner more elongate parasphenoid observed in *Ductilodon*, and a ventral keel in the broad-skulled form. The broad-skulled form also has a much more curved cheek in the dorsoventral plane. The tabulars of the undescribed specimen are more laterally elongated, whereas the tabulars in *Ductilodon* are drawn out more posteriorly, making the overall shape of the skull in the broad-skulled form much wider and shorter with a more rounded snout. The orbit of the undescribed appear shortened in the anterior-posterior plane when compared to those of *Ductilodon*. Our μCT data also show several commonalities between these taxa, including well-developed paroccipital processes of the exoccipitals, absence of a basioccipital, paired exoccipital condyles, a well-developed suture between the pterygoid, exoccipital, and parabasisphenoid, reduced palatine ramus of the pterygoid lateral to greatly enlarged interpterygoid vacuities. We conclude that the Kansas short-horned diplocaulids are both broadly comparable with the classic diplocaulids *Diplocaulus* and *Diploceraspis* as well as broader early tetrapod diversity, and may help resolve this aspect of the 'lepospondyl' origins problem.

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Epigenetic effects on morphological characters and its influence on phylogenetic reconstructions in birds and non-avian dinosaurs

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Morphological data informs all aspects of understanding the paleobiology and paleoecology of fossil organisms, but is central to how we reconstruct the phylogenetic relationships among these organisms. Recently we have seen an increasing push to ever larger morphological character datasets, sometimes into the thousands of individual characters, leading to atomize an animal into smaller and smaller discreet, and theoretically independent, units. One underlying assumption to this is that all these distinct morphologies are suspected to be linked to be modification in the genotype, but recent work has shown that environmental factors can produce heritable changes in the phenotype, without changing its underlying genetic makeup. For example, Botelho et al. (2015) found that embryonic muscle activity that influences the retroversion of the hallux, a previously purported critical adaptation to arboreal life across the theropod to bird transition, from the plesiomorphic condition seen in basal theropods. Here we use pharmacological methods to paralyse chick embryos in early development to examine how epigenetic influences alter the expression of key anatomical characters in the forelimb and pectoral girdle. These traits are important for both generating accurate reconstructions of flight potential but also are used as key features differentiation paravian clades and influencing our understanding of the early evolutionary history of birds. The results of this study will provide valuable insight into a potentially underappreciated method for producing morphological diversity as well as influencing how we view the characters we use to reconstruct the origins and early history of birds and flight.

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Late Pleistocene muskoxen: Using stable isotopes to better understand survival versus extinction

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Populations of the extant tundra muskox *Ovibos moschatus* lived alongside the closely related, yet now extinct, helmeted muskox *Bootherium bombifrons* during the Pleistocene in eastern Beringia (unglaciated Alaska and Yukon). However, tundra muskox were able to persist through the dramatic environmental changes that occurred during the Pleistocene-Holocene transition, while the helmeted muskox suffered complete extinction. As warming occurred at the Pleistocene-Holocene transition, the cold, dry environment of the Mammoth Steppe biome was replaced by wetter conditions with shrubs and woody plants becoming more dominant. Questions persist about the causal mechanisms of why one species survived, while the other did not.

Stable isotope analysis of bone collagen carbon and nitrogen provides dietary and environmental information. Here, a total of 81 late Pleistocene specimens (31 *Ovibos*, 50 *Bootherium*) were analyzed from eastern Beringia. Average stable carbon isotope compositions were similar for both muskoxen species, suggesting that each was an opportunistic mixed feeder, consuming a combination of grasses, forbs and woody plants. On average, nitrogen isotope compositions for *Ovibos* were significantly higher than *Bootherium*, perhaps suggesting *Ovibos* foraged in drier environments while *Bootherium* preferred wetter lowlands areas.

Stable Isotope Bayesian Ellipses in R (SIBER) uses stable carbon and nitrogen isotope compositions of animal tissues to determine isotopic niche size (and hence, by extension, ecological niche size) and to identify an overlap in the use of resources among species. Our results show distinctly separate isotopic niches for the two muskox species, and so they are not believed to have been in direct competition for forage. The larger isotopic niche size of *Ovibos*, however, suggests greater adaptability to a wider range of vegetation types and environmental settings, giving it an advantage over *Bootherium* when facing rapid shifts in available vegetation on the landscape.

A limitation to our current dataset should be pointed out. Results for each species are grouped regardless of temporal considerations. Radiocarbon dates beyond those currently available for 24 specimens are needed to assess temporal variations in the stable isotope data. The nitrogen isotope vegetation baseline varied throughout the late Pleistocene. Hence, the differences in average collagen nitrogen isotope compositions between the two species could be an artefact of age differences. For the purpose of this study, therefore, isotopic niche size information obtained from SIBER provides the most robust insight into late Pleistocene muskox dynamics.

A new Permian-like fauna within a single fossilized stump from the Carboniferous of Nova Scotia

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The fossil record of tetrapods from the Carboniferous of Nova Scotia has been central to understanding some of the earliest phases of tetrapod evolution, including the earliest records of the major groups of tetrapods alive today. Here we report on the discovery of a fossiliferous lycopsid 'tree' stump from the Sydney Mines Formation, Upper Pennsylvanian, Cape Breton Island, that remarkably contains the remains of at least six taxa, both non-amniote and amniote, in various states of preservation and articulation.

Significantly, most of the preserved taxa are otherwise only known by representation in the later, Permian ecosystems of North America. Most notable among these is a virtually complete skull of a large, pantylid recumbirostran, as well as four partial, articulated skeletons of a varanopid synapsid. As such, the new material provides new, earliest records of these taxa and reveals several evolutionary events vastly predate currently known occurrences. For example, CT scanning of the pantylid reveals a highly specialized dental apparatus composed of opposing dental fields on the palate and coronoids. The low, conical teeth of these fields is suggestive of complex oral processing of a diet consistent with high-fibre herbivory, well advanced to that of any known tetrapod of equivalent age. Additionally, the presence of at least three partial, articulated varanopid specimens of equal, subadult size, and an associated very small fourth, alludes to the possibility of a social aggregation – a behavior otherwise known from this clade in the Late Permian. These skeletons are consistent in many regards with mycterosaurines, except for the presence of tall, broad neural spines, suggesting they may represent a new taxon. Furthermore, a fragment of a large proximal femur is also attributable to a varanopid, and approaches the size and morphology of much later occurring varanodontines, such as the Permian-aged *Varanops*. This latter specimen reveals that this early amniote clade had already become much larger, possibly taking on a role of apex predator, well before the start of the Permian.

Together, the implications of this discovery are numerous and include revisions to the tempo of evolution of major tetrapod clades and several new additions to the Upper Carboniferous faunal record. Further detailed analyses of this material will contribute to revising our understanding of the ecosystem composition and dynamics of Upper Carboniferous tetrapod communities.

A new species of nanhsiungchelyid turtle from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada

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We report on a new species of *Basilemys* (Testudines: Nanhsiungchelyidae), based on a nearly complete shell from the Horsethief Member (lower Maastrichtian) of the Horseshoe Canyon Formation of Alberta. The new species is intermediate in age between the Campanian forms *B. variolosa* and *B. gaffneyi*, and the upper Maastrichtian forms *B. sinuosa* and *B. praeclara*. It is also intermediate in its morphology, possessing a unique suite of both plesiomorphic (e.g., divided extragulars) and derived (e.g., square epiplastral beak, pygal wider than long) traits. It is further characterized by an autapomorphic square cervical scale. Phylogenetic analysis assuming parsimony recovers the new species in a polytomy with *B. variolosa* and *B. gaffneyi*, outside the clade formed by the upper Maastrichtian forms *B. sinuosa* and *B. praeclara*. The new specimen provides the first evidence that this genus reached typical large size (~1 m long) in the Horseshoe Canyon Formation, and was not diminutive, as previously thought based on less complete shell material. Although *Basilemys* is usually regarded as terrestrial in habit based on its skull and limb morphology, we note that the low profile of its shell is a derived feature usually indicative of an aquatic mode of life. This suggests that there is yet much to learn about the life habits of this interesting turtle.

A new long-bodied recumbirostran from Mazon Creek, with a full pelage of scales, reveals amniote-like ultrastructural integumentary patterns

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The Carboniferous, Pennsylvanian-aged (309-307 Ma) Mazon Creek Lagerstätte produces some of the earliest fossils of major Paleozoic tetrapod lineages. Recently, several new tetrapod specimens collected from Mazon Creek have come to light, including some of the earliest recumbirostrans. Here we describe a new long-bodied recumbirostran, known from a single concretion (part/dorsal and counterpart/ventral), FMNH 1309, bearing a virtually complete skeleton. We utilize both parsimony and Bayesian methods to conduct phylogenetic analyses using the recent early tetrapod matrix of Pardo et al. (2017), run in the programs PAUP and MrBayes, respectively. Both analyses recover an unresolved basal polytomy among the major recumbirostran clades, and place the new specimen as the sister taxon to the cocytinid *Brachydectes*. Our new taxon represents an important early record of an elongate recumbirostran bauplan, bearing several features linked to fossoriality, including the characteristic recumbent snout. Interestingly, FMNH 1309 also preserves a pelage of scale-like structures, and lacks any

trace of gastralia. Ultrastructural investigation using scanning electron microscopy (SEM) reveals these structures consist of small 'fractal' fibres inconsistent with bone and, instead, suggestive of a keratinous composition. When compared to the ultrastructure of extant reptile and amphibian epidermis compiled from the existing literature, a strong resemblance to the ultrastructure of extant snakes and fossorial reptile scales, which have scales modified for body-based propulsion, is found. On the basis of these data, we identify the structures preserved in FMNH 1309 as epidermal, keratinous scales. We synthesize records of the distribution of integumentary structures across Recumbirostra, noting the loss of gastralia and bony osteoderms as associated with body elongation and increased fossoriality in groups such as lysorophians. Additionally, our new specimen provides the oldest record of keratinous scales in the tetrapod fossil record, and provides an important data point when considering the timing of the origin of amniote-like terrestrial adaptations and of amniotes themselves, particularly given the recent hypothesis that recumbirostrans are eureptiles (Pardo et al. 2017).

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

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

How much did a pterosaur weigh? A case study of a well-preserved *Coloborhynchus* and pterosaur mass estimation

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Mass estimation of pterosaurs has long been controversial, impeded by a poor fossil record and understanding of soft tissue distribution. Previous studies have been suggested to rely too much on modern birds as analogues, or claimed degrees of pneumaticity that are improbable. Here, computed tomography imaging of three-dimensionally (3D) preserved skeleton of *Coloborhynchus robustus* is used to create a 3D skeletal reconstruction, and infer soft tissue body outlines and volumes, using muscular reconstructions as a guide. Membrane volume is estimated based on the inferred ankle attachment point from known fossils, and thickness from recent studies on membrane properties. Densities of different regions are assigned based on previous pterosaur studies and birds, taking into account their differences where possible. The result of the 3D volume reconstruction estimation (3D-VRE) for a *C. robustus* with a 5m wingspan is 30.9 kg. Convex hull volume estimation results in 23.6 kg. A combination of 3D-VRE and convex hull results in an estimated preferred mass of 29.5 kg. This is heavier than estimates from other volumetric studies of similarly-sized, closely-related animals, but similar to those derived from regressions and scaling equations previously used for estimating pterosaur mass. As skeletal correlates are often argued as being a less subjective method of mass estimation due to strong relationships between limb element dimensions and body mass in modern animals, commonly used correlates are also tested for this animal. However, well-supported correlates in both quadrupedal and bipedal, as well as volant and non-volant animals (e.g., circumference or diameter of the humerus or femur) produced substantial over- (humerus) or under- (femur) estimates, and are therefore not currently recommended for use in pterosaurs. Only one skeletal correlate produced a similar mass estimate, that of an avian humerus, though the significant differences in morphology between pterosaurs and birds imply this may be a coincidence. This suggests that volumetric methods, though subjective and time consuming, may be more accurate for pterosaur mass estimation, given the morphological and phylogenetic distance from modern animals.

Variation in the braincase and cranial ornamentation of *Maiasaura peeblesorum* (Ornithischia, Hadrosauridae) from the Campanian Two Medicine Formation of Montana: implications for brachylophosaurin ontogeny and evolution

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The duck-billed dinosaur (Hadrosauridae) tribe Brachylophosaurini includes several closely related genera from the Campanian (Upper Cretaceous) of western North America that have been hypothesized to represent an ancestor-descendant lineage, making these dinosaurs highly significant to studies of evolutionary tempo and mode, and terrestrial biostratigraphic correlation. The iconic "good mother" dinosaur *Maiasaura peeblesorum* from the Two Medicine Formation of northern Montana is universally recognized as a brachylophosaurin, but various relationships to other members within this clade have been recovered in phylogenetic analyses (Gates et al. 2011; Freedman Fowler and Horner 2015). New material of *Maiasaura* is examined to describe morphological variation in the braincase and surrounding skull elements. The smallest of six partial *Maiasaura* skulls examined in this study (ROM 66182) is approximately two thirds as wide as the largest (ROM 66180). Similar to other brachylophosaurins, larger skulls of *M. peeblesorum* have a proportionately wider braincase and a larger, more rugosely ridged nasofrontal contact, which are interpreted as ontogenetic variation. In mature individuals of *M. peeblesorum* the frontal platform incipiently overhangs the supratemporal fenestrae, approaching the condition in *Brachylophosaurus* individuals that have the nasals covering the entire frontals, despite the absence of the latter character in *Maiasaura*. Mature *Maiasaura* skulls have a deep nasofrontal crest with an autapomorphic, vertically oriented, scoop-shaped nasofrontal suture that develops late in ontogeny. In the largest skull examined, the crest is semicircular in anterior view and incorporates flared, concave prefrontals in its lateral margins. Intraspecific variation in *M. peeblesorum* is observed in cranial characters previously discussed as interspecific variation in brachylophosaurins, including the prominence of dorsal depressions on the frontal, and the position of the foramen for the facial nerve (CN VII). A comparison of the cranial ornament and braincase ontogeny in *Maiasaura* to related taxa is discussed in relation to the hypothesis that heterochrony was an important mechanism in the evolution of new brachylophosaurin genera, and its implications for the relationships of *Maiasaura* within Brachylophosaurini.

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Limb evolution in Late Cretaceous marine squamates and the polyphyly of mosasaurs

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Mosasaurs are traditionally considered as a natural (monophyletic) group of Cretaceous marine lizards possessing aquatically adapted appendicular skeletons; specifically, paddle-like limbs (the hydropedal condition), and a loss of connection between the ilium and the sacral vertebrae (the hydropelvic condition). The semi-aquatic intermediates to this derived condition are understood to be the aigialosaurs: a poorly defined group of small, elongate lizards showing an intermediate stage of aquatic adaptations including laterally compressed tails and some reduction and alteration of the appendicular skeleton. The aigialosaurs are conventionally assigned to the stem of the crown mosasaur lineage (i.e., those expressing the hydropedal condition), and consequently, are also referred to as 'mosasauroids'.

Discovery and reanalysis of several species of mosasauroid over the last decade and a half have challenged this conventional understanding of the concept of a 'mosasaur'. The most derived mosasaurs fall into two major groups that may appear externally convergent, but have their own specialized solutions the problem of aquatic living. Certain aigialosaur-grade species show close affinities to one of the two clades within the derived mosasaurs, suggesting multiple independent origins of the derived mosasaur bauplan. However, poor cladistic resolution and a high degree of homoplasy within the Mosasauroidea (a common problem among crown groups) has resulted in tenuous support for this theory.

The discovery of a new species of aigialosaur with an exquisitely preserved forelimb provides new, solid evidence in support of the polyphyletic mosasaur hypothesis. It is this appendage in particular that provides the robustness of this evidence, given that the definition of a 'mosasaur' is so closely tied to the evolution of the hydropedal condition. A thorough re-examination of all described species of semi-aquatic mosasauroid, including *Carsosaurus, Komensaurus, Aigialosaurus, Dallasaurus, Haasiasaurus, Judeasaurus,* and *Vallecillosaurus*, in addition to an examination of a wide variety of derived mosasaur taxa has demonstrated two major limb morphotypes: one with well-ossified and blocky elements, the other with poorly ossified, sub-rounded elements, and a secondary loss of a bony mesopodium. Here, I demonstrate that each morphotype has hypothetical intermediate forms demonstrated by aigialosaur-grade species, providing strong evidence for the multiple, independent evolution and convergence of paddle-like limbs. This model, combined with stratigraphic data, evidence from other skeletal regions, and corroborated by newly produced phylogenetic studies, lead to the conclusion that mosasaurs do not exist in the biological sense, that the term 'mosasaur' must be redefined, and that our understanding of this group's evolutionary history be reimagined.

Redescription of the holotype of *Barbus megacephalus* Günther, 1876 (Teleostei: Cyprinidae)

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Cypriniform fishes, based on ostariophysan relationships, should have an age equivalent to that of Siluriformes or Characiformes, both of which are known from the Late Cretaceous. However, the earliest cypriniforms are not known until the Cenozoic. Within this order, the oldest known fossils of the family Cyprinidae are from deposits believed to be of Eocene age, from the Sangkarewang Formation of the Ombilin Basin in Sumatra, Indonesia. Cyprinids and other fish fossils from this locality were collected over 150 years ago, and many were originally described as belonging to modern genera or species.

One cyprinid taxon collected from the locality was represented by a single, very large specimen presented to the British Museum of Natural History (now the Natural History Museum, London) by Herr R. D. M. Verbeek in 1876. This specimen was studied by Günther (1876) who described it in an extant genus as *Barbus megacephalus*. Further collections from the locality were undertaken by the geologist Dr. K.A.F.R. Musper in 1927 and 1928. His material was studied by Saunders (1934), and included four specimens which she assigned to *B. megacephalus*. Unfortunately, Musper's material cannot be found and is presumed lost. Therefore, the only known specimen remaining for *Barbus megacephalus* is the holotype, NHMUK PV P 9431.

Günter's (1876) description of this fish, as was normal at that time, was quite sparse. He provided measurements and counts, and a few comments on the body form (e.g., page 438 "The snout was particularly long; the eye being situated nearer to the posterior than to the anterior end of the head, close below the upper profile."). Günther (1876: pl. XVIII) also provided an artist's rendition of the fossil, but this also lacked detail. Sanders (1934) indicated her material was not as well-preserved as the holotype and therefore she provided no additional descriptive information and no figures, merely indicating that she thought the species might be better placed in the genus *Labeobarbus*, as that genus was represented by several species in Indonesia that reach a very large size.

The cursory description of the type and the lack of any other material, prevents including what is one of the oldest known cyprinids in any phylogenetic analyses. Although the type is still obscured in some areas by sediment, redescription of the material, including describing features that have been used in morphology-based phylogenetic analyses of extant cyprinids, will allow a better understanding of the relationships of *Barbus megacephalus*, and will also allow this Eocene taxon to be used to inform us about the evolution of characters in the earliest known fossil members of the family.

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Characterizing the anatomical details of the iliosacral joint in extant and fossil lizards

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The iliosacral joint (ISJ) is crucial to terrestrial locomotion in tetrapods, because it transfers the forces of gravity between the appendicular and axial skeletons. Moreover, in obligatorily aquatic tetrapods, the ISJ is heavily modified, or lost altogether in several groups. Despite its importance for understanding aquatic adaptation in tetrapods, the variation in morphology of the ISJ across terrestrial and aquatic lizards, although perceived as important, has been greatly overlooked and scarcely characterized beyond macroscopic osteological point of view.

A recently discovered dolichosaur (Squamata, Pythonomorpha) from Upper Cretaceous deposits of the Apulian Platform (Puglia, Southern Italy), with exceptional preservation of soft tissues and cartilaginous elements, raised questions concerning the early stages of modification of the ISJ in semi-aquatic lizards(e.g., dolichosaurs), to fully-aquatic (e.g., mosasaurs) forms. The new fossil lizard shows the presence of a conspicuous amount of cartilage mediating the contact between both sacral ribs and the posterior process of the ilium. Although the presence of cartilage at such contact is macroscopically visible through osteological observation in most extant lizards, the relative proportion of cartilage in this joint much higher in this new dolichosaur. Whether this feature is related to its aquatic lifestyle or it is a common feature of squamates has yet to be determined, because we have no information on the histology of the lizard ISJ.

There are two main categories of joints: 1) diarthroses or synovial joints, which are the type of joints that allow for greater mobility; and 2) synarthroses (including sutures, synchondroses, and syndesmoses), allowing for no or limited mobility. Our primary goal was to define what type of joint is the ISJ in extant terrestrial lizards, and use it then as a reference for comparison with semi-aquatic and fully-aquatic lizards, both extant and fossil.

A combination of osteological examination, microcomputed tomography (μCT) and serial histology (SH) allowed us to investigate the macro and microanatomical details of the ISJ across several iguanian lizards, a group that includes both terrestrial and semi-aquatic forms, and make some comparisons with key fossil taxa.

Our results show that in terrestrial taxa, abundant articular cartilage is present on both the distal end of the first sacral rib and its corresponding facet on the posterior iliac process, with an intermediary cavity between the two elements surrounded by dense fibrous tissue. All these features together would suggest that this is a synovial joint. However, moving posteriorly through the histological series, towards the contact between the second sacral rib and the ilium, the intermediary cavity disappears and the contact is predominantly characterized by a dense fibrous tissue, with articular cartilage only present at the sacral rib distal end. The lack of a synovial cavity and the increase of a fibrous tissue-based connection in this region is consistent with a syndesmosis, which is a less mobile type of joint. Such transition would suggest that greater mobility is allowed more anteriorly at the ISJ, while posteriorly the motion is somehow limited and the sacral contact becomes firmer. In our terrestrial lizard specimens, the amount of cartilage at the iliosacral contact diminishes going from the first to the second sacral rib; but in the new dolichosaur specimen from Italy, a relatively thick layer of cartilage is still visible also distally to the second sacral rib, giving the impression that a greater mobility of the ISJ is allowed both at the first and second sacral rib.

The variation we describe in the ISJ in terrestrial and semi-aquatic squamates could be related to a high degree of variation in the mobility of the ISJ in lizards, or these could represent successive stages from a weight-bearing ISJ, to a more vestigial, cartilaginous joint. We argue that in order to better understand how squamates repeatedly adapted to life in water, we must first characterize this important structure in terrestrial squamates, and make meaningful comparisons with transitional fossil taxa.

New μCT data on nectrideans reveals unappreciated complexities in early tetrapod evolution

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For the past two decades, phylogenetic analyses of early tetrapod relationships have placed the majority of Paleozoic tetrapods with specialized cranial and axial morphology within a single monophyletic clade, the Lepospondyli, which has alternately been placed on the amniote or amphibian stem. This consensus has led to a view of overall morphological and ecological stasis among early tetrapods with high rates of phenotypic evolution limited to a small number of clades. This consensus has been challenged by recent work showing that one lepospondyl group, Aïstopoda, definitively represent morphological experimentation in Devonian stem-tetrapods, whereas a second lepospondyl lineage, Recumbirostra, is most parsimoniously understood as part of an early diversification of crown amniotes. However, the phylogenetic relationships of the remaining lepospondyl lineages, particularly the Nectridea, remains uncertain. We here present new μCT data collected for two diplocaulids, the sauropleurine *Crossotelos*, and a new urocordylid that amend this deficiency. There are few commonalities between these three taxa that are not shared more broadly among tetrapods. Diplocaulids show a number of features of the braincase, palate, and lower jaw which suggest affinities with temnospondyls, including organization of the occipital arch, extensive fusion of the basipterygoid joint, reduction of the palatine ramus of the pterygoid, and structure of the adductor fossa. Meanwhile, *Crossotelos* shows a number of features consistent with a position within Devonian tetrapod diversity but separate from aïstopods, including a massive Meckelian bone, chamfered sutural relationship between the dentary and infradentary bones, deep notochordal pit in the basiocciput, prominent basipterygoid processes, large slit-like spiracular embayment, and lack of a prominent tabular process of the parietal. The new urocordylid shows an organization of the shoulder girdle and humerus consistent with a phylogenetic position among whatcheeriids and colosteids, but with unique characteristics, including an articulation between the scapulocoracoid and first thoracic rib. Phylogenetic analysis shows that none of the three nectridean taxa studied here fall into the traditional positions of 'lepospondyls' in early tetrapod phylogeny, and do not have an effect on the novel controversial position of recumbirostrans within Amniota. A monophyletic Leposondyli is increasingly untenable and holospondylous vertebrae characterized by thin perichordal ossifications and uninterrupted notochord appeared in numerous convergent lineages. More generally, lepospondyl polyphyly shows that an inclusive Tetrapoda actively experimented in ecomorphospace throughout the Late Paleozoic.

Comparison of hind limb morphology of *Leptoceratops gracilis* (Ornithischia: Ceratopsia) to basal psittacosaurids and derived ceratopsids

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The most derived non-ceratopsid neoceratopsians, leptoceratopsids are a group ranging throughout North America at the end of the Cretaceous. The most basal ceratopsians (psittacosaurids) are bipedal, small-bodied taxa of Asia with a number of diagnostic gracile features. The most derived ceratopsians, the ceratopsids, are large-bodied obligate quadrupeds. Phylogenetically, leptoceratopsids mark a major inflection point in ceratopsian evolution as a clade that potentially retains bipedalism into the latest of the Cretaceous. The best-represented leptoceratopsid, is *Leptoceratops gracilis*, and is well documented from multiple specimens of the Upper Cretaceous of North America from Hell's Creek Formation in Montana to the Scollard Formation in Alberta. Research on this ceratopsian has primarily consisted of biomechanics and/or morphology of the skull and teeth, with no focus on postcrania. The research conferred here compares the hind limb and pes of a 1951 specimen of *Leptoceratops gracilis* (CMN 8889) from the Scollard Formation of Alberta. *Leptoceratops* demonstrates a variety of features to be expected from an intermediate representative between psittacosaurids to ceratopsids, including a straightened femoral shaft, the splaying of the pes, and the reduction of claw-like unguals. These morphologies suggest leptoceratopsids in regards to postcranial development are facultative bipedal animals and share a closer affinity to their Asian ancestors than to their North American sister group.

Palaeoecology of early Pliocene beaver from Ellesmere Island revealed by stable isotopes of coeval plant fossils and bone collagen

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Stable carbon and nitrogen isotope analysis of plant macrofossils and fossil vertebrate remains from a High Arctic Pliocene peat deposit (Beaver Pond site) further our understanding of the ecology of the extinct castorid *Dipoides*. The exceptionally well-preserved assemblages originate from a high-terrace peat layer at Strathcona Fiord on Ellesmere Island, Nunavut, Canada. The site represents a rare example of a North American High Arctic ecosystem during the early Pliocene (4 to 5 mya). Plant species from the macrofossil assemblage indicate a significantly warmer climate than at present, with a *Scorpidium* dominated wetland habitat surrounded by open larch dominated forest-tundra. The larch belongs to an extinct species (*Larix groenlandii*). The remains of the extinct

semi-aquatic Pliocene beaver *Dipoides* are present in the peat deposit, in association with fossil beaver-cut wood. Given the presence of wood-cutting and swimming behaviour in *Dipoides*, the genus is expected to fill an ecological niche similar to that of modern *Castor*. Our study examines *Dipoides* bone collagen $\delta^{13}C$ and $\delta^{15}N$ within the context of a dietary baseline composed of Beaver Pond plant macrofossils. Beaver Pond plant macrofossil $\delta^{13}C$ and $\delta^{15}N$ range from –36.6 to –22.7 ‰ (VPDB), and +0.1 to +4.8 ‰ (AIR), respectively. *Dipoides* (n=5) $\delta^{13}C_{col}$ and $\delta^{15}N_{col}$ values (range –20.8 to –19.1 ‰, mean –20.3 ‰; range +3.2 to +5.8 ‰, mean +4.7 ‰) are higher than those of modern *Castor canadensis*, after accounting for the Suess effect. A Bayesian mixing model (SIAR v.4, Inger et al. 2010, in R v.3.2.4) suggests that aquatic macrophytes (e.g., pondweed (*Potamogeton*), buckbean (*Menyanthes trifoliata*) and pod-grass (*Scheuchzeria*) were consumed in slightly higher proportions than woody terrestrial plants [larch (*Larix*), birch (*Betula*) and red osier dogwood (*Cornus sericea*)]. These findings suggest that *Dipoides* was not only cutting down trees for construction purposes, but that woody terrestrial plants also contributed significantly to its diet. This is a rare example of a palaeodiet reconstruction study that incorporates stable isotope data from contemporaneous plant macrofossil and vertebrate fossil remains.

Concretionary dinosaur footprints and the first report of a dinosaur trackway from the Horseshoe Canyon Formation, Alberta, Canada

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The Horseshoe Canyon Formation has produced abundant skeletal fossils over more than a century of study, but the trace fossil record from the Horseshoe Canyon formation is limited to isolated dinosaur prints, small reptile trackways and burrows of invertebrates. While most formations preserve footprints as molds in beds of concreted rock—sometimes stretching kilometres—this style of preservation has not yet been recorded in the Horseshoe Canyon Formation. However, recent work has uncovered a less obvious preservation type that is prevalent in the Dinosaur Park and Oldman formations. These tracks, called concretionary footprints, are formed by concretion of infilled casts which remain after the softer surrounding molds have weathered away. Recognition of this type of footprint has resulted in increased discovery of similar tracksites elsewhere. Here, we report on one such tracksite—the first dinosaur trackway from the Horseshoe Canyon Formation. Three tridactyl, concretionary footprints in series were exposed from the hillside near Morrin Bridge, Alberta, alongside dozens of partial, weathered tracks. Each footprint in the trackway is greater than 65 cm from the tip of digit III to the heel and the same distance or greater from the tip of digit II to the tip of digit IV. All footprints have widely divaricated digits, large rounded ungual impressions of digit III, and evidence of interdigital padding. Two of the footprints preserve skin impressions in the outer walls of the casts. The trackmaker was likely a hadrosaurid dinosaur based on the size and morphology of the footprints. Footprints peripheral to the trackway vary in size, however, they are oriented near parallel to the trackway. The total evidence observed at this site is consistent with previously described bonebeds and other tracksites, which provides further insight into the social behaviour of hadrosaurid dinosaurs.

Anatomical and histological evidence for caudal autotomy in captorhinids (Eureptilia: Captorhinidae) from the Early Permian Dolese Brothers Quarry, Oklahoma, U.S.A.

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Captorhinids were among the earliest eureptiles to diversify into different ecological niches and disperse across Pangaea by the end of the Permian period. Whereas most of their evolutionary success has been attributed to their dietary specializations, very little attention has been given to another unique aspect of their biology: the ability to autotomize their tails during an attack by a predator. Researchers first noticed small cracks along a series of caudal vertebrae in three partial captorhinid skeletons and argued that these were akin to the autotomy septa along the vertebrae in modern lizards. Using this feature to argue that captorhinids were close to the ancestry of all diapsids, subsequent workers have used the presence of small cracks along the ventral surfaces of the caudal centra as evidence for caudal autotomy in captorhinids, early diapsids, and mesosaurs. Despite the supposed prevalence of this feature in Permo-Carboniferous amniotes, no study had properly examined the autotomy hypothesis beyond gross anatomical comparisons of caudal vertebrae with those of squamates. More specifically for captorhinids, the fact that the proposed autotomy septa never appear to pass through the neural spines of the vertebrae (unlike the condition in lepidosaurs) suggests that these cracks could simply be taphonomic features and warranted more thorough investigation.

In order to determine if these features are indeed evidence of caudal autotomy in captorhinids, we undertook a detailed investigation using histological techniques, Scanning Electron Microscopy (SEM), and comparisons to the autotomous vertebrae of the green iguana (*Iguana iguana*). In addition to re-examining previously described caudal skeletons, we also identified a partially articulated tail of a juvenile captorhinid and over 70 more instances of isolated septum-bearing vertebrae from the Dolese Brothers Quarry in Oklahoma (U.S.A.). Comparisons of sections through several isolated vertebrae, both with and without these septa, confirm that these structures are not taphonomic cracks in the vertebrae, but the result of incomplete ossification of the ventral half of the centrum, which is consistent with autotomy septa in modern lepidosaurs. One vertebra also preserves a partially broken centrum, highlighting how the septum would have aided in propagating a crack through the centrum, passing behind the neural spine, and breaking the centrum in half. We also identified variation in the number of autotomous vertebrae in captorhinds, with many possessing eight or more of these vertebrae at the base of the tail and some larger individuals possessing only four. In these larger individuals, the septa appear to be enclosed by cortical bone, suggesting that larger captorhinids lose the ability to autotomize most of their tail, similar to modern iguanas. Lastly, we extended our comparisons to other amniote caudal vertebrae from the Dolese Brothers Quarry, to other early eureptiles, and conclude that captorhinids are thus far the earliest and only non-lepidosaurian reptiles that exhibited this unique anti-predatory behaviour.

Revisiting *Smilodon* (Carnivora, Felidae) material from Medicine Hat, Alberta

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In the late 1960s and early 1970s, a fieldwork program was conducted by C.S. Churcher and A. MacS. Stalker on the Plio-Pleistocene stratigraphy and vertebrate faunas of the Canadian prairies. Churcher included the sabre-toothed cat *Smilodon* in the late Pleistocene fauna near Medicine Hat, Alberta, marking the most northern occurrence of *Smilodon* by about 1000 km, and the only occurrence of the genus in Canada. However, the material has never been illustrated or formally described, nor is it included in any of the major palaeogeographic databases. Here, we describe this material for the first time. It consists of a left proximal ulna and right proximal metacarpal V, which were ascribed to *Smilodon* by Churcher in his 1969 and 1970 reports to the GSC, respectively.

The length and gracility of the ulna are more consistent with the scimitar-toothed cat *Homotherium*, which has been previously reported from the Pleistocene of Alberta, and we cannot support its referral to *Smilodon*. However, the size, robustness, and morphology of the metacarpal is consistent with *Smilodon*; it has a longitudinally-oriented articular surface for metacarpal IV, a proximal origin of the muscle scar on the palmar surface, and overall robusticity that resembles specimens of *Smilodon* in the collections of the Royal Ontario Museum. Additional work is underway to refine our preliminary taxonomic assessments of these elements. Given that both *Homotherium* and the American lion *Panthera atrox* have been described from the Pleistocene of southern Alberta, it appears that at least three large cat species occurred in this region at that time. The presence of *Smilodon* in Alberta not only greatly expands the northern range limit of the genus, but also adds to our understanding of the large carnivore guild in the Pleistocene of the Canadian prairies.

The lateral pubic process of *Hesperonychus elizabethae* (Theropoda: Dromaeosauridae) and its functional implications for respiration and locomotion

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The Microraptorinae is a clade of dromaeosaurid dinosaurs closely related to birds, characterized by a prominent lateral tubercle or process on the midshaft of the pubis, among other features. Previously, this tubercle has been interpreted as a muscle attachment site with little evidence or functional reasoning. The holotype of the microraptorine *Hesperonychus elizabethae*, a partial pelvis discovered in Alberta, allows detailed examination for functional morphology. Comparison to its closest living relatives (i.e., crocodylians and birds) as an extant phylogenetic bracket offers reasonable interpretation of soft tissue attachment sites. Pelvic soft tissue of *H. elizabethae* is reconstructed based on extant phylogenetic bracketing and direct observation of attachment sites.

Inspection of the lateral pubic process of *H. elizabethae* reveals a highly unusual texture for muscle attachment. Osteological correlates of trunk, pelvic, and tail muscles that attach to the pubis can be identified elsewhere apart from pubogastralial ligaments. The lateral process is therefore reinterpreted as an anchor for pubogastralial ligaments. In this location, well-preserved dromaeosaurids have gastralia, extant crocodilians possess cartilage and ligaments connecting to gastralia, and theropods ancestral to Dromaeosauridae have robust pubic boots for ligament attachment. The presence of the lateral process is also correlated with reduction of the pubic apron, from which locomotory muscles originate. Thus, the lateral process serves primarily to maintain a connection to the gastral basket, and secondarily functions as a pulley for pubic locomotory muscles to avoid interference with this pubogastralial connection. This unique morphology among microraptorines suggests that a pubogastralial connection remained important and that some pelvic locomotory muscles may have required unique organization for hindlimb manipulation, both possibly related to the acquisition of four-winged flight in this clade.

Histological analysis of the gastralia of *Deinocheirus mirificus* from the Nemegt Formation of Mongolia

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The Late Cretaceous Gobi of Mongolia preserves one of the best dinosaur fossil assemblages in the world. In 1965, the Polish-Mongolian expedition collected the forelimbs and pectoral girdle of *Deinocheirus mirificus*, a taxon now identified as a basal ornithomimid based on the recent discovery of two relatively complete skeletons by the Korean-Mongolian International Dinosaur Project. In 2006, an expedition lead by Philip Currie rediscovered the quarry for the 1970 holotype specimen (Z. Pal. No. MgD-1/6). The sand that that infilled the quarry was sieved resulting in the recovery of approximately three dozen small fragments of ribs and gastralia. One of gastralia fragment (KID-412) was histologically examined.

The internal structure of the gastralia is similar to that reported for secondarily ossified tendons from other theropod dinosaurs. The sample has approximately 10 complete osteons per 1mm^2, with far more partially reworked osteons. The bulk of these are very small (< 100 μm), but increase in diameter towards the core of the bone (> 600μm). Many of these latter Haversian canals are filled with calcite minerals which is typical for fossils collected from the Nemegt Formation. Possible canaliculi are also found in some of the osteons; if confirmed, these would be the first evidence of canaliculi in a basal ornithomimosaur. The structure of the periosteum and the lack of lines of arrested growth suggest that the holotype of *Deinocheirus mirificus* represents a fully grown adult.

Evidence for age-related social structures in *Gryposaurus* from the Oldman Formation (Campanian) of Alberta, Canada

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The Oldman Formation of the Milk River region of southern Alberta, Canada, is notable for the large number of juvenile and sub-adult dinosaur specimens that have been collected relative to equivalent horizons of the Belly River Group in other parts of the province. Between 2004 and 2010, the Southern Alberta Dinosaur Project, a joint project of the Cleveland Museum of Natural History and the Royal Ontario Museum, excavated a monodominant *Gryposaurus* sp. bonebed (Wendy's Bonebed) from the base of the Oldman Formation on the Pinhorn Grazing Reserve on the south slopes of the Milk River approximately 34 km SW of Manyberries, AB. Histological evidence derived from six tibiae (e.g., the lack of an external fundamental system, the limited development of the medullary cavity, and the lack of any secondary osteons) indicates that the individuals represent a mixed group of early (less than one year) and late (approaching the end of their second year) juveniles. The bonebed, thus, probably preserves individuals from at least two growth stages originating from at least two separate broods. This conclusion is supported by the differences in the number of Lines of Arrested Growth (LAG) (one LAG in the largest specimens; no LAGs in smaller specimens) and number of alternating zones of reticular and circumferential tissue (two reticular-circumferential couplets in larger specimens; one couplet in smaller specimens) between the largest and smallest specimens. Bone microstructure data also indicates that the gryposaurs experienced rapid growth and achieved approximately 70% of adult size before the end of their second year.

The parautochthonous nature of the bonebed, and the lack of small neonate and large adult material, suggests that the bonebed represents an isolated group of juveniles. This group may have separated itself from a larger social grouping, possibly as an evolutionary strategy to allow greater allocation of resources to altricial hatchlings. Based on data from well-preserved mass mortality sites in Asia (i.e., the ornithomimid *Sinornithomimus dongi* in the Djadokhta Formation of inner Mongolia, as well as *Protoceratops* and *Psittacosaurus* assemblages), it has been proposed that some ornithischian juveniles may have congregated together away from the rest of the population during the season when adults would be preoccupied with rearing altricial hatchlings. Evidence for juvenile sociality in North American taxa is less conclusive, as truly autochthonous bonebeds with complete or near-complete articulated skeletons are rare, but the taphonomic and histological profile of the *Gryposaurus* bonebed offers a relatively robust data set that suggests the phenomenon of juvenile sociality was likely not limited to Asian ornithischians.

Re-grafting early reptile phylogeny by increased taxon sampling and multiple optimality criteria

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Morphology-based phylogenetic relationships among reptiles has sparked intense debate and discussions over the last decades. Whereas molecular-based phylogenies have most often found an archosaur-turtle sister-group relationship, the morphological signal has always provided conflicting results across different data sets for the placement of turtles and other major reptile clades, such as their placement with parareptiles vs. within diapsids. Most recent data sets have consistently found turtles within diapsids, closely allied to sauropterygians, but those data sets have never included a deep species-level taxon sampling of the major reptile lineages. Most existing data sets on early reptile phylogeny also focus on diapsid reptile relationships only, thus not considering parareptiles and early evolving amniotes along with diapsids, nor have considered a significant revision of existing morphological characters or personal assessment of the majority of the taxa included in those data sets. Here we present a new early reptile phylogenetic data set, with deep species level sampling in which all taxa have been personally observed by us (95 taxa and 315 morphological characters). We investigated this data set utilizing multiple optimality criteria of phylogenetic inference (equal weights and implied weighting maximum parsimony, and Bayesian inference analysis), including relaxed morphological clocks for divergence time estimates, applying the fossilized birth–death tree model and combined tip and node dating. Our preliminary results indicate the paraphyly of parareptiles, and that the distinct clades of "parareptiles" are all nested within diapsids, as part of the early evolution of the later group. We also find strong support for the placement of marine reptiles forming a single clade, closely allied to archosaurs. These results shed light on why turtles have more recently been regarded by several authors as diapsid reptiles, as we find that the majority of reptiles are actually within Diapsida, including turtles and "parareptiles". The results also call upon the relevance of increased taxon sampling across multiple taxonomic groups of interest, careful and explicit criterion of morphological character construction, and the importance of personal observation of anatomical data for morphology-based phylogenetic analyses.

Early Palaeocene ichthyofauna from the Ravenscrag Formation, southern Saskatchewan, Canada

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The Late Cretaceous Western Interior Seaway was reduced to a narrow body of water in the far north towards the end of its existence and gradually disappeared in the Palaeocene, with a few scattered and isolated water bodies in central Canada. Thereafter, the freshwater ichthyofaunas took over the area, with a large number of diverse taxa represented in the different Palaeogene formations, notably the Ravenscrag Formation and the Paskapoo Formation in southern Saskatchewan and Alberta respectively. The ichthyofauna of the Paskapoo Formation has been well studied. In contrast, the sedimentology as well as the ichthyofauna of the Ravenscrag Formation have not been studied in detail. The early Palaeocene Ravenscrag Formation, representing fresh water riverine environments, crops out in several sites in southern Saskatchewan, particularly around the towns of Evans, Eastend, Roche Percee and Ravenscrag. This formation overlies the Cretaceous Frenchman Formation. The Ravenscrag Formation of Saskatchewan has yielded diverse vertebrate faunas including mammals, fishes, frogs, salamanders, turtles, champsosaurs and crocodiles. The ichthyofaunas from the UAR2A (= Roche Percee) locality from eastern Saskatchewan and the Croc Pot locality from western Saskatchewan are here described. The ichthyofaunas are diverse including the following fish taxa: *Lepisosteus*, Amiidae, Osteoglossomorpha, Acanthomorpha, Holostean A, Siluriformes, Esocidae, Gonorhynchiformes, ?Hiodontidae. Identified taxa have been compared to those reported from the Palaeocene of Montana, USA. Studies of the Palaeocene faunas will help bridge the faunal gap between the Late Cretaceous Frenchman Formation and the early Eocene to Oligocene Cypress Hills Formation. The high abundance of some taxa and the documentation of the different taxa sheds light on the high diversity of ichthyofaunas of both localities. The diverse fish taxa obtained represent a mosaic of environmental conditions.

Names, narrative, and imagery: effectively communicating the past

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Palaeontology is a science that co-exists as an elusive consumer product. It is reliant on government funding, museum patronage, and universities, but exists primarily as the indigestible circuitous domain of professionals. However, it is possible to better communicate palaeontological research, as newly uncovered species can be crafted to have charisma, winning the hearts (and wallets) of the public and financial sponsors. Media is a key vehicle for this, and increasingly social media determines the reach. Research on social media interaction has found that readers tend toward the heuristic system model, wherein information is processed peripherally with a heavy reliance on cognitive shortcuts. In this presentation, an improved approach to palaeo-science communication is proposed and described. Researchers should engage with the heuristic system model with introducing a new species, by using 1) a memorable name, 2) clear engaging narrative, and 3) striking imagery. Case examples will

be presented of recently announced species (*Zuul*, *Hallucigenia*, etc.) that experienced immediate integration into popular culture, in contrast to comparative species that did not. Mechanisms behind the viral popularity of certain species, the benefits of virality, and testimonies from the public will be discussed. The benefits to be reaped from improved scientific communication include increased museum attendance, enhanced public interest, and influence on the career paths of students.

The faunal composition of a Late Cretaceous marine bonebed from Saskatchewan

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The upper Campanian-lower Maastrichtian Bearpaw Sea deposits of southern Alberta and Saskatchewan have produced multiple specimens of large marine reptiles, including the holotypes of three plesiosaurs. However, the diversity of the vertebrate fauna from the seaway is generally poorly documented. Royal Saskatchewan Museum palaeontologists discovered a Bearpaw Formation bonebed near the town of Herschel, SK in the 1990s and collection has continued there over multiple field seasons. Through these collecting efforts, nearly 3,000 specimens have been found. However, most specimens consist of isolated elements, with few examples of associated fossils being recovered. Elasmosaurid, polycotylid, mosasaurine, and toxochelyid fossils comprise the marine reptile diversity from the site. Interestingly, there appears to be an abundance of juvenile marine reptiles, indicated by relatively small and poorly ossified elements and a high occurrence of disarticulated plesiosaur vertebrae, which is another indicator of individual immaturity. Additionally, numerous teeth and vertebrae representing both bony and cartilaginous fishes have been found. The teeth are diagnostic of actinopterygiian groups such as Enchodontidae, Pachycormidae, and Ichthyodectidae. Most of the chondrichthyan teeth represent Lamniformes, but specimens of Hybodontidae and Callorhinchidae are also present. The fish vertebrae are the least well understood, but at least six morphotypes, including both cartilaginous and osseous forms, have been identified. Based on the faunal composition of the Herschel bonebed, this Bearpaw Sea locality appears to have preserved a productive, shallow system that provided a refuge for juvenile marine reptiles.

Fused caenagnathid (Dinosauria: Theropoda) dentaries from the Wapiti Formation of northern Alberta, and the ontogeny of mandibular features in Caenagnathidae

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The dentaries of caenagnathid oviraptorosaurs are highly diagnostic, and robust enough to be relatively well represented in the Late Cretaceous fossil record of Asia and North America. A recently collected pair of fused, nearly complete dentaries from the "DC Bonebed", a fluvial locality on the Wapiti River near Grande Prairie, represents the first definitive caenagnathid from the Upper Cretaceous Wapiti Formation of northern Alberta. While the Wapiti Formation is temporally extensive, the DC Bonebed is probably approximately contemporaneous with the Dinosaur Park Formation of southern Alberta.

The Wapiti specimen bears a close resemblance in general shape to dentaries of *Leptorhynchos* from the Dinosaur Park Formation and the Aguja Formation of Texas, sharing their short, strongly upturned symphyseal region and high depth to length ratio. The mandible also resembles *Leptorhynchos* in the form of the network of shallow vascular grooves in the symphyseal region. However, the Wapiti mandible clearly lacks one diagnostic feature of *Leptorhynchos*, namely two pairs of eminences that define anterior occlusal grooves, and also differs from southern Albertan *Leptorhynchos* mandibles in having deeper fossae medial to the lingual ridges, less well-developed prominences between the lateral occlusal grooves, and Meckelian grooves with less extensive exposure on the ventral surface of the mandible and less subdued medial margins.

The Wapiti mandible is considerably smaller than other known specimens of *Leptorhynchos*, raising the possibility that its morphological differences from these specimens reflect immaturity. This would imply that certain features presumably linked to the occlusal function of the mandible become better defined with age, whereas at least some vascular features are more ontogenetically stable. If the prominences between the lateral occlusal grooves are indeed positively allometric, they presumably play a functional role in the feeding system, even if they represent degenerate interdental septa as was recently suggested for caenagnathids in general. Regardless, the Wapiti caenagnathid represents the northernmost occurrence of the *Leptorhynchos* mandibular morphotype, and underscores the viability of this type of jaw structure over a wide latitudinal range in the Campanian.

Morphological variation and phylogenetic relationships of the species of *Armigatus* (Teleostei, Clupeomorpha, Ellimmichthyiformes) with implications for the biogeography of the group

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Clupeomorph fishes of the extinct genus *Armigatus* (Teleostei, Clupeomorpha, Ellimmichthyiformes) were a group of pelagic fishes restricted to the shallow marine environments of the eastern Tethys region, contributing to the overall diversity of the ellimmichthyiforms in that region during the Late Cretaceous. The group includes five species described from the present-day circum-Mediterranean region. The oldest fossil record of the group is described from the Cenomanian deposits of Lebanon that yielded three species of *Armigatus*, the type species *A. brevissimus* from Hakel and Hajula, and *A. namourensis* and *A. alticorpus* described from Namoura. The other two younger species are known from Cenomanian–Turonian deposits of Morocco, *A. oligodentatus*, and Campanian deposits of Croatia, *A. dalmaticus*. With the new species being described, the phylogenetic relationships within the genus remain unresolved due to the lack of sufficient information for some members of the genus, namely *A. alticorpus*, and overlapping ranges of some diagnostic morphological traits between *A. namourensis* and *A. brevissimus*.

Here we report material from Hakel, Lebanon housed in the Royal Tyrrell Museum (Alberta, Canada). Two mass mortality slabs, TMP 1998.65.11 and TMP 1998.65.12, preserve multiple clupeomorphs including two species of *Armigatus*, *A. namourensis* and *A. alticorpus*, previously known only from Namoura, Lebanon. Preservation of the skull elements and caudal skeleton of the *A. alticorpus* specimens provides necessary information for addition of the species in a phylogenetic analysis. Results of the phylogenetic analysis indicate close affinities of *A. alticorpus* to the two younger species, *A. oligodentatus* and *A. dalmaticus*. The three species together (*A. alticorpus* (*A. oligodentatus* + *A. dalmaticus*)) belong to a separate lineage diverging from their sister-clade, (*A. brevissimus* + *A. namourensis*). Additionally, comparative examination of the multiple specimens of each species enabled us to establish a set of morphological traits which allow a more reliable delimitation of the species of *Armigatus*; this includes number of abdominal scutes, vertebrae, predorsal bones, as well as position of the dorsal fin.

The new fossil material indicates faunal similarity between Cenomanian localities in Lebanon, Hakel and Namoura. The relatively high species diversity and older age of the fossils suggests that the eastern part of the central Tethys could be a potential centre of origin and radiation of the group. This hypothesis is congruent with the results of the ancestral range reconstruction which indicate origin of *Armigatus* in the eastern central Tethys and successive dispersal north (*A. dalmaticus* from Croatia) and west (*A. oligodentatus* from Morocco).

Oviraptorid eggshell fragments from the Nemegt Formation, Mongolia identified using standard histological analysis

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Eggshell fragments from Mongolia were collected and analyzed to determine if they could be identified as being derived from a known ootaxon. Based on oviraptorid skeletal material collected at the same time from the same locality, it was hypothesized that the egg fragments were also from this taxon. Standard histological analysis of one eggshell fragment identified mammillary cones and pores characteristic of the Elongatoolithidae oofamily. These structures are similar to those found in previous studies of eggshell material that contained oviraptorid embryos. The eggshell fragments are tentatively assigned to the oofamily Elongatoolithidae, but further descriptions of the associated skeletal material are necessary to confirm the taxon. If this material is determined to be from hatchlings it could have important implications on the parental care and development of oviraptorids.

How long is the neck? Conflicting criteria for the cervicodorsal transition in crocodylomorph archosaurs

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The number of cervical vertebrae is highly stable in mammals, but variable in reptiles. The transition between the cervical and dorsal regions is most unambiguously defined by taking the anteriormost vertebra linked to the sternum by rib segments as the first dorsal. However, this traditional definition cannot be applied to most crocodylomorphs and other non-avian reptiles in the fossil record, because of the cartilaginous nature of their sterna and sternal ribs.

Students of fossil crocodylomorphs have used various characters to diagnose the cervicodorsal transition, guided by comparisons to extant crocodylians. Most commonly, the first dorsal has been identified as the anteriormost vertebra in which (1) the parapophysis is located dorsal to the neurocentral suture; (2) the diapophysis projects laterally rather than ventrolaterally; or (3) the zygapophyseal facets are subhorizontal rather than steeply inclined. However, authors have occasionally identified the first dorsal based on other criteria such as neural spine morphology, centrum length, or absence of a ventral keel. No consensus exists regarding how the cervicodorsal transition in fossil crocodylomorphs should be pinpointed, and the various morphological indicators used in

practice have never been systematically evaluated to determine how they correlate with one another or, in extant crocodylians, with the classic criterion of sternal connectivity.

Data from extant crocodylians and fossil crocodylomorphs, combined with descriptions from relevant literature, indicate that the change in parapophyseal position is consistently followed by the change in diapophyseal orientation, which in turn is followed by disappearance of the foramen costotransversarium formed by the vertebra and the rib. The change in diapophyseal orientation consistently takes place on the 7th or 8th presacral, but the other two changes are less positionally stable. In extant crocodylians, sternal connectivity indicates that all three changes take place in a transition region comprising the last two cervicals and first three dorsals, and that nine cervicals are present. However, the change in zygapophyseal orientation is more variable, taking place before the dorsal migration of the parapophysis in *Crocodylus*, after the dorsal migration in the notosuchian *Simosuchus*, and seemingly not at all in the basal crocodylomorph *Junggarsuchus*. Zygapophyseal orientation is thus unsuitable as a criterion for diagnosing the cervicodorsal transition in fossil crocodylomorphs, and comparisons of cervical and dorsal vertebral counts across taxa should be explicitly based on one or more criteria that vary in a consistent manner.

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

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Microfossil sites (more commonly called microsites) are localities where small fossil remains of vertebrates have been concentrated, usually due to low-energy fluvial environments. The majority of documented microsite material from southern Alberta has been collected from the Dinosaur Park Formation with comparatively little from the Foremost and Oldman formations, and, to an even lesser extent, the Horseshoe Canyon Formation (HCF). This has led to difficulty in assessing the faunal turnover of vertebrates that are better represented through microfossil material throughout the Late Cretaceous of North America. Here we describe a new microsite from the HCF with an unusual faunal assemblage, characterized by an abundance of troodontid and anuran material, theropod and ornithopod perinates, and the first fossil eggshell from the HCF.

Examination of the eggshell suggests it belongs to a troodontid nester, probably *Albertavenator*. At this locality we find both large fossils and microfossils in close association, suggesting less taphonomic bias than other microsites. The fossil assemblage at this locality therefore suggests that a nesting site for troodontids was nearby and that there is non-random association between troodontids and perinate material from other dinosaurs. Although we find no direct evidence of predation, it is likely that the altricial hadrosaur perinate found here were a food source for the precocial fledgling *Troodon*. Similarly, the presence of anurans and other perinates, like ceratopsians and theropods, may be the result of targeted predation by *Albertavenator*.

A histological examination of the ontogeny of caenagnathid dentaries

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Caenagnathidae is a clade of mid- to Late Cretaceous toothless theropod dinosaurs found in Asia and North America. Caenagnathid growth, development, and variation is poorly understood as most caenagnathid specimens are preserved as isolated elements. The dentary is a commonly preserved element in the fossil record; as a result, many studies of caenagnathid taxonomy and morphology are based on the dentaries. A thorough understanding of the growth and development of these elements is vital for assessing the morphological and ontogenetic variation. This study examines the histological characteristics of four caenagnathid mandibles from the Dinosaur Park Formation representing an ontogenetic series. Transverse thin sections of the mandibular symphysis were photographed under both plane and cross-polarized light, and their histological features were described. The early ontogenetic stages were characterized by rapidly-deposited woven bone, high vascularity, and high density of osteocyte lacunae indicating rapid growth. Even in the youngest individual, the mandibular symphysis is completely fused with no evidence of a suture or calcified cartilage. This rapid fusion in caenagnathids would allow for precocial young capable of processing their own food. Throughout ontogeny, the mandibles show a decrease in vascularity and osteocyte lacunar density, an increase in lamellar bone and secondary osteons, an expansion of the pneumatized cavities, and the formation of growth lines along the ventral margin of the mandibles. The toothless condition in caenagnathids has previously been hypothesized to result from ontogenetic tooth loss with the lingual ridges and grooves representing vestigial alveoli. However, we found no evidence of dental tissues nor the distinct histological signals expected of tooth-bearing structures in these regions of the mandibles. These descriptions add to our knowledge of the growth and development of caenagnathids, and the identification of an ontogenetic series will aid in the taxonomic classification of partial or incomplete caenagnathid skeletons.

A new, basal actinopterygian from Nova Scotia: stem group survivorship in the early Carboniferous

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The vertebrate fossil record of the earliest Carboniferous is notoriously poorly-sampled, obscuring a critical interval in the evolution of modern vertebrate diversity. Recent studies of diversity across the Devonian-Carboniferous boundary propose a vertebrate mass-extinction at the end-Devonian, and recent phylogenetic and molecular work suggests that important actinopterygian divergences may have occurred in the earliest Carboniferous, as part of a broader recovery fauna. However, the morphological data necessary to test this are limited. Here, we describe a partial actinopterygian skull, including diagnostic elements of the posterior braincase, from the Tournaisian Horton Bluff Formation of Blue Beach, Nova Scotia. The braincase surprisingly shows an open spiracular groove, a supratemporal-intertemporal complex, and lateral dorsal aortae that pass through parallel open groves in the ventral otoccipital region; characters which, in combination, are typical of Devonian forms. Phylogenetic analysis places it deep within the actinopterygian stem, among Devonian moythomasiids and mimiids, hinting at greater survivorship of plesiomorphic actinopterygians across the end-Devonian mass extinction. With high lineage survivorship in tetrapods and lungfish across the Devonian-Carboniferous boundary and high vertebrate diversity at other Tournaisian localities, this hints at a more gradual turnover between Devonian and Carboniferous vertebrate faunas.

Early archosauriforms recently discovered in China

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Here I summarize our recent studies of early archosauriforms from China, including those of non-archosaur members of the clade as well as non-crocodylomorph pseudosuchians. As in many other places in the world, these archosauriforms are all found in Triassic-age deposits. Since the discovery in 1936 of the first early Triassic archosauriform of China – *Proterosuchus* (then *Chasmatosuchus*) *yuani* – numerous additional genera of Chinese non-archosaur archosauriforms and non-crocodylomorph pseudosuchians have been named, numbering around 15 by the year 2000. However, many of these archosauriforms are too fragmentary to have been included in any phylogenetic studies. Therefore, it is crucial to find better specimens of these poorly known species in order that they may be reviewed using modern-day standards in taxonomy and phylogeny. Moreover, the known taxa represent limited lineages of Archosauriformes, and no indisputable phytosaur or rhynchosaur fossils have been found in China. Considering the many exposures of Triassic deposits which have not yet been fully explored, there should be good opportunities to find new archosauriforms and better specimens of known taxa in China. Since 2000, the Canadian Museum of Nature has successively established partnerships with a number of institutes and museums of China for the purpose of better documenting Chinese archosauriforms.

A number of joint-research projects with the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences in Beijing, the Zhejiang Museum of Natural History (ZMNH) in

Hangzhou, and the National Museum of Natural Science (NMNS) in Taichung, have produced several significant accomplishments. In 2001, we described a new pseudosuchian, *Yonghesuchus sangbiensis*, and restudied *Turranosuchus dabanensis*; the discovery of the former constituted at the time the stratigraphically highest record of Archosauriformes in the terrestrial Triassic of China. In 2006, we described a new non-crocodylomorph pseudosuchian, the poposauroid *Qianosuchus mixtus*, from Triassic marine limestones. *Qianosuchus mixtus* represents the first archosauriform that can be confirmed to have led an aquatic or semi-aquatic lifestyle in the Triassic seas. In 2012, we reported another archosauriform from the Triassic marine limestones of China, *Diandongosuchus fuyuanensis*, which was subsequently reinterpreted as the first phytosaur found in China and presents phylogenetically the basal-most member of the group. The discovery of *D. fuyuanensis* is therefore significant to our understanding of the origin and paleogeography of Phytosauria. Most recently, we collaborated with researchers from the Virginia Polytechnic Institute and State University in the USA to describe a new basal archosauriform, *Litorosuchus somnii*, from marine limestones dating to the early Middle Triassic. It is an armored and semi-aquatic animal, which indicates that archosauriform diversity in terms of both ecology and morphology appeared much earlier than was previously thought.

In addition to the aforementioned new archosauriforms, a project with the Shanxi Museum of Geology also restudied material from several terrestrial Triassic archosauriforms from China. In 2013, we clarified certain anatomical structures of *Shansisuchus shansisuchus* on the basis of a newly collected skeleton. Our reexamination confirmed the presence of the two antorbital fenestrae in the skull of this taxon. Furthermore, we revealed an unusual morphology of the intercentrum for *S. shansisuchus*, which is big and bow-shaped rather than small and wedge-shaped, clamping over rather than inserting between the ventral edges of the vertebrae.

Collaborations between the Canadian Museum of Nature and various Chinese institutions continues. New archosauriform fossils from Triassic marine deposits are currently in preparation, and better preserved material from both terrestrial and marine deposits are now under study. This includes a nearly complete, three-dimensionally preserved skeleton of *Diandongosuchus fuyuanensis* and a cluster of 12 skeletons referable to *Wangisuchus tzeyii*, a questionable euparkeriid. The study of these taxa will certainly continue to build the growing body of evidence that there was a significant diversity in mode of life among early archosauriforms, and will furthermore help resolve character optimizations outside Archosauria during the Triassic recovery from the end-Permian mass extinction.

Stratigraphy, biostratigraphy and x-ray fluorescence of mudstone horizons in the Dinosaur Park Formation, Dinosaur Provincial Park, Alberta

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This research aims to determine if the apparently cyclic stratigraphic packages in the Dinosaur Park Formation (DPF) in Dinosaur Provincial Park (DPP), Alberta correlate with dinosaur biostratigraphy and turnover events. X-Ray Fluorescence (XRF), spectral gamma-ray, SediGraph, and X-Ray Diffraction (XRD) analyses on selected heterolithic and mudstone samples collected from measured stratigraphic sections in DPP helped to recognize the stratigraphic packages. These data were compiled alongside published stratigraphic positions of dinosaur, other vertebrate, and palynological fossil occurrences. Twelve facies were characterized using the presence or absence

of laminae, pedogenic features, roots, transported plant material, grain-size, and colour. The vertical positions and lateral extents of muddy facies indicate up to five allogenically controlled mudstone horizons in the DPF, which are interpreted to represent the landward expressions of marine flooding surfaces. The repetitive nature of stacked facies associations suggests that higher frequency sea-level fluctuations affected sediment deposition during the overall 3rd order transgression represented by the entire DPF. XRF analysis of powdered samples using an Olympus hand-held machine as well as spectral gamma ray analysis revealed chemically distinct horizons with changes in Ti, Cr, Sr and Zn and Th, K and U concentrations respectively. These chemical changes are present at significant lithological and biostratigraphic boundaries, and may represent changes in oxygen/organic content as well as the proportions of certain clay minerals (i.e., illite, montmorillonite). Correlation of elemental concentrations, stratigraphic flooding surfaces, and biostratigraphic intervals suggests that ~12 m-thick packages representative of 4th (or 5th) order base-level cycles influenced the sedimentary environments, as well as the distribution and composition of fossil assemblages, in the Dinosaur Park Formation.

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