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Mark Powers and Ryan Wilkinson

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Abstracts

Skeletal anatomy and systematic placement of the Permian actinopterygian *Brachydegma caelatum* based on new data from µCT

Thodoris Argyriou

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The sparse Permian record of actinopterygian fishes remains relatively understudied. As a result, the origins of the morphologically diverse actinopterygian clades of the Triassic, and with them the origins of surviving major lineages, are incompletely understood. One of the few three-dimensionally preserved Permian actinopterygians is *Brachydegma caelatum* Dunkle 1939, an enigmatic species from the Artinskian (early Permian) of Texas. *Brachydegma* has had a volatile systematic history, being affiliated with *Elonichthys*, acrolepids, crown holosteans, and, more recently resolved as a crownward member of the neopterygian stem. This ambiguity in phylogenetic placement stems from limited character information available for *Brachydegma*, which is restricted to superficial details of the external skeleton. Using computed microtomography (µCT) I investigated the internal anatomy of the two known specimens. Surrounding matrix shows considerable growth of dense (likely iron) minerals that make segmentation difficult, but nevertheless µCT yields considerable new morphological data highlighting an unusual mosaic of characters. Widely distributed actinopterygian traits revealed in *Brachydegma* include: an aortic canal; a persistent oticooccipital fissure; a perforate hyomandibula; five branchial arches; clavicles capping the anteroventral processes of the cleithra; and a notochord partially constricted by paired neural and haemal elements. Derived features of *Brachydegma* with a more restricted distribution among actinopterygians include: a parasphenoid stalk that underlies the otic and the anterior part of the occipital regions; well-developed uncinate processes on the epibranchials; and multiple basibranchial ossifications. Distinctive—and potentially autapomorphic—traits include: a broad interorbital septum and a peculiar hyomandibula with a thin dorsal and a much wider ventral limb. These features reinforce recent verbal and cladistic arguments excluding *Brachydegma* from the neopterygian crown, but the unusual combination of features in this genus and the instability of relationships among 'early' actinopterygians precludes a more precise placement at present.

The power of predation: Ground-truthing adaptive escalation as an evolutionary driver

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Adaptive escalation (Vermeij 1987) is an evolutionary theory proposing that an increased predation rate creates increased competition between predators, leading to an increase in predator taxonomic diversity, which in turn leads to a further increase in predation. This 'run away' predation leads to an increase in predator avoidance in prey species, which increases prey diversity (Vermeij 1987; Van Valen 1973; Aberhan et al. 2006). Given sufficient time, adaptive escalation is suggested to drive major biotic transitions (Vermeij 1987, 1987).

The theory was first proposed to explain the fourfold increase in predator taxonomic diversity during the so-called Mid-Mesozoic Marine Revolution (Vermeij 1997; Bambach 2002), which saw the replacement of the long-standing Paleozoic-type benthic faunas, dominated by epifaunal and immobile suspension-feeding organisms, with infaunal, mobile faunas more characteristic of modern benthic marine communities (Aberhan et al. 2006). Most significant biotic transitions are mediated by external events such as bolide impacts, ocean acidification and mass volcanism, which transcend biological interactions and 'reset' the diversity on large scales, allowing for the radiation of new groups into unoccupied niches (Miller 1998; Alroy 2010). Biotic transitions, or even smaller biotic trends, that are instead driven by biological interactions such as predation and competition are much more difficult to define and study in the fossil record. As an example in vertebrate palaeontology, we are unsure of whether an increase in large theropod diversity on Laramidia during the Late Campanian was linked to the increase in megaherbiavore dinosaur diversity during the same time interval. Similarly, we are unsure if and how the decline in large theropod diversity to one species (*Tyrannosaurus rex*) between the Campanian and Late Maastrichtian in Canada is linked to a similar decline in megaherbivore dinosaur diversity.

Due to the Mid-Mesozoic Marine Revolution's spatial and temporal extent (the revolution was global and took 115 million years, between the mid-Jurassic [~180Ma] and the Late Cretaceous [65Ma]), it provides a rare opportunity to study a biologically-driven biotic transition with a reasonable degree of integrity. Despite this, owing in part to the difficulty of linking predator abundance with predation intensity in the benthic marine fossil record (Roy and LaBarbera 1994), few attempts have been made to actually address the fundamental underlying assumption in the adaptive escalation model: that an increase in predator taxonomic diversity ultimately leads to an increase in predation rate.

In this study, I examined if and how predator taxonomic diversity is linearly correlated with an increase in predation from both a modern and a paleontological point of view. I performed a meta-analysis of modern ecological studies to determine whether increased predation in modern marine systems could be explained by an increase in predator taxonomic diversity. The results of this meta-analysis suggest that predator taxonomic diversity generally has a positive effect on predation in marine experimental systems. However, high heterogeneity between studies may indicate that other factors, such as predator identity and density, may also play a significant role in the effect predation has on prey abundances. To investigate evidence of increased predation in the fossil record, studies of drilling predation occurrences throughout the Phanerozoic were compiled to assess the type and frequency of this type of predation through geologic time. These results of these reviews were inconclusive, suggesting that while evidence of predation did increase in the Mid-Mesozoic marine revolution, it had increased once before in the late Paleozoic. This earlier increase in predation was unrelated to a similar increase in predatory taxonomic diversity, suggesting that the two factors are not necessarily tightly linked.

Ground-truthing evolutionary theories such as adaptive escalation is an important step in understanding diversity patterns in the fossil record. While our ability to do this on large scales may be limited (we cannot conduct experiments over geological timescales), gaining an understanding the strengths and shortfalls of modern ecological systems to inform us of paleobiodiversity patterns is crucial in moving forward in the science of paleoecology.

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Turnover in freshwater turtle diversity in the latest Maastrichtian (66Ma) Frenchman Formation, Saskatchewan, Canada

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Fossil turtles are widespread and abundant in Late Cretaceous deposits in North America (Holroyd and Hutchison 2001), making them ideal for the study of paleobiodiversity. In practice, turtle genera are readily identifiable from fragmentary remains, which is a distinct advantage when dealing with fossils from microvertebrate sites. As shell fragments from different taxonomic groups are assumed to have the same preservational potential, the obscuring effect of taphonomy in determining diversity within the group is less problematic in turtles than in other vertebrate groups (Holroyd and Hutchison 2002). For these reasons, many paleobiodiversity and paleoenvironmental studies have focused on fossil turtles (i.e., Holroyd and Hutchison 2001; Holroyd and Hutchison 2002; Brinkman 2003; Eberth and Brinkman 2012; Quinney et al. 2013). Changes in Late Cretaceous turtle diversity has in the past been attributed to climate change (Brinkman 2003). However, recent studies have suggested that factors such as availability of wetland habitat, aridity, landscape instability, barriers to migration (Quinney et al. 2013), or habitat heterogeneity (Holroyd and Hutchison 2001) could play more important roles in influencing turtle diversity patterns. For these reasons, the diversity of fossil turtles is an important indicator of environmental changes that are subtler and less easily discerned than changes in climate.

The latest Maastrichtian ('Lancian') Frenchman Formation of southern Saskatchewan represents that last half-million years of the Cretaceous period in a near unbroken sequence of fluvial and coastal sediment. Highly fossiliferous and particularly rich in microvertebrate fossil sites, the Frenchman Formation is bounded at its top by the Cretaceous-Paleogene (K-Pg) Boundary, providing an excellent opportunity to study paleobiodiversity up to and across the end-Cretaceous mass extinction event. The Frenchman Formation has one of the highest diversities of fossil turtles in the Late Cretaceous of North America. With at least 16 known freshwater turtle genera (Bamforth 2013), the diversity is second only to that found in the time equivalent Hell Creek Formation of the United States, which boasts 19 genera (Hutchison and

Archibald 1986). Turtle shell fragments are among the most common elements in vertebrate microsites. Other elements such as limbs, cervical and caudal vertebra, girdle elements and rare cranial material have been collected from late Maastrichtian sites across southern Saskatchewan. Frenchman Formation turtle species comprise six families; Trionychidae (soft-shelled turtle), Baenidae (extinct pond turtles), Chelydridae (snapping turtles), Nanhsiungchelyidae (extinct tortoise-like turtles), Adocidae and Pleurosternidae (both extinct freshwater turtles of unknown affinity).

With the exception of the trionychids (soft-shelled turtles), which are common throughout the formation, the proportional representation of turtle genera shifts moving upsection towards to K-Pg Boundary. At the base of the formation, baenid (pond turtle) species and the Nanhsiungchelyid *Basilemys* (a tortoise-like turtle) are common, but become progressively less common towards the K-Pg Boundary. Conversely, chelydrids (snapping turtles) and the pleurosternid *Compsemys* are both uncommon at the base of the formation, but together make up an average of 50% of the turtle occurrences at the top of the formation.

Based on the known or inferred biology of these turtle families, it is suggested herein that the turnover in turtle fauna found in the Frenchman Formation may be attributed in part to an increasing marine influence towards the K-Pg Boundary. The turtle families that increase in proportional occurrence towards the K-Pg Boundary either have salt-tolerant descendants (trionychids and chelydrids), or have been found to predominate in locations where an inferred marine influence was present. While there is no evidence to suggest that the turtle families that decline in proportional abundance towards the K-Pg Boundary were necessarily salt intolerant, an increasing marine influence nonetheless implies a potential change in habitat and drainage pattern, which may have contributed to the turnover in turtle fauna. For example, as the fully terrestrial Basilemys is inferred to prefer inland-like habitats (Brinkman 1990; Peng 1998), a shift towards more coastal-like habitats could potentially drive a decline in the proportional occurrence of *Basilemys*.

In the uppermost Hell Creek Formation (coeval with the uppermost Frenchman Formation), a small marine transgression known as the Cantapeta Advance was documented in North Dakota (Murphey et al. 2002). As this interfingered marine unit is found less than 600 km from most Frenchman Formation exposures in Saskatchewan, it is possibly that the transgression reached Saskatchewan just prior to the end-Cretaceous mass extinction. The turnover in turtle fauna within the Frenchman Formation, along with several other biological lines of evidence, do suggest an increasing marine influence towards the K-Pg Boundary.

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Cranial anatomy and systematic position of *Aelurosaurus* (Synapsida, Gorgonopsia) based on a ct-reconstruction

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Gorgonopsia is one of the major clades of non-mammalian synapsids, and included the dominant predators in tetrapod faunas of the late Permian. Gorgonopsian taxonomy is highly problematic, due to a lack of precise diagnoses and thorough descriptions of individual species and their respective type specimens. Although significant progress has recently been made in revising the taxonomy of the largest gorgonopsian species (rubidgeines), small-bodied gorgonopsians remain poorly understood. Here we present new data on small gorgonopsian anatomy and relationships, based on a reanalysis of the cranial anatomy of MB.R.999, a gorgonopsian skull from the late Permian of South Africa housed in the collection of the Museum für Naturkunde, Berlin. The anatomical analysis of MB.R.999 has been undertaken with the help of high-resolution computer tomography (CT scanning) and neutron imaging technologies, and the subsequent 3D reconstruction yields insights into otherwise inaccessible features of the skull. We have identified this specimen as *Aelurosaurus felinus*, permitting a detailed redescription of this historic taxon. *Aelurosaurus felinus* can be recognized by its extensive dentition on the palatine and the pterygoid, delta-shaped palatine bosses, high maxillary tooth count (five postcanines), and sharply curved transverse processes of the pterygoid. A parsimony-based phylogenetic analysis of Gorgonopsia revealed a basal position for *Aelurosaurus* within gorgonopsians, close to *Eriphostoma* and *Gorgonops*. CT scanning also revealed new insights on tooth replacement in *Aelurosaurus*. In MB.R.999, tooth replacement occurs most rapidly in the canines. A functional and an erupting replacement canine are present in the upper canine alveoli, with an additional replacement canine forming below the functional one. Given that the canines have been interpreted as crucial for killing prey in gorgonopsians, rapid canine replacement would have been an important adaptation for maintaining individual fitness.

Tooth migration in the hadrosaurid dental battery

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Hadrosauridae, or duckbill dinosaurs, are characterized by a unique dental complex called a dental battery. This dental battery is composed of multiple vertically stacked columns of teeth, or tooth families, that interlock with adjacent tooth columns. Each tooth family contributes multiple teeth to the occlusal surface. This feature is a result of an accumulation of three to six successional teeth within each tooth family and the tight spacing between tooth generations. This complex grinding surface allowed for efficient grazing on tough vegetation, including the grit attached to low-lying plants.

Previous work on the hadrosaurid dental battery initially interpreted this unique structure as a solid block of teeth that were cemented together, but a recent study clearly concluded that soft tissues and ligaments held the battery together. This would have allowed for fine-scale eruptive movement of the teeth and provided compressive resistance during occlusion. However, investigation into the interactions between teeth in a full hadrosaurid dental battery is required before these interpretations can be confirmed and/or improved. For this study, the first histological thin-sections of an entire adult dental battery were prepared along the occlusal plane, as well as a nearly complete perinatal dental battery. Considering adults have approximately eight times more teeth than perinatal individuals, an ontogenetic approach was used to further test whether any shifts in these interactions changed through ontogeny.

The adult dental battery revealed signs of extensive tooth migration (teeth drifting from their original positions within the jaw), including active remodeling of the alveolar bone as a result of gradual repositioning of tooth generations within the battery. The directionality of the remodeling of alveolar septa also indicated an antero-posteriorly variable path of tooth migration. The four most posterior tooth families of the adult migrated posteriorly while the remaining tooth families had a progressive anterior trajectory. The alveolar bone and teeth migrate anteriorly or posteriorly based on bone remodeling and the displacement of successive generations of teeth at these positions. In the perinatal individual, all of the alveolar septa are angled anteriorly suggesting that anterior tooth migration is extensive early in ontogeny and the most posterior tooth migrate posteriorly later in ontogeny.

Although the mechanisms behind tooth migration in the hadrosaurid dental battery require further investigation, accommodation of new tooth families during jaw development and/or opposition of forces during mastication and occlusal wear may have strong influences. Regardless of the reason, the degree of movement within the dental battery is only possible due to the presence of a complex network of ligamentous connections between the teeth and alveolar bone.

Avian traces of the Gates Formation (Early Cretaceous: Albian) of northwest Alberta and northeast British Columbia: first report of Ignotornidae in Canada

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Initial work (McCrea, 2000; McCrea et al., 2014) outlined several possible novel footprint morphotypes of shorebirds from the Gates Formation (Early Cretaceous: Albian) from within the open pit coal mine near the community of Grande Cache, Alberta. Royal Tyrrell Museum specimen RTM 2016.036.0003 is a track slab preserving the natural casts of two distinct avian traces. One trace is of small, semipalmate avian that preserves sinusoidal digit III impressions, and inconsistently preserve impressions of a functional digit I (hallux). The morphology and size of the tracks is consistent with Ignotornidae (Fig. 1).

Figure 1. RTM 2016.036.003, natural cast track slab from within Grande Cache Coal (Gates Formation: Albian), northwest Alberta. Two avian ichnotaxa are preserved on this slab: *Aquatilavipes* ichnosp., and a track type that represents Ignotornidae. Present in the Early Cretaceous of China, Colorado, and Korea, this is the first occurrence of Ignotornidae in Canada.

This sinusoidal digit III impression is not uncommon to see in the traces of both extinct and extant avians as an extramorphological feature. In Ignotornidae, *Ignotornis mcconnelli* does exhibit a sinusoidal digit III that is inconsistently preserved within trackways. The sinuous look to digit III is likely the result of incomplete preservation of the digital pads in fine grained sediment. This extramorphological feature is demonstrated in the erosion of tracks in RTM 2016.036.0003: tracks that preserve the deepest impressions demonstrate this sinusoidal feature, while the digits that are eroded to the level of the track surface are more straight. Individual tracks within trackways of extant *Actitis macularius* (Spotted Sandpiper) may show digit III impressions that are sinusoidal. Sinusoidal digit III impressions in Spotted Sandpiper tracks are not consistent throughout the trackway, and occur predominantly in tracks that are made on sediment with high water content: one can observe the digit III impression transition from straight to sinusoidal with a change in the water content of the track-bearing sediment (Fig. 2).

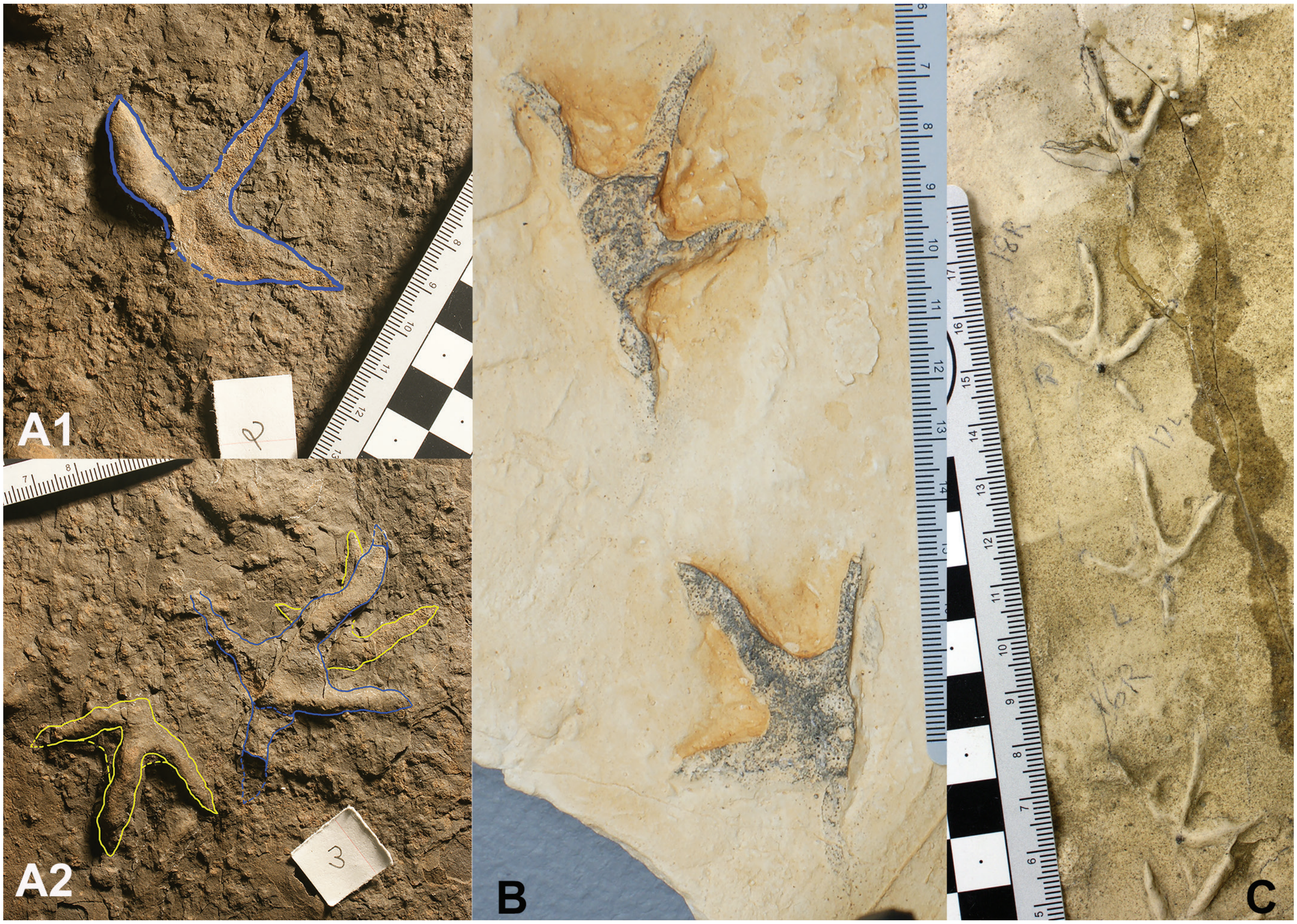

Figure 2. Comparison of sinusoidal digit III impressions of Gates Formation Ignotornidae to extinct and extant avian traces. A1, eroded track 2 from Trackway 1 of RTM 2016.036.0003, showing a straight digit III impression; A2, intact track 3 from Trackway 1 of RTM 2016.036.0003 showing an apparent sinusoidal laterally directed curve of digit III; B, replica of University of Colorado Museum of Natural History UCM 203.5, replica of *Ignotornis mcconnelli*, showing a sinuosity to digit III impressions; C, Peace River Palaeontological Resource Centre specimen PRPRC NI2010.004, plaster cast of tracks of extant *Actitis macularius* (Spotted Sandpiper), showing the transition from a straight digit III impression to a digit III impression that is laterally curved. The only difference between the tracks is the substrate consistency: the tracks that show the curved digit III were made on sediment that was saturated.

The track slab also preserves small avian traces that are similar in morphology to *Aquatilavipes swiboldae*, first described from the Gething Formation (Early Cretaceous: Aptian) of the Peace River Canyon of northeast British Columbia (Currie 1981). At the time of their description *A. swiboldae* were the oldest avian traces known. The occurrence of *Aquatilavipes swiboldae* in the Gates Formation extends the temporal range of *Aquatilavipes* ichnosp. in western Canada, which is congruent with the temporal range of specimens referable to *Aquatilavipes* ichnosp. worldwide (Azuma et al. 2002; Alfinson et al. 2004; Huh et al. 2012; Lockley et al. 2015.) *Aquatilavipes* ichnosp. is known from several localities in what was once Laurasia, and has a broad temporal range (Valanginian – Campanian).

A second track specimen collected from the Gates Formation of northeast British Columbia (PRPRC 2014.05.001) contains the natural molds of two avian ichnotaxa. The predominant avian track type is likely that of *Aquatilavipes* ichnosp. The second avian track type, while faintly preserved, is comparable in size and morphology with Ignotornidae (Fig. 3).

Currently, there are no avian ichnotaxa described from Canada that possess a functional digit I. The tetradactyl avian traces from both Grande Cache, Alberta, and from Roman Mountain, British Columbia, compare favorably with ichnotaxa within Ignotornidae in that the tracks have a wide total (DIVII-IV) divarication, digit II impressions consistently shorter and wider than impressions of digits III and IV, and comparable in pace and stride length with *Ignotornis mcconnelli* (Lockley et al. 2009).

These tetradactyl avian traces represent the first documentation of Ignotornidae from Canada, and the first report of Ignortornidae in the Gates Formation. Preliminary multivariate statistical analyses show that both the Roman Mountain and the Grande Cache Ignotoridae are more similar to *Ignotornis* ichnosp. (*Ignotornis mcconnelli, Ignotornis yangi*) than to *Hwangsanipes* ichnosp. and *Goseongornipes* ichnosp., based on the large divarication between digits I-II. However, the Gates Formation ignotornids are significantly different from all other tetradactyl avian ichnotaxa known from the Cretaceous Period. The possibility that the Gates Formation Ignotornidae represent novel avian ichnotaxa is under investigation.

The known diversity of avian footprints from the Early Cretaceous of North America is growing. McCrea et al. (2015) described *Paxavipes babcockensis* from the Boulder Creek Formation (Aptian-Albian), and *Limiavipes curriei* was described from the Aptian Gething Formation (McCrea et al. 2014), both from northeast British Columbia. As more research is conducted on the avian ichnology of the Early Cretaceous of North America, it is likely the diversity of North American avian ichnotaxa will approach that known from the Early Cretaceous of China and Korea.

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A new approach to pythonomorph phylogeny and implications for independent radiations of Cretaceous marine squamate groups

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During the Cretaceous, terrestrial squamates exhibited a remarkable radiation into the oceans of the world. One group in particular–the Pythonomorpha–was responsible for at least three major radiations: the ophidians (including aquatic hind-limbed snakes), the dolichosaurs (elongate, semi-aquatic lizards), and the mosasauroids (including the giant, open-ocean, predatory mosasaurs). The Pythonomorpha has a long history of study dating back to the early 1800s, when early pioneers of paleontology and comparative anatomy such as Conybeare, Cope, Cuvier, Kornhuber, Kramberger, Mantell, Meyer, and Owen were recognising and describing these fossils. Recent decades have seen a renewed interest in this group, resulting in an explosion in the number of species described and revised. These studies have prompted questions surrounding the origins and evolutionary trajectories of lineages within Pythonomorpha: specifically regarding independent evolution, coevolution or convergence of specific traits. The investigation of these questions necessitates a well-resolved phylogeny; however, no phylogenetic study has specifically attempted to resolve the relationships within the whole of the Pythonomorpha. Instead, the focus has generally been to contextualize a single specimen, or to determine the internal relationships of the ophidians, the dolichosaurs, or the mosasauroids. Broader level comparisons have been coincidental, usually due to the choice of outgroups or ingroups. This study is the first to focus on the relationships at the base of the Pythonomorph lineage using a comprehensive selection of basal members. It shows multiple independent incursions into the marine environment, indicating that many of the traits uniting all or most of this group (axial elongation, limb reduction, the development of paddles and flippers) were independent acquisitions showing similar–though slightly different–solutions to the problem of aquatic adaptation. This in turn, can help explain the variation in success between these three groups: the dolichosaurs remain small and become rare after the Cenomanian/Turonian boundary event; the mosasauroids become large, cosmopolitan predators that go extinct at the end of the Cretaceous; and the ophidians continued to radiate successfully, but primarily in terrestrial environments.

Taxonomic implications of the rediscovery of the type localities of the Late Cretaceous Mongolian sauropods *Nemegtosaurus mongoliensis* and *Opisthocoelicaudia skarzynskii*

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The Polish-Mongolian Palaeontological Expeditions (1965-1971) recovered two sauropods from the Nemegt Formation of the Nemegt Basin, Mongolia. A complete skull found in Central Sayr at the Nemegt Locality became the holotype of *Nemegtosaurus mongoliensis* Nowinski 1971, and an almost complete skeleton lacking the skull and neck became the holotype of *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka 1977. Although both *Nemegtosaurus* and *Opisthocoelicaudia* are sauropods that were found in the same formation only 50 km apart, they were initially assigned to Dicraeosaurinae and Camarasauridae respectively. Because the anatomical parts known for each did not overlap, there was no way of determining whether or not they were more closely related. As the anatomy of titanosaur sauropods became better known in the 1990s, it was proposed that both of the Mongolian sauropods were members of Titanosauria (Calvo et al. 1998a, b). Their overlapping geographic and stratigraphic distribution has led to the persistent suspicion that they belong to the same species, and that there is only one sauropod taxon in the Nemegt Formation (Wilson 2005).

There are two straightforward ways to resolve the problem of whether or not *Nemegtosaurus* and *Opisthocoelicaudia* are synonymous. Either a new sauropod specimen with both the skull and enough diagnostic postcranial material needs to be found and collected in the Nemegt Formation, or more of the holotypes of these two taxa need to be recovered. Since 1965, more sauropod material has been found in the Nemegt Formation, including more than thirty partial skeletons (Currie 2016) and many footprint sites (Currie et al. 2003). This includes a second beautifully-preserved skull of *Nemegtosaurus* (Maryanska 2000, Wilson 2005). However, none of these specimens have overlapping cranial and postcranial material, and cannot resolve the problem of whether or not *Nemegtosaurus* and *Opisthocoelicaudia* are the same taxon.

In 1965, R. Gradzinski found the original skeleton of *Opisthocoelicaudia* on the fifth day after arrival at Altan Uul IV (Kielan-Jaworowska 1969). It was a huge undertaking to collect this specimen, in part because it required an enormous quarry to excavate such a large animal, and in part because it was in an area that could not be accessed by motorized vehicles. Gradzinski produced fairly accurate maps of several of the Polish-Mongolian Palaeontological Expedition localities, on which many of the dinosaur quarries were pinpointed (Gradzinski 1969). Nevertheless, it took us many years of prospecting at Altan Uul IV before we relocated the quarry of *Opisthocoelicaudia* (Currie 2013, fig. 7). And that was only possible because R. Gradzinski supplied additional photographs and sketches that could be used in the field to relocate the quarry. One of the reasons that it was difficult to find is that most of the quarry had been filled with wind-blown sand. For this and other reasons, no attempt has been made to reopen the quarry to see if there are any additional bones that can be recovered.

While the *Opisthocoelicaudia* was being excavated in 1965, several of the members of the Polish-Mongolian Palaeontological Expedition made a short trip to Nemegt on June 15th, and this let to the discovery of another sauropod (Kielan-Jaworowska 1969). In Central Sayr of Nemegt, M. Kuczynski found a skull encased in a wall of hard sandstone, and Maryanska was able to identify the fossil as a sauropod because of its protruding, peg-like teeth. They did not have the tools and supplies needed to remove the specimen, which was covered by more than a metre of rock. Therefore, Kuczynski and Skarzynski returned to the site several days later with the necessary supplies and tools, and then three days later returned to the camp at Altan Uul IV "with the rare, beautiful skull carefully wrapped in wood shavings and cradled in a spacious box" (Kielan-Jaworowska 1969). Gradzinski (1969) marked the location of the quarry on his map of Nemegt. In the Nemegt Formation, it is very rare to find the articulated skull and lower jaws of any dinosaur without finding associated postcranial bones. Therefore we looked for the quarry where the skull came from for more than a decade in the hope of finding parts of the skeleton that might overlap with the holotype of *Opisthocoelocaudia*. Unfortunately, the hand-drawn map of Gradzinski (1969) suggested it was up a side gulley of Central Sayr, whereas when we finally found the site in 2016, it was in fact in the next side canyon. The distance was not that far (about 25 meters) from where it had been marked on the map, but the topographic features were different than expected. One of us (FF) initially found a sauropod ungual and an assortment of fragmentary sauropod bones at the bottom of a cliff. Returning to the site with others later the same day, an opisthocoelic vertebral centrum and both ends of a femur (Fig. 1) were also found in the talus at the bottom of the hill. The source of the material was traced to a level in the face of the cliff, where the shaft of the femur was found. A few meters further over at the same level (Fig. 2), the distal ends of an articulated tibia, fibula and astragalus were protruding from the cliff. The presence of sauropod bones, a stone cairn, quarrying material (plaster and burlap), wood shavings (used by the Poles for packing up specimens), and an empty can stamped with the same numbers (P 341, Fig. 3) as cans found in the 1965 Polish-Mongolian camp all confirmed that this is probably the correct site. The *Nemegtosaurus* holotype was recovered from the interfingering interval of the Baruungoyot and Nemegt formations, and the *Opisthocoelicaudia* locality at Altan Uul IV is also within the lower beds of the Nemegt Formation.

The femur shaft was removed from the cliff and reunited with the other fragments that were found on the talus pile. The bone is virtually complete, and compares well with the femur of *Opisthocoelicaudia* in dimensions and morphology. The partial centrum is clearly opisthocoelic and confirms that *Nemegtosaurus* had the same kind of caudal vertebrae. The astragalus and pedal ungual are also consistent in morphology and size with the same bones in *Opisthocoelicaudia*. The site will be reopened in 2017 to collect the tibia and fibula, which are extending straight into the rock from the cliff face. Hopefully at that time, more bones will also be recovered from the bone level. At this time, it seems more likely than ever that *Nemegtosaurus*

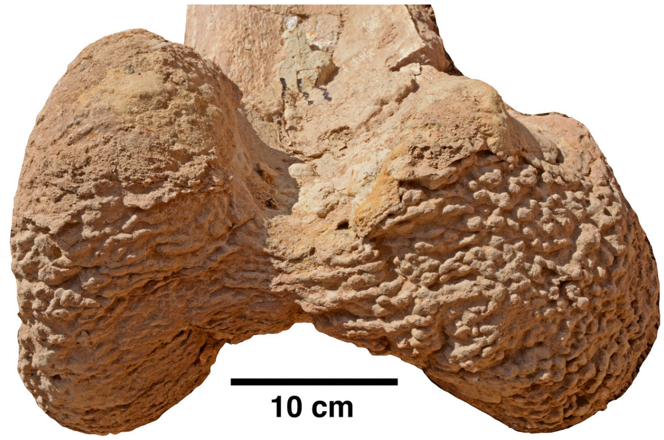

Figure 1. Distal end of right femur in distoposterior view showing the heavily textured surface for attachment of the joint cartilage.

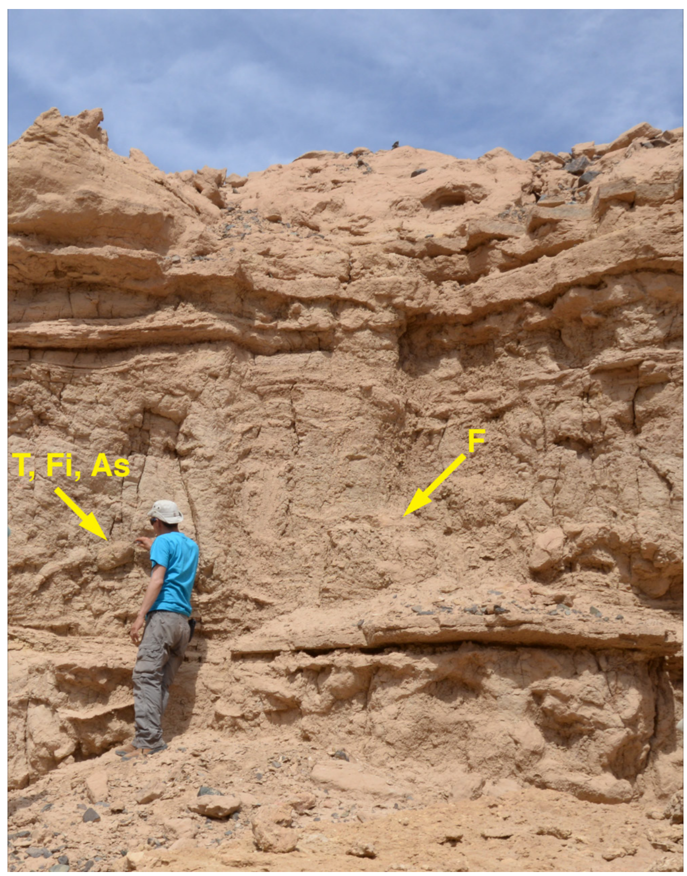

Figure 2. Cliff face with sauropod bones in situ. Both ends of the femur were found in the talus at the bottom of the cliff. Abbreviations: As, astragalus; F, femur; Fi, fibula, T, Tibia.

and *Opisthocoelicaudia* are congeneric. However, even though no differences can be seen in the overlapping bones of the two type specimens, these bones are not particularly diagnostic for sauropods either. Additional recovery of bones from the *Nemegtosaurus* quarry, further research, and additional analysis will be necessary to resolve this taxonomic conundrum.

Figure 3. Tin can lid stamped with P 341 found at the sauropod site. Many cans of this same type were found in the 1965 Polish-Mongolian Palaeontological Expedition camp. 'P' and 'PL' identifies canned goods that were made in Poland, and '341' is a product number that we have not identified yet.

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Timing of cranial ornamentation development in *Prosaurolophus maximus* (Hadrosauridae: Saurolophinae): Implications for display and sexual maturity

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Crest ontogeny has been well documented in hadrosaurs, especially in the Lambeosaurinae sub-family. The crest ontogeny of the Saurolophinae sub-family has been relatively poorly understood, with only a few species having a described ontogenetic series. The cranial ornamentation of hadrosaurs has been hypothesized to have been used for display due to the positively allometric growth of the crest relative to the rest of the skull. However, despite numerous well-studied growth series, the ontogenetic changes in crest morphology of hadrosaurs have yet to be linked to biological age and age of sexual maturity. Here we studied an ontogenetic series of *Prosaurolophus maximus*, a saurolophine hadrosaur with a small nasal crest, in order to assess the timing of changes in crest morphology. Crest morphology was examined in three specimens, including two small individuals (TMP1983.64.3 and TMP1998.50.1) and one large individual (TMP1984.1.1). The number of lines of arrested growth (LAGs) observed in histologic sections of the tibiae was used to estimate the biological age of each specimen. Our results indicate that the crest is poorly developed at two years of age (TMP1983.64.3), and by three years of age (TMP1998.50.1) the crest has adopted the overall shape observed in larger individuals, but lacks the robustness and excavated circumnarial depression seen in the larger specimens. By five years of age (TMP1984.1.1), the crest is fully developed and has achieved the morphology typically observed in the largest specimen of the species. Interestingly, despite size classification as an adult due to a comparable skull size to the largest known *P. maximus* specimen (USNM 12712), histological sections reveal that TMP1984.1.1 is still undergoing rapid growth and has not reached skeletal maturity (identified by thinly-spaced LAGs). Thus, the crest of *P. maximus* is fully formed at a very young age, well before the animal reaches skeletal maturity, and could have been used for display.

A morphometric analysis of Albertan hadrosaur humeri and pubes

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Morphometric analyses can provide great insight into palaeobiology, palaeoeology, and evolutionary trends. To date, few studies have used morphometry to compare lambeosaurine and saurolophine postcranial morphologies. The goal of this study was to identify morphologic trends in postcranial elements between lambeosaurines and saurolophines, and to identify morphologic trends in hadrosaur postcranial elements over geologic time. Sixty humeri and 50 pubes from the Judith River and Edmonton groups were measured. Humeral measurements included: total length, distal width, shaft width, deltopectoral crest length, and proximal width. Pubic measurements included: pre pubic neck height, height at the iliac peduncle, height of the post pubic neck, and length from the iliac peduncle to the branch between the post pubic process and the ischial peduncle. Complete and partial elements were analysed as a single data set. To account for incomplete specimens, a series of regressions were made, comparing all possible measurement pairs. The difference in paired measurement ratios were assessed with t-tests. On average, saurolophine humeral shaft widths are 13% thicker than the shaft widths of lambeosaurines, relative to the humeral distal width. This trend, however, was not seen in relation to any other humeral measurements. The relative large sizes of the deltopectoral crests in lambeosaurines compared to those of saurolophines were not found, as previously reported by other authors. The post pubic neck of *Edmontosaurus* is on average 26% taller than in Judith River hadrosaurs. This may indicate a reduction or shifting of the acetabulum and/or a strengthening of the posterior portion of the pubis. Further work needs to be done on morphological trends, both taxonomic and over geologic time, in the pelvic girdle of hadrosaurid dinosaurs to better understand the significance of these results.

A new troodontid from the Horseshoe Canyon Formation (Maastrichtian) of Alberta, Canada

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Troodontid material from the Maastrichtian of North America is extremely rare, beyond isolated teeth from microvertebrate sites. Here we describe troodontid frontals from the early Maastrichtian Horseshoe Canyon Formation (Horsethief Member). The most complete specimen is notably foreshortened when compared to numerous specimens referred to *Troodon* from the Dinosaur Park Formation, and exhibits several characteristics that distinguish it from other members of the family. Morphometric analyses demonstrate shape differences between the Horseshoe Canyon frontal and other North America troodontids, and show that proportional differences are independent of size. We therefore recognize a new taxon diagnosed by the following autapomorphies: 1) primary supraciliary foramen is truncated anteriorly by the lacrimal contact, 2) superficial (ectocranial) surface of the frontal proportionally shorter than all known troodontids, with a length to width ratio under 1.25, and 3) frontal-parietal joint in which an enlarged lappet of the frontal extends medially to extensively overlap the lateral region of the anteromedial process of the parietal. Interestingly, tooth and jaw morphology from the single relatively complete dentary recovered from the Horsethief Member of the Horseshoe Canyon Formation cannot be distinguished from dentaries and teeth from the Dinosaur Park Formation. If the dentary and teeth from the Horsethief dentary prove to belong to the new taxon, extensive overlap in tooth morphology between the Dinosaur Park and Horseshoe Canyon formations reinforce the notion that tooth morphotypes do not exhibit strong correspondence to species alpha diversity, and may encompass multiple closely-related taxa.

Paleocene-Eocene mammal communities were robust to invasion

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The Paleocene-Eocene transition in North America was marked by a rapid global warming event of 5° to 10°C (PETM; ~56 Ma) that followed an abrupt carbon isotope excursion lasting 21 ky or less. During the PETM, mammals decreased significantly in body size due to anagenetic (within lineage) evolution. The PETM is also coincident with the immigration of the Perissodactyla, Artiodactyla, and Primates into North America from Eurasia, which also led to significant body size change. The PETM is thus ideal for understanding the role of invasion and morphological evolution in the assembly of mammal communities. We assembled a database of 571 species and their associated body sizes that included the vast majority of species that cross the PETM in North America. We created a time scaled composite phylogeny for all species in the sample based on a recently published phylogeny of early Cenozoic mammal genera. Using the Net Relatedness Index, we calculated the phylogenetic relatedness of species in the same community across the PETM. We also calculated body size dispersion as the average of the pairwise differences among co-occurring species. We found that, the phylogenetic structure of mammalian communities remained stable across the PETM, a pattern that is invariant to the tree dating method, uncertainty in tree topology, and resolution of the tree. Similarly, body size dispersion and faunal turnover in the spatial dimension (beta diversity) remained stable. We suggest that invasion by new taxa had little impact on Paleocene-Eocene mammal communities and that their resilience to invasion may indicate that niches were not saturated. We note that invasion in the modern world is unprecedented due to transplantation of species by human activities. We suggest that human activities have so dramatically altered modern biotas that the once high resilience of mammal communities to invasion may have been lost.

A new oviraptorid (Dinosauria: Theropoda) provides a rare glimpse into social behaviour in dinosaurs

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The Nemegt Formation of Southern Mongolia is one of the richest dinosaur-producing formations in the world. At least 30 genera are known from the Nemegt Formation, including ankylosaurs, hadrosaurs, sauropods, and theropods. The abundance of these deposits has unfortunately attracted the attention of fossil poachers, and dozens of poached skeletons are suspected to hail from the Nemegt Formation. In 2006, Mongolian customs officers confiscated two important poached specimens. The first is a spectacular block of three articulated juvenile skeletons, representing a new species of oviraptorid theropod. This new taxon is characterized by a domed cranial crest, a functionally didactyl hand, and a short tail. In addition to the skeletons in the block, the second poached skeleton is an even younger individual. An unpoached, partial adult skeleton from Guriliin Tsav verifies the suspected provenance, and together the skeletons constitute an excellent ontogenetic series. This series indicates that the cranial crest is present early in development, and is positively allometric. Appendicular skeletal proportions change little throughout ontogeny, but the tail becomes relatively shorter and the chevrons longer. Additionally, the pygostyle fuses throughout development, which is consistent with its proposed function as a sexual display structure. In addition to anatomical and ontogenetic insights, the skeletons in the block are important for our understanding of oviraptorid and theropod behaviour. The three individuals are in sleeping posture, and would have been in contact in life. In addition to a remarkable instance of behaviour captured in the fossil record, the specimens also represent the first evidence of communal roosting in dinosaurs. The evolutionary origins of communal roosting in modern birds are debated, and this specimen highlights the possibility that this behaviour was inherited from their dinosaurian ancestors. In light of the oviraptorid style of synchronously laying paired eggs, the identical young ages of the individuals in the block suggest that they may be siblings. If this were the case, it would lend support to synchronous-breeding hypotheses of communal roosting evolution. Beyond the behavioural implications, this new taxon highlights the diversity of Nemegt oviraptorids, and raises questions of why and how this ecosystem could sustain this diversity.

Paleoecology of a vertebrate microfossil assemblage from the easternmost Dinosaur Park Formation (Upper Campanian) Saskatchewan, Canada: Reconstructing diversity in a coastal ecosystem

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The Belly River Group (BRG) comprises an eastward thinning paralic to non-marine Campanian clastic succession in the Western Canadian Sedimentary Basin. The three formally recognized formations of the BRG in the western Canadian Plains are, in ascending order, the Foremost, Oldman, and the Dinosaur Park formations. In Alberta, the BRG is well known for its rich and diverse vertebrate fauna. The Dinosaur Park Formation in particular is one of the most productive dinosaur bearing units in the world. Outcrop of the BRG in Saskatchewan is, in contrast, much sparser, more widely distributed, and often difficult to access. Despite this paucity of available outcrop, localities where the BRG is exposed in Saskatchewan represent the north-easternmost occurrence of the Group. As such, the Saskatchewan BRG holds considerable potential for addressing longstanding questions about large-scale spatial diversity patterns during the late Campanian period. In particular, questions about how the proximity of the Western Interior Sea influences diversity could be addressed in a much broader and more temporally expended scale by studying the paleoecology of vertebrate assemblages between Alberta and Saskatchewan. In recent years, several micro- and macrofossil sites from the BRG have been identified throughout southwest Saskatchewan. These sites contain diverse vertebrate assemblages, including chondrichthyans, osteichthyans, turtles, champsosaurs, crocodiles, salamanders, birds, mammals and dinosaurs.

A ~42 metre section of upper Campanian sediments in Saskatchewan Landing Provincial Park in southwest Saskatchewan, represents the easternmost outcrop of the Dinosaur Park Formation in the Western Interior Basin. Between 2010 and 2015, the RSM and McGill have collected macrofossil material from several dinosaur taxa, including hadrosaurs, ceratopsians and theropods. In addition, hundreds of microvertebrate fossils have been collected, expanding our understanding of the rich microvertebrate fauna present during the late Campanian period in Saskatchewan. In this study, palynology, ichnology, sedimentology, and vertebrate paleontology are integrated to determine paleoenvironmental and paleoecological conditions in the region. The site is interpreted as having been deposited under marginal-marine conditions near a shoreline undergoing transgression by the encroaching Bearpaw Sea. The vertebrate fossil assemblage found at this locality is highly diverse, and offers new insights into late Cretaceous ecosystems living near paleocoastlines. This ongoing research could provide critical insights into the large scale diversity patterns, as well as the drivers of that diversity, that were occurring in the late Campanian of North America.

Trapped in time: Investigating the morphology and paleoecology of a previously unreported lizard specimen in amber

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Vertebrate inclusions in amber deposits are rare in the fossil record, known for only a few localities and time slices. Yet their 3D preservation of both hard and soft tissues offer paleontologists a detailed glimpse into the biology of extinct life that is not possible through other preservation methods. Here we will discuss a new study on a previously unreported fossil lizard specimen preserved in amber that has been housed in the collections of the Queen's Miller Museum of Geology. As the specimen lacked locality data we have undertaken Fourier Transform Infrared Spectroscopy (FTIR) and stable isotopic (C, H) analysis to investigate the paleoenvironmental conditions of the depositional environment. The highly negative Carbon-13 isotopic signal suggested that our sample is derived from Angiosperm resin and of Neogene in age from an area of high precipitation. FTIR shows a similar spectrum to other vertebrate bearing deposits from the Dominican and suggest that our sample is from this region. Using high resolution X-ray Microscopy scans we have reconstructed a 3-D digital model to document the morphology and paleoecology of this specimen as well as several invertebrate inclusions found in the same sample. We determined the lizard is a gecko based on several major synapomorphies such as fused frontals, reduced cervical count and short parietal supratemporal process. The high phalangeal index and recurved claws suggests a scansorial lifestyle, though toe pads are not preserved. Several morphological differences, including a thin quadrate and tooth shape indicate that our specimen is not part of the *Sphaerodactylus* complex that is commonly preserved in this region and link it to the mostly terrestrial eublepharids. By combining techniques and using cut edge 3-D scanning technology has allowed for a unique glimpse into the paleobiology of this specimen and the ecosystem in which it lived.

Assessing the relationship between acrodont implantation and reduced tooth replacement: comparisons between the dentitions of extinct and extant acrodont reptiles

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Acrodonty is a form of tooth implantation where the tooth is ankylosed to the apex of the jaw; this is unlike the mammalian condition thecodonty, where the tooth sits within a socket. Extant reptiles possessing acrodont dentitions are mostly found within the squamate lineage Acrodonta, and lack tooth replacement (monophyodonty). Although not all extant acrodont reptiles fall within this clade, they are all restricted to Lepidosauria and exhibit at least reduced replacement (oligophyodonty). This reduction in replacement has resulted in an association between oligophyodonty and the evolution of acrodont implantation (Zaher and Rieppel 1999). This association between replacement and implantation breaks down when considering extinct reptiles with acrodont dentition, which are found in several eureptilian groups outside of Lepidosauria. The earliest acrodont reptile, *Opisthodontosaurus* is unusual in exhibiting continuous tooth replacement (polyphyodonty) through ontogeny, and none of the wear adaptations seen in modern acrodont amniotes. In this study we examine tooth implantation and histology in *Pogona vitticeps*, an extant acrodont agamid lizard, that shows no external or histological signs of replacement, and compare it to *Opisthodontosaurus* (Reisz et al. 2015), the earliest acrodont amniote from the early Permian. This comparison is crucial when attempting to determine which characteristics diagnose acrodont implantation, and which might have resulted separately as an adaptation to oligophyodonty. Modern chamaeleonid and agamid squamates exhibit adaptations to prolong the life of their dentition, such as having mineralized tissues that infill the pulp cavity of the teeth, this permits extended erosion of the crown surface without the possibility of exposing the pulp cavity (Throckmorton 1979; Dosedělová et al. 2016). These new histological data presented for Pogona vitticeps, and Opisthodontosaurus, show that acrodont implantation is not universally associated with any of the dental adaptations commonly associated with reduced tooth replacement. Our findings also suggest that the evolution of acrodonty predates the Lepidosauria and the evolution of oligophyodonty. These findings highlight the need to consider the fossil record and the diversity of dentitions in extinct reptiles in order to tease apart functionally and phylogenetically informative features of amniote dental growth and replacement patterns.

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Assessing the provenance of a pachycephalosaur skull

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A pachycephalosaur skull-cap was surface collected near Drumheller by an amateur fossil-hunter before the Alberta Historical Resources Act was extended (July 5, 1978) to protect Alberta fossils. It was taken to British Columbia and was kept in a private collection for many years before it was donated to the Qualicum Beach Palaeontological Museum. Two of us saw it there in January 2010. Because the skull-cap is well-preserved and scientifically important, arrangements were made with the director (Graham Beard) and the amateur collector to donate the original specimen to the University of Alberta in return for a cast. It is now catalogued in the collections of the Laboratory for Vertebrate Palaeontology as UALVP52676.

Unfortunately there was little precise information on when and where it was collected. According to the collector's account and his daughter's diary it was recovered from the badlands on the east side of the Bleriot Ferry. The dark, chocolate-brown colour of the bone is consistent with other bones recovered from this locality, but does not provide any information about the level the specimen may have been washed from. At least two members (Horsethief, Morrin) of the Horseshoe Canyon Formation are exposed in this area. Because of the uncertainty about the provenance of the fossil it was decided to see if it was possible to retrieve enough sediment to make a palynological preparation. The sediment that was to be checked in biostratigraphic and palaeoenvironmental studies for fossil spores and pollen was removed from the dinosaur fossil while it was being cleaned up, and the palynological preparation was done using standard techniques by Geolab in Medicine Hat.

The recovery was poor, but enough spores and pollen were recovered for comparison with different localities and stratigraphic levels in Alberta, and in particular with the members of the Horseshoe Canyon Formation that are exposed at Bleriot Ferry. Approximately 25 species of spores and pollen have been identified. Most of them have a long range and will not help in narrowing in on the stratigraphic level that the skull is coming from. However, there are a few species from the Aquilapollenites suite that have shorter stratigraphic ranges, and support assignment of the specimen to the Horseshoe Canyon Formation, but not to any particular horizon in that formation.

A new alligatorid from the Margaret Formation (Eocene), Ellesmere Island, Nunavut

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In the 1970s, Mary Dawson and her team discovered a diverse early Eocene terrestrial fauna on Ellesmere Island, Nunavut. The fauna comes from the Margaret Formation that has been dated to Wasatchian North American Land Mammal Age. The collection consists of a wide range of mammals, including primates, bats, multituberculates, carnivorans, and perrisodactyls. The more rare fishes include gars, amiiforms, and pikes, and a small representation of scapherpetontid salamanders have a minor representation. Numerous freshwater turtles, squamates, and even a giant ground bird (represented by a phalanx) were recovered. Of note is the single medium-bodied crocodylian. This taxon was originally referred to *Allognathosuchus* sp. on the basis of a relatively complete mandible. The molariform dentition and robust proportions of the jaw were comparable to the Wasatchian *Allognathosuchus heterodon* and Bridgerian *A. polydon*. However, these traits are now known to be more general for Alligatoridae.

Additional material of this crocodylian was recently returned to the Canadian Museum of Nature in its original collection bags. Preparation and analysis of this new material has yielded a more complete picture of the skeletal anatomy of this taxon. The taxon is larger than originally thought. The original mandible indicated an animal approximately 1.5 m long whereas the new material suggests the body length is actually close to 3.5 m. Its molariform dentition is remarkably heterotrophied to a greater degree than that of any other known alligatoroid. The same applies to the mandible. The ectopterygoid-maxilla and ectopterygoid-jugal contacts are equally robust, suggesting a durophagous diet. The postcranial anatomy is comparable to other alligatorids with robust vertebrae, thin scutes, and relatively short, robust limbs. Numerous bivalves were included in the sample bags and may have been a major portion of the crocodylian's diet.

Enough autapomorphies are present to distinguish this alligatorid as a new taxon. Phylogenetic analysis recovers the new taxon within a clade of *Alloganthosuchus* and Procaimanoidea. The geographic occurrence is also unique to this Ellesmere Island alligatorid. It is the highest latitude crocodylomorph ever recovered, by over 1000 km poleward. How a predator of this size survived the 24 hour darkness of long winters at this latitude is puzzling. Revision of this High Arctic crocodylian is an important addition to the crocodylian fossil record, and lends insight to the fascinating Eocene ecosystem of Ellesmere Island.

Tooth attachment histology in mosasaurs, snakes, and crocodilians: a comparative approach for understanding the evolution of tooth attachment and implantation in amniotes

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Squamates present a unique challenge to our understanding of the evolution of amniote tooth attachment. Mammals and crocodilians have a complex ligamentous mode of tooth attachment where teeth sit within a dental groove or discrete circular sockets, a condition known as thecodonty. By comparison, most lizards exhibit pleurodonty or acrodonty, where teeth are fused to a single wall or to the crest of the jaw respectively. These differences in the nature and geometry of tooth attachment among modern amniotes have enforced a long-standing view that squamates possess a plesiomorphic form of tooth attachment and that crocodilians and mammals have independently evolved a histologically complex tooth attachment system that includes a periodontal ligament. However, this interpretation is now at odds with a growing number of reports of complex, ligamentous forms of tooth attachment in numerous extinct amniote lineages, including many eureptiles. What remains to be determined is if squamates produce the same tooth attachment tissues as those of the traditionally "thecodont" groups or if crocodilians and mammals have convergently evolved a novel suite of dental tissues.

To address this question, we compare the histology and development of tooth attachment tissues in extinct marine mosasaurids, modern snakes, and the crocodilian *Caiman sclerops*. The teeth of the two squamate taxa are surrounded by extensive tooth attachment tissues, making them ideal for histological sampling. Thin sections reveal that, contrary to previous interpretations, mosasaurs and snakes indeed possess a periodontal ligament, but unlike the condition in *C. sclerops*, the ligament completely calcifies after the tooth erupts. The bulk of the osteocementum forming the roots of mosasaur teeth and the "bone of attachment" at the bases of snake teeth are actually composed of large networks of thick calcified collagen fiber bundles that are identical in shape and topology to those of a periodontal ligament. Studying ontogenetic stages of mosasaur teeth reveals that the ligament calcifies from the root surface outwards, eventually meeting the surrounding socket bone to form a stable ankylosis. When compared to attachment tissue development in crocodilians, these findings indicate that differences in the timing and extent of this calcification, and not the de novo evolution of dental attachment tissues, dictate the nature and geometry of tooth attachment in reptiles.

T-U-R-T-L-E power at the Canadian Museum of Nature

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The Canadian Museum of Nature in Ottawa is known for its historic collection of Upper Cretaceous dinosaurs from Canada. Perhaps less appreciated is the museum's excellent collection of fossil turtles, made by the likes of the Sternberg family, Loris Russell, Wann Langston, Jr., and others over the last century. Until recently, many of these turtles have remained in their original plaster jackets. However, considerable focus has been given to preparing them over the last year-and-a-half, combining the efforts of in-house preparators and volunteers alike. The results have been tremendous, with 15 specimens prepared so far. Included among the finds are partial growth series of the baenid *Plesiobaena* and the trionychoid *Aspideretoides*, the collections' first

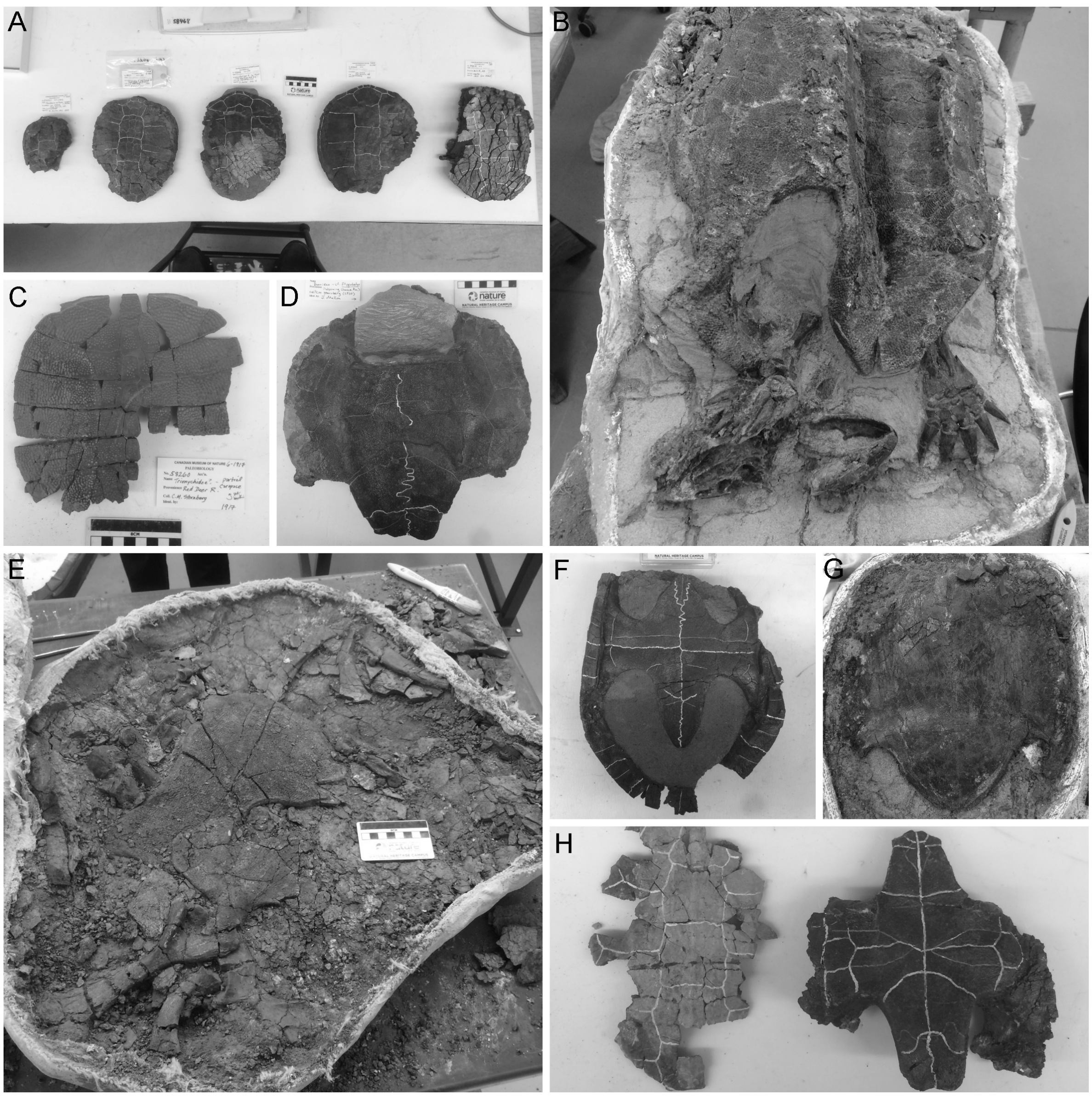

Figure 1. Select recently prepared turtles at the Canadian Museum of Nature. A, *Plesiobaena* growth series; B, mostly complete skeleton of *Basilemys*; C, carapace of *Aspideretoides*; D, plastron of *Stygiochelys*; E, shell and partial postcranium of *Axestemys*; F, plastron of *Judithemys*; G, plastron of *Adocus*; H, carapace and plastron of *Boremys*.

examples of the macrobaenid *Judithemys* and the chelonioid *Kimurachelys*, one of the few shells of the baenid *Stygiochelys*, a complete shell and rare associated postcrania of the giant trionychid *Axestemys*, an exquisite skeleton and first known skull of the nanhsiunchelydid *Basilemys varialosa*, and a new species of *Basilemys* from the Horseshoe Canyon Formation of Alberta (Fig. 1).

The new *Basilemys* species (Fig. 2) is intermediate in age between the Judithian/Kirtlandian forms *B. varialosa* and *B. nobilis*, and the Lancian forms *B. gaffneyi* and *B. praeclara*. It is also intermediate in its morphology, possessing a unique suite of both primitive (e.g., divided extragulars) and derived (e.g., square epiplastral beak, pygal wider than long) traits. The new species is further characterized by a protruding epiplastral beak and cinched vertebral scale 1. Preliminary cladistic analysis using parsimony finds the new species as the sister taxon to the Lancian forms. The specimen is significant for being the first diagnostic *Basilemys* collected from Edmontonian strata, which represent a time of low turtle diversity owing to cool climatic conditions.

These newly revealed finds speak to the wealth of information still contained in unprepared storage at the Canadian Museum of Nature. Ongoing preparation efforts will continue to reap this bounty in due time. Interested students of fossil turtles stand to greatly benefit from visiting the museum's collections.

Figure 2. Nearly complete shell of *Basilemys* n. sp. from the Horseshoe Canyon Formation of Alberta. A, carapace; B, plastron.

The "Six Peaks Dinosaur Track Site": A diverse fossil vertebrate track site from the Gaylard Member of the Gething Formation (Early Cretaceous: Aptian) from the Carbon Creek Basin, northeastern British Columbia

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The earliest published reports of vertebrate tracks from western Canada are from the Gething Formation strata exposed along the Peace River Canyon of northeastern British Columbia (McLearn 1923). Sternberg (1932) described the first ever Cretaceous fauna from tracks found at several large-scale track surfaces from the Gething Formation, establishing six new ichnogenera and eight new ichnospecies of dinosaur prints. These are *Irenesauripus mclearni* (medium theropod), *I. occidentalis* (large theropod), *I. acutus*, (large theropod), *Columbosauripus ungulatus* (small theropod), *Irenichnites gracilis* (small theropod), *Gypsichnites pascensis* (small ornithopod), *Amblydactylus gethingi* (large ornithopod) and *Tetrapodosaurus borealis* (ankylosaur).

In the 1970's, the Provincial Museum of Alberta sent out a series of four expeditions between 1976–1979 to document as many tracks and track sites as possible before Peace River Canyon was flooded upon completion of the Peace Canyon Dam, which occurred in the fall of 1979. Results from these expeditions added a new ornithopod ichnotaxon *Amblydactylus kortmeyeri* (Currie and Sarjeant 1979) and a new avian ichnotaxon, *Aquatilavipes swiboldae* (Currie 1981), along with many novel observations of terrestrial vertebrate communities and behaviour (Currie 1983; 1989; 1995). Since the late 1970s there have been very few tracks and track sites from the Gething Formation found outside of the Peace River Canyon (McCrea et al. 2014). However, one additional avian ichnotaxon (*Limiavipes curriei*) was collected from the south shore of the Williston Reservoir, from the Gething Formation just a few hundred metres west of the W.A.C. Bennett Dam, as were slabs containing small, non-dinosaurian reptile tracks, very similar to turtle tracks (McCrea et al. 2014).

In 2008, a local resident, Mr. Barry Mireau, reported finding several dinosaur tracks at a locality within the Carbon Creek Basin. Though fossil tracks had been previously found in Carbon Creek Basin (Currie, 1989), Mr. Mireau's report was from a novel locality. The site was exposed in a ~6,000 m^2 clearing, established as a result of industrial activity. While only a few tens of square metres were uncovered, there were scores of vertebrate tracks (mostly theropod) evident (Fig. 1), many exhibiting lengthy trackways.

Due to the site's proximity to a public road no research was started until the resources became available to do it properly. The first field work on the site began in the summer of 2016, and it was shortly after this work began that the name "Six Peaks Dinosaur Track Site" was proposed. The name refers to six prominent mountains that surround the Carbon Creek Basin and most of these mountains feature prominently in the histories of local First Nations.

Preliminary surveys in the spring of 2016 indicated that at least 6,000 m^2 of the track surface was lightly covered (1 metre or less) with friable mudstone. The clearing was produced as a result of logging activity a few decades ago, likely as a borrow pit for the mudstone as road fill for logging. Mechanical excavation marks on the track surface indicate the removal of the overlying mudstone, but continued industrial activity at the site was foiled by the impenetrable sandstone that comprised the dinosaur track surfaces.

The site is situated on a southwest dipping (~10º) anticline limb which drops off to steep valleys on its north and south sides. The east portion of the track surface has a similar, but less steep drop off. The west side continues downslope into forest cover, but the surface likely extends at least another 200 metres which could add as much as 12,000 m^2 or more track surface. The goal of the 2016 field work was to excavate as much of the track surface as possible with the ultimate objective of uncover approximately 3,000 m^2 for this project over five years. Approximately 750 m^2 of the surface was excavated in 2016, revealing over 1,200 prints and scores of vertebrate trackways.

Most of Sternberg's ichnotaxa described from the Peace River Canyon are present at the Six Peaks Dinosaur Track Site, with the exception of *Tetrapodosaurus borealis*. *Amblydactylus kortemeyeri* described by Currie and Sarjeant (1979) from the Peace River Canyon has also been identified at the Six Peaks Dinosaur Track Site. Other notable absences include the avian ichnotaxa *Aquatilavipes swiboldae* and *Limiavipes curriei*. No turtle tracks have been recognized to date.

There are a few vertebrate ichnotaxa present at the Six Peaks Dinosaur Track Site that had never been reported from any previously documented site from the Gething Formation. This includes a very few tracks (no trackway) that closely resemble *Magnoavipes* isp. which were produced by small- to mid-sized theropods. There is also the rather unexpected presence of a pair of lengthy sauropod trackways (Fig. 2), two trackways of large, functionally four-toed theropods, and a several tracks of a large avian with a distinct hallux impression. The sauropod trackways bear some similarity to those of the ichnogenus *Parabrontopodus*. The large, tetradactyl theropod tracks seem unprecedented in the literature, and are quite distinct in morphology from the few ichnospecies within the tetradactyl theropod ichnogenus *Saurexallopus*. The large avian prints with hallux impressions are similar to ichnotaxa within the Ignotornidae.

The site is dominated by tracks and trackways of theropods, mostly those of *Irenesauripus acutus*. Trackways of both saurischians and ornithischians exhibit bimodal orientation to present day east and west. Very few trackways were exposed that trended in other orientations.

Figure 1. A pair of large theropod tracks (*Irenesauripus acutus*) from the Six Peaks Dinosaur Track Site. Picture taken shortly after this site was reported (Fall, 2008).

Next to *Irenesauripus acutus*, *Gypsichnites pascensis* is the most common vertebrate ichnotaxon at the Six Peaks Dinosaur Track Site. Based on the morphology of a few pes prints, including the holotype, it has been speculated that *Gypsichnites pascensis* might be the product of a theropod dinosaur (McCrea 2000; Diaz-Martinez et al. 2015). However, there is a wide variety of preservation of trackways identified as *G. pascensis* at the Six Peaks Dinosaur Track Site, and a great many of them display manual impressions. *Gypsichnites pascensis* is certainly an ichnotaxon produced by ornithopods that were generally quadrupedal. These prints were some of the first ones made on the track surface when the substrate was still saturated with water. In fact, one of the first such trackways made on this surface was of an animal that evidently experienced difficulty walking on such waterlogged substrate as it exhibits lengthy foot slip marks and even shows a trace of a stumble and recovery.


Figure 2. Capture from a generated 3D model of the ninth pes print (right) of a large sauropod from the Six Peaks Dinosaur Track Site. Total length 85cm.

A very rare locomotion event was recorded at the Six Peaks Dinosaur Track Site. A well-preserved, lengthy, and easy to follow theropod trackway exhibits a series of four deliberate course changes. The trackway of 27 footprints (23 present, 4 missing) first has a general eastward bearing, then the animal's pace and stride decrease into the first course change to the south, then back to the east, then strongly to the south then to resume its eastward course for the remainder of the exposed trackway. It is difficult and often unwise to speculate about the motives and behaviours of extinct animals, but the surface was likely to have had some areas of standing water which this particular theropod may have been trying to avoid.

The sauropods were among the last animals to cross the surface as their prints obliterate, or deform a number of tracks and trackways at the Six Peaks Dinosaur Track Site. The two trackways are from two different animals,(one large, one smaller) progressing in two different directions, one to the north west and the other gently curving to the northeast. One sauropod pes print was completely excavated and was so deep that is not only penetrated through the track surface, but also penetrated three or more underlying sedimentary layers. It nevertheless shows the larger, clawed digit traces (I-III) clearly, and the smaller unclawed digits (IV-V) as well.

There is less than one metre of vertical section exposed at the site with seven distinct bedding planes which are thinly bedded (0.5 cm – 1 cm scale) and overall show a fining upward sequence from a basal layer of heavily burrowed sandstone to the top layer comprised of a dark, friable mudstone. The five lower beds all display tracks, although it is the middle of these that is the most widely exposed and is the main track layer for the Six Peaks Dinosaur Track Site.

Almost all of the prints contained infill from the overlying sedimentary layer and required preparation to fully expose them (Fig. 3). The main track layer is quite lithified, having a substantial amount of carbonates filling the interstitial spaces between grains. The infilling material does not normally have carbonates present and is generally less lithified than the main track layer. The infilling layer does contain small bivalves, gastropods and ostracods which were observed and collected during infill removal of tracks.

Replica latex and platinum-cure moulds of 96 tracks (some singles, most in trackways) were collected, as were thousands of high-resolution photographs for 3D digital modeling. The entire excavated surface was traced on

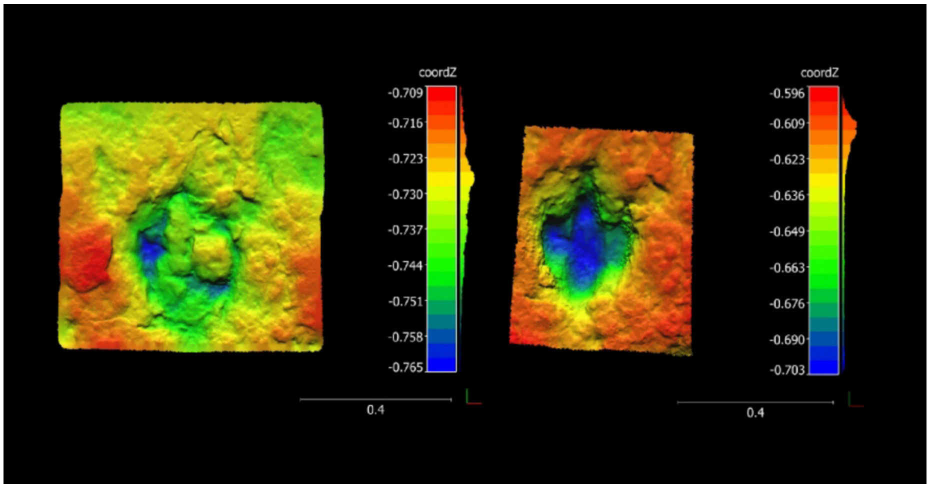

Figure 3. Captures from generated 3D models of a *Gypsichnites pascensis* pes print. Left: print before infill removal. Right: print after infill removal. Vertical and horizontal scales in metres.

1:1 scale on a series of overlapping, transparent plastic sheets, and detailed measurements were collected on 231 in situ tracks in 22 trackways. Twelve vertebrate ichnotaxa (morphotypes) have be recognized at the site to date.

On October 17, 2016, the Six Peaks Dinosaur Track Site received Section 17 status (conditional withdrawal from disposition) via British Columbia's Heritage Branch within the Ministry of Forests, Lands and Natural Resource Operations.

Acknowledgements

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Inferring the evolution of the cyclostome body plans through reconstruction of stem conditions

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Cyclostomes (hagfish and lampreys) constitute the only living lineages of jawless vertebrates, but neither hagfish nor lampreys readily serve as an outgroup to gnathostomes for comparative purposes. It remains a puzzle in what traits they are primitive, and even the status of cyclostomes as a clade has been questioned repeatedly by phenotypic data. These challenges reflect a general problem of the emphasis on crown groups. The extant hagfish and lampreys each have specialized and divergent morphology, whereas few fossil forms have been assigned unambiguously to the stems of the crown lineages of cyclostomes.

In hagfish, the origin of the crown group represents a key node to distinguish primitive (symplesiomorphic) versus degenerative (autapomorphic) characters in their quasi-vertebrate morphology. Molecular clock places this node in the latter half of the Mesozoic Era, but no unambiguous fossil hagfish has been known to date. The poorly preserved *Myxinikela* and *Gilpichthys* from the Carboniferous of Illinois are putative stem members but remain controversial. Aided by phase-contrast synchrotron radiation scanning of preserved soft tissues, I report a new fossil from the early Late Cretaceous of Lebanon that (a) nests within the crown group of hagfish and (b) provides a hard minimum calibration point compatible with molecular clock estimates.

In lampreys, the dramatic metamorphosis from a filter-feeding larva to a blood-sucking adult has generated conflicting interpretations of early vertebrate evolution. Nevertheless, multiple hypotheses posit the larvae as a surrogate for the last common ancestor of the living vertebrates. If cyclostomes form a clade, however, the larval lamprey-like first crown-group vertebrate is equally parsimonious with the alternative — a secondary acquisition of a filter-feeding larval stage within lampreys. To contrast these hypotheses, I describe an ontogenetic series of a stem lamprey and test whether the larvae exhibit skeletal correlates of filter feeding or predatory/ectoparasitic habits.

Lates (Perciformes, Latinae) in the Pontian (latest Miocene) of Ukraine

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A series of articulated centra representing a perciform fish of the genus *Lates*, is in the collections of the Ukraine National Museum. The specimen likely represents a distinct species, and can be differentiated from other species of *Lates*, including *L. gregarius* from the mid-late Miocene of Moldova, by several features, such as the size of the primary lateral fossa of the second centrum, the shape and ornament of the neural spine of the third centrum, and the thickness of the striated bone between the two fossa laterally on both the fifth and sixth centra.

The specimen was collected from Pontian (latest Miocene) marine deposits of Ukraine, with an estimated age of 6.04 to 4.7 Ma. During this time period, the Paratethys had its most northern reach with waters extending well into southern Ukraine. The specimen documents the presence of *Lates* in the northern Paratethys in the latest Miocene; this is the latest occurrence of the genus in marine waters of the area. After the Pontian, species of *Lates* are no longer found in the marine waters of the Mediterranean region although they persisted in freshwaters of Israel until the Pleistocene and are still found in Africa today. We suggest that latines were extirpated from the Mediterranean and Paratethys by the rapidity of the changes in salinity that occurred in the Tethys Mediterranean basin and Paratethys Black Sea basin as a result of the Messinian Salinity Crisis.

Articulated ornithomimid material from the upper Maastrichtian Scollard Formation of Alberta

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Ornithomimids, or bird-mimic dinosaurs, are a diverse clade of theropods whose remains are abundant in Upper Cretaceous sediments of Alberta. However, diagnostic ornithomimid remains are largely unknown from the lower Scollard Formation (upper Maastrichtian), creating a gap in our understanding of ornithomimid diversity and evolution leading up to the Cretaceous-Paleogene (K-Pg) mass extinction event. Here we describe articulated and associated ornithomimid material (TMP 1993.104.1) from the Scollard Formation, discovered near Rumsey in southern Alberta. TMP 1993.104.1 consists of an articulated left forelimb (distal half of the humerus, antebrachium, and manus), as well as articulated gastralia, the distal right antebrachium, and isolated right metacarpals and phalanges. Analysis of the specimen involved thorough morphological examination and evaluation of morphometric data for comparison to other known ornithomimid remains. Lack of cranial and additional post-cranial material (such as the metatarsals), which are typically used to diagnose ornithomimid taxa, makes precise identification challenging, but

the moderately-curved, non-raptorial manual unguals are diagnostic for the family Ornithomimidae. The length proportions of metacarpals (MC), where MC I > MC II > MC III, used to distinguish the genus *Ornithomimus* from other ornithomimids, is observed in TMP 1993.104.1. Histological examination of the humerus revealed the presence of primary osteons, areas of condensed cartilage similar to the juvenile feathered *Ornithomimus* (TMP 2009.110.1), and only two distinct lines of arrested growth (LAGs), indicating TMP 1993.104.1 is a juvenile individual. The temporal and stratigraphic separation between TMP 1993.104.1 and other ornithomimid taxa suggest that TMP 1993.104.1 may potentially represent a new species. Ultimately, TMP 1993.104.1 provides new information on the diversity of ornithomimids in Alberta prior to the K-Pg extinction.

Revised homologies of the ilium in mosasauroids — Insights on the plesiopelvic-hydropelvic evolutionary transition

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The systematic situation of mosasauroids is considered to be quite problematic due to the non-monophyly of the group as frequently recovered in phylogenies. A more effective way to refer to the two major groupings within Mosasauroidea (Squamata: Pythonomorpha) seems to be the terminology based on the morphology of the sacral region (i.e., pelvic girdle and sacral vertebrae): 1) plesiopelvic mosasauroids, which retains a terrestrial-like configuration of the articulation between the pelvic girdle and the two sacral vertebrae; 2) hydropelvic mosasauroids, where the bony contact between the column and the hip is lost, or possibly extremely reduced. As a consequence of the plesiopelvic-hydropelvic transition, the pelvic girdle is shifted downward relative to the column, and the articular contact between ilium and sacrals is lost, to the extent that no sacral vertebrae can be identified. The downward shifting of the pelvic girdle not only allows more space for the attachment of caudal muscles on the vertebral column at the trunk-tail border, but it also results in deepening and greater lateral flattening of the body in this region. All these modifications lead to a complete shift towards an obligatory aquatic lifestyle in hydropelvic mosasauroids, in comparison to plesiopelvic mosasauroids which potentially retain a functional sacrum. What is still unclear is if this transition happened only once or multiple times within Mosasauroidea.

By reviewing the available material on mosasauroid appendicular elements, and comparing it to extant lizards, we tried to clarify the morphological details regarding the plesiopelvic-hydropelvic transition. The identification of the homologous structures for the ilium in plesiopelvic and hydropelvic mosasauroids helps in understanding how this modification of the sacral region happened. More basal (i.e., plesiopelvic) mosasauroids possess an ilium with a posteriorly elongated rod-like process, while in more derived (i.e., hydropelvic) mosasauroids, the elongated iliac process projects anterodorsally. However, these two elongated processes of the ilium are by no means homologous. Confusion may arise instead regarding another process that in the land-to-water transition appears quite modified as a consequence of the new anatomical arrangement in mosasauroids, and that in some basal extinct pythonomorphs appears to be extremely long (e.g., *Aigialosaurus dalmaticus*, and a new taxon from Italy). The ilium in most lizards possess another extension on the anterior or preacetabular margin that overlaps onto the pubis when the pelvic elements are in articulation. For terrestrial lizards, the pelvic bones fuse during onto-

geny, and the interdigitating suture makes this anteroventrally oriented process difficult to see. The pelvic bones in plesiopelvic mosasauroids already appear to never fuse during ontogeny, a paedomorphic feature that is considered to be an adaptation to the aquatic environment. When the pelvic elements are unfused, the preacetabular anteroventrally oriented process of the ilium still overlaps the pubis, and it gives to the pubic facet of the ilium a quite distinct sinusoidal morphology, in contrast to an almost straight facet for the ischium. In hydropelvic mosasauroids, this process disappears, and both pubic and ischial facets on the ilium extend equally and straight in mediolateral view. The posteriorly oriented iliac process present in plesiopelvic mosasauroids is the same as any extant terrestrial lizard, and is characterized by the presence of articular facets for the sacral ribs, through which it is connected to the vertebral column. Our observations suggest that the anterodorsally oriented process of the ilium in hydropelvic mosasauroids results from the elongation of the supracetabular anterior tubercle of a plesiopelvic ancestor. It is commonly present in extant terrestrial lizards (e.g., *Iguana*, *Varanus*). Support for our hypothesis is found in: 1) the lack of articular facets for sacral ribs along the anterodorsally oriented iliac process of hydropelvic mosasauroids; 2) the same anatomical position of this process in hydropelvic mosasauroids, extant terrestrial lizards, and potentially basal mosasauroids (e.g., *Aigialosaurus dalmaticus*); 3) the presence of a possible surface of attachment for the iliopubic ligament on the tip of the anterodorsal process of hydropelvic mosasauroids (e.g., tylosaurines, mosasaurines), similar to the condition in extant terrestrial lizards.

An examination of atlas-axis complex in tyrannosaurids, with a new interpretation of the proatlas articulation

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The amount of variation in the atlas-axis complex is poorly understood in dinosaurian taxa due to a lack specimens that preserve this part of the vertebral column. Elements of the complex are relatively small and usually only coossify in more mature specimens. And even in associated and articulated skeletons, the front of the neck is often obscured by bones from the back of the skull. The proatlas is the most frequently lost element of the atlas-axis complex, and there is still debate regarding how and where it articulates within the complex. Interpretations of its position in articulation range from the primitive condition of forming an arch between the atlas and the exoccipital of the skull, to it essentially being a cervical rib of the atlas. Atlas-axis complexes of several tyrannosaurids from Alberta were studied, and a well-preserved complex of *Daspletosaurus* sp. suggested a new interpretation of how the proatlas articulates with the skull and the neck. As theropods evolved over time, the proatlas shows increasing incorporation into the condylar articular surface of the atlas, and a ligamentous attachment with the exoccipitals demonstrates a possible ancestral condition to avian theropods. A posterior process on the proatlases causes a reduction, or even loss of contact between the odontoid process and occipital condyle. The anatomy of the complex is also consistent with the long, flexible necks of non-avian theropods. This characteristic is shared with Aves, although neck morphology varies highly because of the wide range of feeding adaptations in birds.

Theropod pelvic musculature and the transition to knee-driven locomotion

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Theropod dinosaurs were obligate bipeds that relied on hindlimb bones and muscles for locomotion. Analyzing theropod pelvis and hindlimb anatomy with comparison to their closest living relatives allows reasonable identification of muscle configuration and attachment sites, which offers a new perspective on locomotory adaptations. Tail-driven locomotion is ancestral for theropods, however, living theropods (birds) exhibit knee-driven locomotion. This transition, regarding both anatomy and musculature, has significant implications and constraints concerning the evolution of bird-like, knee-driven locomotion. Hindlimb musculature is reconstructed based on extant phylogenetic bracketing and direct observation of muscle attachment sites for caenagnathids, dromaeosaurids, ornithomimids, troodontids, and tyrannosaurids from Alberta. The results indicate disparate locomotory styles in theropods from Alberta. Trends in the evolution of theropod pelvic musculature shed light on the stepwise transitions towards bird-like muscular configuration. The arrangement of locomotory musculature in caenagnathids and dromaeosaurids suggests they were not well-adapted for rapid cursoriality. Ornithomimids and troodontids appear built for speed and capable of rapid cursorial locomotion. Tyrannosaurids possess powerful hips that served for attachment of strong muscles for supporting and moving their enormous body mass. The progressive change from tail-driven to knee-driven locomotion is tracked by the morphology of the pelvis and the rearrangement of pelvic musculature. The loss of the supraacetabular crest at the base of Pennaraptora probably coincides with a major transition towards primarily knee-driven locomotion and bird-like posture.

A new articulated fossilized Acipenseridae from Dinosaur Provincial Park, Alberta, Canada

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Articulated fossilized skeletons of Acipenseridae are rarely found in the Late Cretaceous sediments of North America, although fragmentary fossils such as scutes and pectoral spines are relatively common. During field work in southern Alberta in 2016, an articulated specimen of Acipenseridae, UALVP 56596, was discovered which preserves the cranium and the anterior portion of the postcranial skeleton including the dermal scales and pectoral fins with fin rays. The specimen was recovered from the Dinosaur Park Formation (Campanian) in Dinosaur Provincial Park, Alberta, Canada. Although there are five extinct acipenserid taxa reported from the Late Cretaceous sediments of North America, three of them (†*A. albertensis*, †*A. eruciferus*, and †*A. ornatus*) are named based on isolated dermal elements, scutes, spines and a poorly preserved partial skeleton, which may not be diagnostic. If these elements are not diagnostic, these taxa would be considered nomina dubia. The other two acipenserids, †*Priscosturion longipinnis* and†*Protoscaphirhynchus squamosus*, are based on articulated material.

UALVP 56596 has several characters that appear to be unique, including dermatocranial bones strongly ornamented with anastomosing ridges, large, laterally expanded dorsal and lateral scutes with spines, and an extensive cover of smaller dermal scales. In comparison to the previously described articulated skeletons, UALVP 56596 shows notable differences in the dorsal scutes and clavicles. These characters allow us to identify the new specimen as a new taxon of Acipenseridae from the Late Cretaceous of North America. The existence of UALVP 56596, along with an articulated specimen of †*Priscosturion longipinnis* (TMP 90.104.6) from the upper Judith River Formation in Alberta, another as yet undescribed specimen of an articulated partial skeleton (TMP 96.150.1), and numerous other elements from the Dinosaur Park Formation that have a different morphology from UALVP 56596, indicate that there were multiple acipenserid taxa in the ichthyocommunity in the western coastal area of the Western Interior Seaway in the Campanian. Along with fossils of other large fish taxa such as guitarfishes and gars from this area, a remarkably diverse aquatic ecological community in the region during this time is suggested.

Diapsid reptile phylogeny and the origin and early radiation of lepidosaurs

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Lepidosaurian reptiles comprise one of the most diverse groups of tetrapods with almost 10,000 living species of squamates (lizards, snakes and amphisbaenians), and sphenodontians (represented by a single living taxon: *Sphenodon*), with both lineages estimated to have originated during the Early Triassic. However, the origins and early radiation of lepidosaurs remain largely enigmatic as a result of several factors, including: the oldest unequivocal fossils currently attributed to the Squamata are from the Middle Jurassic; available studies of broad level/deep-time diapsid reptile relationships provide very limited sampling of either fossil or living lepidosaurs (often, Squamata being represented as a single terminal unit); morphological and molecular evidence of squamate relationships disagree on what is the earliest squamate clade (iguanians vs dibamids and geckoes).

Here, I provide the first phylogenetic dataset with a deep sampling of the major diapsid and lepidosaurian lineages (living and fossil) at the species level in order to identify the composition and early evolution of lepidosaurs. All taxon scorings were based on personal observation of specimens and/or 3D CT scans from 51 collections from around the world, making it the largest species sample ever collected for investigating the origin of lepidosaurs—over 150 species. Additionally, molecular data from 10 nuclear/mitochondrial loci (7,230 base pairs) available in the GenBank database were sampled and aligned for the extant lepidosaurs component of the dataset. Importantly, the current dataset implements rigorous criteria for character construction in order to avoid biological or logical biases in the morphological dataset. Finally, I applied multiple methods of phylogenetic investigation to the morphological and combined evidence dataset: maximum parsimony, maximum likelihood, and Bayesian inference (non-clock and clock based analyses using total evidence dating) also testing for performance improvement by the partitioning of morphological data.

The results indicate novel relationships among diapsids and re-shape the lepidosaurian tree of life. Previously proposed early lepidosaurs are found to belong to other lineages of reptiles. Importantly, heretofore unrecognized squamate fossils are found as the earliest squamates, dating back to the Early Triassic, thus filling what was thought to be a fossil gap of at least 50 million years. In most results (morphology only and combined data) geckoes are the earliest squamate crown clade, iguanians are always found as later evolving squamates, and scincomorphs are polyphyletic, thus providing important agreements between morphological and molecular data concerning squamate evolution.

Palaeoecological and morphometric study of the Late Cretaceous shark fauna from the English Chalk

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The Late Cretaceous Chalk of Southern England spans from the Cenomanian to the Campanian stages and has yielded diverse genera of sharks, represented mainly by isolated teeth. Morphometric analyses of these teeth demonstrate how their shape and size varied through time, which in turn provides information on the evolution of body size and feeding strategy in these genera of sharks. A total of 875 lamniform shark teeth were studied from the Chalk deposits of England, representing eight genera of extinct shark. Assemblages were studied across the Cenomanian/Turonian boundary and from the Lower, Middle and Upper Chalk lithostratigraphic divisions. Eleven different morphometric measurements were obtained from these shark teeth and the data were analysed using ANOVA and Principal Component Analysis (PCA). The Cenomanian/Turonian boundary marks a major crisis in marine ecosystems associated with an oceanic anoxic event and the analyses focussed on determining whether any significant changes occurred in the shark fauna at that time. Results show that shark teeth became generally smaller and narrower across the Cenomanian/Turonian boundary. Since no shark species became extinct across the boundary but the morphology of these teeth underwent measurable and significant change, we suggest that a shift in the feeding behaviour of these sharks occurred at this time. Upper Chalk teeth have very similar shapes to Lower Chalk specimens, indicating a return to pre-Turonian feeding behaviours, but are significantly larger, indicating that the body sizes of lamniform sharks increased through the Late Cretaceous.

Reassessing Mosasaurini based on a systematic revision of *Mosasaurus*

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Mosasaurus hoffmannii was first discovered in the phosphatic chalks of the Maastricht type formation in the Netherlands and is the namesake of Mosasauridae, a family of extinct marine squamates. The famous fossil that came to be known as the 'Grand Animal de Maestricht' was described before the first dinosaur and long before the concepts of extinction and evolution gained traction within the scientific community. Although *M. hoffmannii* is a species with historic and taxonomic importance, it has been imprecisely diagnosed for more than 200 years, and the genus has not been completely reviewed in terms of the plethora of species that have been assigned to it over time. I herein present diagnostic features of *M. hoffmannii*, use the morphology of the type species as the basis of comparison for thirteen species of *Mosasaurus* in current usage from around the world, and combine the results of morphological and phylogenetic analyses to revise the systematics and taxonomy of mosasaurs and its closest relatives. Each of the mosasaur fossils included in this study was examined first-hand. Based on the morphological assessment, it was determined that several of the species currently assigned to *Mosasaurus* exhibit morphologies that differ notably from the type species. The phylogenetic analyses did not recover a monophyletic *Mosasaurus*, a finding which supported the morphological interpretations. However, if the genus *Mosasaurus* is revised to include only those taxa that exhibit morphologies most similar to *M. hoffmannii* (*M. lemonnieri*, *M. missouriensis*, and a specimen from Belgium, which had previously been assigned to *M. hoffmannii*, but whose morphology differs slightly from both *M. hoffmannii* and *M. lemonnieri*) the monophyly of the taxon can be maintained. This restricted interpretation of *Mosasaurus* forms a monophyletic clade along with the other taxa included in this study; this grouping of *Mosasaurus* and the taxa to which it is closely related can be called Mosasaurini. The sister group to *Mosasaurus* was found to be composed of the highly derived mosasaur *Plotosaurus* and other taxa with numerous unornamented teeth. Another group within Mosasaurini includes *Moanasaurus*, which was previously only known from New Zealand. Due to the morphological similarities between the type species, *Moanasaurus mangahouangae*, and specimens from Japan and Belgium that were formerly assigned to *Mosasaurus*, the results from this study indicate that *Moanasaurus* was more diverse and achieved a wider distribution than was previously understood. These findings for *Moanasaurus* were representative of Mosasaurini as a whole: better understanding of *Mosasaurus* and more inclusive sampling allows for greater appreciation of the diversity and distribution of the clade.

Data from the Chinese Triassic on the diversification of poposauroid archosaurs

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The crocodylian-line archosaur clade Poposauroidea contains two major subgroups. The geographically widespread Ctenosauriscidae represent an Early-Middle Triassic radiation of sail-backed taxa with a plesiomorphic, carnivorous dentition, whereas several predominantly Late Triassic and North American taxa form an advanced clade of bipedal, non-sail-backed, often edentulous poposauroids. Chinese poposauroids include the semi-aquatic Middle Triassic basal form *Qianosuchus*, the ctenosauriscid *Xilousuchus* from probable Lower Triassic strata, and the enigmatic Middle Triassic taxon *Lotosaurus*. Furthermore, a large partial ilium recently recovered from the Middle Triassic of Shanxi Province preserves key anatomical features that suggest it represents an early member of the advanced poposauroid clade. Among Chinese poposauroids, *Lotosaurus* is noteworthy because it is morphologically unusual and known from abundant material, almost all from a bonebed in Hunan Province that was initially interpreted as an early Middle Triassic (i.e., Anisian) tidal flat deposit. However, sedimentological and taphonomic reassessment of the site suggests a floodplain setting where dozens of individual *Lotosaurus* likely died around a failing water source during a drought, while detrital zircons indicate a probable late Middle Triassic (Ladinian) or even early Late Triassic (Carnian) age. Anatomically, *Lotosaurus* resembles ctenosauriscids in being sail-backed and quadrupedal, but resembles the most derived poposauroids in being edentulous. Previous phylogenetic analyses have recovered *Lotosaurus* as either a very basal poposauroid or a member of the advanced clade, close to the edentulous forms *Shuvosaurus* and *Effigia*. Our anatomical reappraisal of *Lotosaurus* suggests an alternative position just outside the advanced clade, which would imply that the sail-backed condition characterises a grade including *Lotosaurus* and ctenosauriscids whereas edentulousness has a more complicated, homoplastic distribution among poposauroids. Taken together, *Lotosaurus* and the new poposauroid ilium from Shanxi indicate that the diversification of relatively derived poposauroids was a complex process with Middle Triassic roots visible in the Chinese fossil record.

Jane M. Colwell-Danis: Canada's first academically-trained female vertebrate paleontologist

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Jane M. Colwell (Fig. 1) was born in Fort Stockton, TX, on 8 May 1941. By age four she was already an avid rock hound and developing a strong natural history interest, including fossils and especially those of a small size. She attended University of California Berkeley from September 1959 to July 1965, getting her Master's degree in vertebrate paleontology. She found being a woman there hard, troubled more so by some men's opposition to women in academia, one professor even telling her that "women belonged in the kitchen". While pursuing her degree, she had a part-time job in Berkeley at the Lawrence Radiation Laboratory assisting on the hydrogen bubble chamber experiments headed by Dr. Luis Alvarez. The project lead to him winning the Nobel Prize in Physics in 1968. For her Master's thesis, she studied the cranial and dental anatomy of a middle Miocene leontiniid notoungulate from La Venta, Columbia. Try as she might, work and family obligations got in the way of publishing her thesis. Others, unaware of her thesis, formally named her material *Huilatherium*, and later she was finally able to contribute to a study on this genus (Villarroel and Colwell-Danis 1997).

Fig. 1. Jane Colwell, seen here in her 1962-1963 departmental and yearbook photograph. Image from Frank, 1963.

After graduation, in the fall of 1965 she came to Alberta with a letter of recommendation from Dr. Wann Langston Jr. She began working for Dr. Richard C. Fox at the University of Alberta (UA). Her arrival marked the occasion of the first academically-trained female vertebrate paleontologist to be employed in Canada. She was a fossil preparator of dinosaur and other material, some of a quite delicate nature. In May 1966, she was made part of the faculty's academic staff, but still mostly did technical work. She then began three successive seasons of fieldwork, prospecting in Dinosaur Provincial Park (DPP) mostly for Late Cretaceous mammals. Expectations were to find one or two such specimens per season "if she was lucky", but by the end of the first summer, and working alone, she found eighty. She had similar successes in the next two years; current UA records have her collecting 677 fossil specimens of all types (mostly microvertebrates), including a *Leidyosuchus* crocodile skull. In September 1967, she participated in the first ever helicopter lift of an ornithomimid dinosaur skeleton. In the summer of 1968 she met her future husband, a paleontological technician working in DPP, left her job in Edmonton, and went to Ottawa to join him. There she soon worked in various paleontological capacities in lab, research assistant, and collections management roles under Drs. J.A. Jeletzky and Dale A. Russell. Her hiring in Ottawa marked the first time an academically-trained female vertebrate paleontologist worked for the federal government. In 1973, she wrote the popular softcover booklet "The Age of Dinosaurs in Canada" (Danis, 1973). Daughters were born in 1971 and 1974.

The Danis' moved back to Alberta in 1979, her husband joining the Paleontology Department of the Provincial Museum of Alberta (PMA). She joined PMA field expeditions and did some fossil collecting. In 1982, she became the PMA's paleontology collections manager and was the first woman with an earth sciences degree to be hired into a paleontological position by the provincial government. With the upcoming building of the Tyrrell Museum of Palaeontology (TMP), it was her job to train and supervise a small team of movers and pack up the entire fossil collection and move it to Drumheller. Some 45,000 catalogued fossils and plaster field jackets weighing a combined 110 tons were safely transferred. From 1983-1991, she served in a variety of collections management functions and did more fieldwork; TMP catalogue records identify her as collecting about 1,920 fossils of all types. During this time, she was a member of the Society for the Preservation of Natural History Collections and gave conference presentations on topics such as collections moving and storage, and field locality data preservation (Danis 1987, 1988, 1989). 1991 was a bad year; her failing marriage ended and early that year, government downsizing resulted in her being one of four Tyrrell staff being laid off, she the only academic lost. She later became the Seniors Coordinator for the Town of Drumheller. Retiring in 2008, she returned to the TMP as a regular volunteer. With a microscope and tweezers, she sorted Late Cretaceous microvertebrate concentrate until the fall of 2015. Her present health keeps her away from the museum, but microvertebrate concentrate, tweezers, vials, and a head-mounted magnifier delivered to her retirement apartment means she can now do about one hour of sorting per day.

The role of women in vertebrate paleontology has increased dramatically over the past three decades. But Jane, pursuing an earth sciences career in the late 1950s to mid-1960s presented an enigma to some of her male (and female) students and teachers, and later, some of her co-workers. At Berkeley, she was often the only woman in her earth sciences classes and was passed over on some opportunities solely because of her sex. She was probably born a couple decades too soon, but despite the continued negativity from some men during schooling and her career, she persevered, remaining strong and determined. A pioneer, she also did help lead the way and inspire other women to follow in her field and for that, her 2,597 UA and TMP fossils collected, and other museum work, we owe Jane a debt of gratitude.

The author is well along in writing Jane's biography as part of his "Remember Me" series and seeks to meet people who have anecdotal stories or images of her.

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Ceratopsian dinosaur survives a broken neck

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Globally, Dinosaur Provincial Park (DPP) is the best locality to recover examples of dinosaur teeth and bone bearing evidence of past injuries and disease. Paleopathologic specimens are both abundant and well preserved, allowing for a variety of invasive and non-invasive studies. Dental trauma consists of broken teeth in theropods large and small. Trauma is the most common osteopathy recognized. Tyrannosaurids exhibit healing face-biting lesions with about 50% of individuals affected. Among saurischians of all sizes, broken toes, ribs, fibulae and vertebral fusions predominate. Healing pedal phalanx and rib fractures, frills with supernumerary fontanelles and fracture injuries are reported in ceratopsians. Trauma in ankylosaurs is also known in smaller numbers. Osteopathy in hadrosaurs is extremely well represented with rib and other fractures, but especially common are injured caudal vertebrae with broken neural spines and crushed centra which have split into two (typically) or more pieces with subsequent imperfect fusion and sometimes fusion to adjoining injured vertebrae.

Paleopathologies of these types occur in demonstrable patterns but occasionally something completely unexpected is recognized. An isolated adult ceratopsian cervical vertebra collected in 2001 (DPP, bonebed 47) represents a remarkable example of severe centrum fracture with advanced healing. It exhibits a proximal endplate crack up to 2 cm deep and up to 6 mm wide. The visible crack begins roughly mid-centrum length on the midline floor of the neural canal, progresses anteriorly to the dorsal endplate rim, then is angled ventrally and laterally over a distance of 5.4 cm. The crack stops 1.5 cm from splitting the centrum into two subequal parts. The walls and edges of the crack show smooth, reparative and remodeled bone. The endplate crack grossly resembles healing hadrosaur caudal vertebrae that show traumatic centrum splitting (Tanke and Rothschild 2015). The posterior endplate was eroded away before fossilization and the trabecular bone is well exposed. Much of the trabecular pattern is of normal wall thickness and irregular arrangement. However, on the opposite side of the crack, the trabecular bone has thickened and shows stressed linear patterns associated with the reparative bone actively knitting across the fracture line. The new trabecular bone is orientated at right angles to the crack and forms to a linear pattern analogous to that recently reported in the oldest known bone fracture (Bishop et al. 2016). This altered linear trabecular pattern associated with, and at right angles to, the crack confirms that a healing fracture is indeed preserved. There is no evidence to suggest genetic defect, a degenerative, or predisposing infectious condition lead to the centrum fracture. The fracture is pre-mortem as it shows advanced, but not total, repair. Healing rates of bone fractures in dinosaurs are unknown; however, some evidence points towards healing rates similar to extant avians (Straight et al. 2009). This cervical vertebra provides evidences for a broken neck that was not immediately fatal, indicating the injured animal lived on for at least weeks or months after being injured.

An extensive review of dinosaur osteopathy and related conditions (Tanke and Rothschild 2002) revealed no examples of dinosaurs surviving a broken neck — not unexpected as it is often fatal in extant animals. Etiology of the condition is unknown; Tanke and Rothschild (2015) posited conspecific tail trampling to explain the crushed and split caudal vertebrae in hadrosaurs, however that etiology does not explain this instance. Being traumatic in origin, it could be related to a serious fall or an aggressive interaction with a conspecific (i.e., Farke 2014; Farke et al. 2009). Similar, but less extensive lesions in cervical centra reported in extant Soay Sheep were ascribed to head-butting (Clutton-Brock et al. 1990). Whatever the cause, the survival of an animal that is both large and possessing an enlarged and heavy head and with so serious a neck injury, is remarkable.

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Examples of pathologies in terrestrial vertebrates from the Early Permian of Richards Spur locality, Oklahoma, USA

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Evidence of pathologies in the Paleozoic are quite rare, and have largely been limited to gross morphological comparisons (Reisz 1979). Most described paleopathologies can be attributed to trauma of the limbs and ribs, with little documented evidence of disease in early Permian material (Reisz et al. 2011). The Doles Brothers limestone quarry near Richards Spur, Oklahoma, USA, is unique in having the richest collection of tetrapod fauna in the world (Macdougall and Reisz 2012), as such it represents a fertile faunal assemblage from which to sample pathologies. In this study we collect and describe examples of pathological material from Richards Spur. With this we have been able to demonstrate that both traumatic and infectious pathologies are present at this locality, and are not restricted to any one taxa, but rather span across the major terrestrial clades including: Amphibamidae, Seymouriidae, Synapsida, Reptilia and Parareptilia. Additional work will focus on differentiating between pathologies that originate from trauma versus disease, as well as potential etiological hypotheses, by using a combination of gross morphological comparison, CT scans, scanning electron microscopy as well as histological analysis. The study of fossil abnormalities can be a powerful tool in documenting hypotheses of lifestyle, behavior, species interactions, immune response and healing patterns of extinct taxa, as well as providing powerful diagnoses of extant disease evolutionary history and phylogenetic distribution (Hanna 2002). Analyses of larger sample sizes, as in this study, can be useful in deducing the relationship between particular abnormalities and how these might help characterize distinct taxa (Hanna 2002). Finally, a rigorous description of osseous macroscopic deformities can help inform the reproducibility of bone response to environmental conditions across phylogeny, which makes the cause of the variations from the normal state more readily deduced (Rothschild 2009). With this study we hope to better understand the difference in bone response to trauma versus disease and to better illuminate the role of paleopathologies in phylogenetic distribution, conservation of osteological response to disease, as well as helping to identify the reproducibility of testable etiological hypotheses (Rothschild 2009).

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Preliminary results of an investigation into the preservation of soft tissue structures in bone from the Dinosaur Park Formation

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In recent years, several papers have claimed that soft tissue can be preserved within bone matrix of extinct vertebrates, some dating back well over 100 million years. Work conducted on specimens from Montana, has suggested sediment type may influence preservation of tissues and original proteins. Preliminary results of a dissolution of bone samples from 25 specimens of vertebrate remains from the Dinosaur Park Formation (76.3-74.4 MA) of southern Alberta indicate an unexpectedly high rate of tissue preservation. Samples were placed into a 0.5 M solution of (ethylenedinitrilo)tetraacetic acid, disodium salt, dehydrate (EDTA) for two months to dissolve mineral components. Imaging was performed using compound microscope and micro CT scanning. Of the 25 specimens sampled there are 16 dinosaur, 3 turtle, 3 champsosaur, 2 crocodilian, and 1 fish samples. All specimens studied were collected from the Dinosaur Park Formation to reduce stratigraphic variation that may influence preservation. Specimens were chosen based on sediment type and degree of articulation. To test this, approximately half of the samples originated from sandstone and the other half originated from mudstone. A second factor that may influence tissue preservation is the degree of articulation and thus the time exposed to the environment prior to burial. Approximately half of the samples were collected from articulated or closely associated skeletons, and the other half of the specimens were collected from isolated bones or specimens from micro vertebrate sites. Of the 25 specimens collected all dissolved enough to obtain sufficient data except the champsosaur vertebrae. The slow dissolution of the vertebrae is likely due to the high density of the cortical bone. Of the 22 specimens that produced results, 20 specimens were positive for soft tissues. Although these results indicate that there is no correlation between soft tissue preservation and sediment type, nor degree of articulation of specimens, crystal growth of several different minerals observed within vessels suggests if haversian canals are sealed by precipitated minerals, tissues may preserve in situ.

Flipped classrooms as a model for inclusive education in post-secondary courses

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While inclusive education has become the norm within primary classrooms, it has not received the same level of attention at the post-secondary level. However, with the steady increase in the proportion of students attending colleges and universities, the number of students with a learning disability has risen in kind. Students with learning disabilities have, by definition, average to above average intelligence, but have underlying difficulties that prevent them from receiving, processing and expressing information. Many instructors are unaware of

how to implement methods that promote inclusion and foster the success of students with learning disabilities in their classes, and the potential benefits for all students that these changes can provide. This research focuses on a case study from an introductory vertebrate palaeontology course where inclusive techniques were used, and examines which aspects of instructional theory can be efficiently applied in a post-secondary setting. It is intended to be used as a guide for post-secondary science instructors on how to effectively modify their instructional methods without requiring large amounts of additional preparation time.

Discovery of a new dercetid fish (Neoteleostei: Aulopiformes) from the Turonian of Colombia

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The family Dercetidae is an extinct group of marine fishes characterized by an elongate body and pronounced rostrum formed by extended jaws. The temporal range of the group extends from the Late Cretaceous to the Paleocene, with nearly 35 species described from the Tethyan deposits of North Africa, the Levant, Europe, Mexico, and Brazil. The fossil record of the Dercetidae from South America is scarce and has been restricted to the Brazilian outcrops.

A new dercetid is reported from a Turonian deposit of Boyacá, Colombia. A single articulated specimen, preserved in part and counterpart, was originally discovered in the stone slabs while paving a walkway at the Monasterio de la Calendaria, which were extracted from a nearby quarry where fossiliferous lower to middle Turonian rocks of the San Rafael Formation crop out. The specimen differs from other dercetid species by the following unique combination of morphological features: lack of the scutes on the flanks of the body, roofed post-temporal fossa, single row of small conical teeth on the dentary and maxilla, toothless premaxilla ornamented with pronounced longitudinal striations and protruding forward far beyond the anterior end of the dentary, presence of a single pair of the transverse processes associated with the abdominal vertebrae, and relatively large pectoral fins positioned high on the body. The specimen represents a new species and potentially a new genus of Dercetidae, and the first member of the group reported from Colombia. The new specimen fills in a gap in the distribution of dercetid fishes in the Western Tethys region, and together with the other dercetids from Mexico and Brazil, i.e., *Brazilodercetis*, *Robertichthys*, and *Rhyncodercetis*, the new taxon provides insights into the faunal connections between the Eastern and Western Tethys.

A dinosaur eggshell assemblage from the lower Maastrichtian St. Mary River Formation of southern Alberta

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Dinosaur eggshells have been reported from several Upper Cretaceous formations in Alberta, spanning an age between the upper Santonian (Milk River Formation) and upper Maastrichtian (Willow Creek Formation), but are unknown from intervening lower Maastrichtian strata. Here we report a dinosaur eggshell assemblage from the lower Maastrichtian St. Mary River Formation of southern Alberta, a rock formation preserving abundant dinosaur tracks yet frustratingly little skeletal remains. Eighty-four eggshell fragments recovered from seven localities were measured and their structure described via scanning electron microscopy and radial thin sections. Four theropod ootaxa (*Continuoolithus* cf. *C. canadensis*, *Montanoolithus* cf. *M. strongorum*, *Prismatoolithus* cf. *P. levis*, and an unidentified ootaxon) and a single hadrosaur ootaxon (*Spheroolithus* cf. *S. albertensis*) were identified. The eggshells collected from the St. Mary River Formation records a lower diversity of ootaxa than in the Oldman and Willow Creek formations, the underlying and overlying, respectively, terrestrial formations, although this potentially could be an artifact due to small sample size. With exception to the unidentified theropod eggshell, all ootaxa identified in the St. Mary River Formation are present in the upper Maastrichtian Willow Creek Formation while only some of the ootaxa are present in older formations. Comparison of eggshell thickness among the St. Mary River and other Upper Cretaceous formations of Alberta support the hypothesis of an overall increase in theropod eggshell thickness, and concomitant increase in body size of small theropods, between the upper Santonian and upper Maastrichtian.

Assessing bite force and cranial kinesis in *Tyrannosaurus rex* using a physical model

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The possibility that theropod dinosaurs may have exhibited some degree of cranial kinesis merits close examination due to the extensive cranial kinesis found in their modern descendants, the birds (Bock, 1964; Larsson, 2008; Holliday and Witmer, 2008). It has been suggested that *Tyrannosaurus* may have had limited streptostyly due to the presence of an articular condyle on the proximal end of the quadrate, allowing the quadrate to rock backwards and forwards along the quadratosquamosal joint (Molnar, 1991; Holliday and Witmer, 2008). Swinging the quadrate forwards in this way as the animal closed its jaws could have driven palatal kinesis by displacing the palatal bones in the forward direction, which in turn would have led the maxillae to bow outwards (Larsson, 2008). This study examines whether streptostyly and palatal kinesis could occur by this mechanism through the construction of a physical model using 3D printing technology. It was found that palatal kinesis is indeed possible in the model, but requires a mobile maxilla-jugal contact as well as a mobile quadrate. The model was also used as a base to reconstruct jaw musculature in clay, and bite forces were calculated according to physiological cross sectional area and lever arm mechanics. The jaws closed in the natural position with the quadrate forward were found to produce a bite force of 13,520 to 14,335 N at a single posterior tooth, which corresponds most closely to previous estimates based on the force required to produce bite marks found on a Triceratops pelvis (Erickson et al., 1996). Due to the limitations of the physiological cross sectional area method, it is unclear if palatal kinesis played a role in increasing bite force. Instead, it may have served as a mechanism to widen the jaws to reduce stress while biting. In addition to providing insights on cranial kinesis and bite force, this study demonstrates the usefulness of 3D printing to create models for experimentation.

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Ontogenetic variation in the bone histology of caenagnathid mandibular symphyses

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Caenagnathidae is a group of middle to late Cretaceous theropod dinosaurs found in Asia and North America. The isolated nature of their remains means their growth, development, and variation is difficult to study, as skeletal morphology is the primary investigative tool used in palaeontology. This study examines the histological characteristics of four caenagnathid mandible specimens suspected to represent an ontogenetic series from the Dinosaur Park Formation of Alberta, Canada, to identify trends or patterns in the cell- and tissue-level features of these dinosaurs. Thin sections of the mandibular symphysis were examined with light microscopy and their histological features were observed and described. The thin sections were interpreted as an ontogenetic series with the later stages characterized by a reduction in the rate of growth, an increase in lamellar bone, and an accumulation of secondary remodelling structures such as Haversian canals throughout ontogeny. Lines of arrested growth indicated an increased developmental age in two of the specimens. Additionally, developmental and growth patterns including the rapid fusion and obliteration of the mandibular symphysis and the widening of the mandible at the symphysis were identified in later ontogenetic stages. The concentration of Haversian canals along the occlusal margin and lingual ridges suggests remodelling as a histological response to high levels of repeated stress. These descriptions add to our knowledge of the growth and development of Caenagnathidae and the identification of an ontogenetic series may aid in the taxonomic classification of partial or incomplete caenagnathid skeletons.

Life history of hadrosaurids from the Dinosaur Park Formation of Alberta, Canada

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The Upper Cretaceous Dinosaur Park Formation (DPF) of southern Alberta is one of the best sampled and intensely studied dinosaur fossil assemblages. Its record of articulated skeletons and microvertebrates shows that hadrosaurids dominated in terms of relative abundance. Although partial ontogenetic series are known for most taxa, the lack of monodominant hadrosaurid bonebeds has prevented detailed studies related to their life history. To investigate growth patterns of DPF hadrosaurids, Brinkman (2014) considered the entire DPF as an attritional (time-averaged) assemblage and generated a size-frequency distribution of hadrosaurid long bones (n=58). Assuming a strong correlation between size and age, he identified three distinct size classes (hatchlings, yearlings, and adults) and suggested that DPF hadrosaurids attained near-asymptotic body size in three years. Interestingly, this inferred rapid growth pattern conflicts with osteohistological estimates of 6-8 years for penecontemporaneous hadrosaurids from the Two Medicine Formation of Montana (Cooper et al., 2008; Woodward et al., 2015). Therefore, these studies suggest either extreme variation in hadrosaurid growth rates or poor performance of size-frequency distributions to accurately estimate ontogenetic age in attritional mass death assemblages.

For this study, I tested the proposed size-age relationship of DPF hadrosaurids by combining size-frequency distributions and long bone histology. The sample size was considerably expanded (n>450) and subjected to an osteohistological analysis across multiple elements (n=36; humeri, femora, tibiae). The newly constructed size-frequency distribution reveals four relatively distinct peaks, which form a positive parabolic distribution consistent with patterns exhibited by attritional assemblages. When integrated with the osteohistological growth mark data, the peaks progressively align with age and reveal that the yearling size class is not present in the distribution. If not due to preservation, this may suggest DPF hadrosaurids had high survivorship until two years of age if they managed to survive the initial hatchling mortality rate or that juveniles were segregated from the main herd. A preliminary growth curve analysis revealed asymptotic body size was attained in five years with minimal variation.

Osteohistology shows that growth rates of DPF hadrosaurids are similar to taxa from Montana and have less variation than inferred from size-frequency distributions alone. The data suggests size-frequency distributions of attritional samples may overestimate the growth rate and should be paired with osteohistology to provide more accurate interpretations. Clarification of the DPF size-frequency pattern is significant because it has implications for hadrosaurid growth strategies and may provide further insight on taphonomic preservation patterns in the DPF biocenose.

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