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A reconsideration of the aïstopod *Lethiscus stocki* via micro-Computed Tomography (microCT), with implications for tetrapod phylogeny

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Given advances in computer processing power we revisited microCT dataset of *Lethiscus* the oldest lepospondyl. Digital dissection shows for the first time the structure of the skull, revealing extremely primitive morphology despite its derived body plan, including a spiracular notch, parasphenoid lacking a broad basal plate, palatal fang-pit pairs, meckelian ossifications, and previously noted notochordal atlantoccipital articulation. The braincase is elongate and atop a dorsally projecting septum of the parasphenoid, similar to what is seen in stem tetrapods such as embolomeres. This morphology is consistent with that seen in a second aïstopod, *Coloraderpeton*. Phylogenetic analysis of a newly expanded matrix of stem tetrapods, including critical new microsaurian braincase data, demonstrates lepospondyl paraphyly, placing aïstopods deep on the tetrapod stem, whereas recumbirostrans are displaced into amniotes. These results show that stem group tetrapods were much more diverse in their body plans than previously thought. Furthermore, our study requires a change in commonly used calibration dates for molecular analyses, and emphasizes the importance of taxonomic and character sampling for early tetrapod evolutionary relationships.

Early Permian amphibamid *Pasawioops* (Amphibamidae, Dissorophoidea): An ontogenetic series

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Amphibamids (Temnospondyli: Dissorophoidea) were small, amphibian taxa that were mostly present during the Early Permian (~270 to 300 Mya). These taxa are generally considered to be close relatives of modern amphibians (lissamphibians). Thus, detailed analysis of their morphology and phylogenetic relationships sheds light on the evolution of lissamphibians and the origin of several unique traits. Amphibamids are additionally interesting because for some taxa larval, juvenile and adult specimens have been found, allowing researchers to discern the ontogenetic progression of morphological traits. However, because many amphibamids have a more juvenile appearance than other amphibians (e.g., comparatively large orbits and small body size), distinguishing between ontogeny dependent traits and diagnostic traits of taxa is of utmost importance. The goal of the present research is to first document the detailed morphology of the skull of the recently described amphibamid *Pasawioops* (*OMNH 73019) using novel CT data, and to second explore the nature of ontogeny dependent traits in this taxon through comparison with a recently referred specimen of *Pasawioops* (**MCZ 1415). We found the smaller OMNH 73019 specimen differs from MCZ 1415 in the following traits: the skull bones are not as tightly sutured, the anterior skull has a more rounded appearance, and the jaw articulations do not extend as far posteriorly beyond the occiput. Together, these data indicate that OMNH 73019 likely represents a more juvenile specimen of *Pasawioops* and the observed differences between specimens are consistent with previously posited juvenile traits in amphibamids. This suggests the nature of ontogeny dependent traits may be more conserved across Amphibamidae than previous thought.

*OMNH = Oklahoma Museum of Natural History

**MCZ = Museum of Comparative Zoology, Harvard

Palaeontological partnerships with Canadian National Parks: a case study from Saskatchewan

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With the centennials of the Canadian (2011) and American (2016) National Park systems, much discussion has been generated about the shifting relevance of National Parks to modern society. Whereas parks were originally established to protect natural ecosystems/heritage sites, they now also strive to provide meaningful visitor experiences (Parks Canada Agency 2013). Parks Canada is also dedicated to supporting scientific research in National Parks, especially where it aids in the understanding of ecosystems and heritage resources. Partnerships with outside organizations that can bridge all three of these principles – ecological/heritage preservation, visitor experience, and research – are therefore desirable and beneficial. One example of such a partnership exists between Grasslands National Park, Saskatchewan (SK) and the Royal Saskatchewan Museum (RSM), in collaboration with McGill University.

Grasslands National Park (GNP) in southern Saskatchewan was established in 1981 to protect the native grassland ecosystem. Originally called the Killdeer Badlands, the area is known for its fossil heritage: George Mercer Dawson collected the first dinosaur fossil in Canada from the Park's East Block in 1879. Despite this, for the first two decades after its establishment, palaeontology in GNP was minimal, with concerns that fossil collection would disrupt the delicate ecosystem. It was not until the 2000s that a renewed effort by the RSM and McGill to explore and document the palaeontological resources in GNP brought the park's fossils back into focus. During prospecting trips in 2001, 2007, and 2008, over 375 fossil localities were identified in the East Block. Attaining permits to collect the fossil material led to discussions with Parks Canada about the need to collect palaeontological resources in order to protect them, as well as how the ecological impact of collection could be minimized. These discussions led to the establishment of a GNP Palaeontology Team, comprised of members from Parks Canada GNP, the RSM, McGill and other outside institutions, to discuss issues related to palaeontology in the Park. In 2014, a formal Memo of Understanding was established between the RSM and GNP, establishing guidelines about how palaeontological resources in the Park were to be dealt with.

In 2010, Parks Canada began to develop the East Block's Rock Creek Campground, establishing the Rock Creek Visitor Centre and hiring new seasonal staff. GNP also began to introduce visitor experience programs that focused on palaeontology. The most popular of these is a program, now in its third year, grew directly out of the partnership established between GNP, the RSM and McGill. Known as 'Fossil Fever', this program involves GNP staff bringing visitors out to an active RSM/McGill fossil site in the East Block, with the visitors given an opportunity to help with the excavation. Programs such as these highlight the benefits of partnering with a National Park, allowing research to be undertaken while providing education and visitor experience, while ensuring the preservation and protection of Canada's valuable heritage resources.

Literature Cited

Parks Canada Mandate from Parks Canada 2013-14 Report on Plans and Priorities, Pg. 3

Parks Canada, Guiding Principles and Operational Policies, Part II, Section 3.2.8



Figure 1. The East Block of Grasslands National Park, SK contains some of the finest exposures of latest Cretaceous rock (including the Cretaceous-Paleogene Boundary) in the province. In 1874, George Mercer Dawson collected Canada's first dinosaur fossil from this area.

Morphological and histological analysis of a new large-bodied caenagnathid specimen (Theropoda: Oviraptorosauria) from the Hell Creek Formation (Montana)

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*ROM 65884, a partial caenagnathid skeleton from the Hell Creek Formation (Montana) is described and identified as belonging to large-bodied taxon similar in size to the recently described, coeval taxon *Anzu wyliei* (Lamanna et al. 2014). The new specimen includes three caudal vertebrae, dorsal rib, gastralia fragments, fragments of the pubis, an almost complete fibula, partial metatarsals (MT II-V), and a pedal phalanx. Although the fragmentary nature and lack of overlapping elements do not allow definitive assignment to *Anzu*, ROM 65884 differs from *Caenagnathus collinsi* (Bell et al. 2015), another large-bodied caenagnathid, in the presence of a distinct ridge on the posteromedial shaft of the second metatarsal. ROM 65884 was used to assess osteohistological variability in caenagnathids for the first time. Osteohistological thin sections of ROM 65884 indicate it was actively growing due to the predominance of primary fibrolamellar bone in the outer cortex, spacing of lines of arrested growth (LAGs), and the absence of an External Fundamental System (EFS) within the tibia. LAG counts were found to vary between the tibia, rib, and pedal phalanx. Osteocyte lacunar density (OLD) varies greatly between sampled skeletal elements: tibia, 51913 Osteocyte Lacunae (OL)/ μm^3 (SD of 1429 OL/ μm^3); pedal phalanx, 41046 OL/ μm^3 (SD of 4973 OL/ μm^3). OLD also varied within the tissues of a given bone. For example, vascular patterns within the pedal phalanx differed considerably, with the ventral having more secondary remodelling and relatively higher OLD count (average of 45078 OL/ μm^3 +/- 1255 OL/ μm^3) than the lateral side which grew more slowly and had a lower OLD count (average of 37013 OL/ μm^3 +/- 1736 OL/ μm^3). These histological results are consistent with the variation observed in other theropods, such as ornithomimids (Cullen et al. 2014).

*ROM = Royal Ontario Museum

Literature Cited

- Bell, P.R., P.J. Currie, and D.A. Russell. 2015. Large caenagnathids (Dinosauria, Oviraptorosauria) from the uppermost Cretaceous of western Canada. *Cretaceous Research* 52: 101-107.
- Cullen, T.M., D.C. Evans, M.J. Ryan, P.J. Currie, and Y. Kobayashi. 2014. Osteohistological variation in growth marks and osteocyte lacunar density in a theropod dinosaur (Coelurosauria: Ornithomimidae). *BMC Evolutionary Biology* 14: 231.
- Lamanna, M.C., H-D. Sues, E.R. Schachner, and T.R. Lyson. 2014. A new large-bodied oviraptorosaurian theropod dinosaur from the latest Cretaceous of Western North America. *PLoS ONE* 9: E92022.

Brain evolution in Rodentia and a deeper understanding of the ancestral condition for the brain of Euarchontoglires

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The brain of rodents has rarely been studied from the perspective of the fossil record, and little is known of the process of brain evolution in this group. What's more, rodents are members of Euarchontoglires and could help form a better understanding of the ancestral condition for this group, augmenting what has been learned from primates. In this study, I describe the first fossil and extant virtual endocasts for Rodentia. The analysis of primitive members of the Ischyromyidae family, *Ischyromys typus* (Oligocene), *Paramys copei* and *P. delicatus* (Eocene), reveals that exposure of the midbrain is likely to be primitive for rodents (Bertrand et al. 2016; Bertrand and Silcox 2016) as has been observed for Primates (Silcox et al. 2010). Decrease in the proportion of the olfactory bulbs and increase in neocortical surface area may have occurred through time in rodent evolution similar to Primates, but with less intensity in Rodentia (Bertrand and Silcox, 2016). Ischyromyid rodents exhibit variation in EQ through time, with some Eocene taxa displaying a higher EQ (e.g. 0.84, *P. copei*) compared to Oligocene species (e.g. 0.51-0.77, *Ischyromys typus*; calculated using a rodent-specific EQ equation; Pilleri et al. 1984), demonstrating that the group did not show a simple increase in EQ through time. The study of the virtual endocast of the early squirrel *Cedromus wilsoni* and extant members of Sciuridae suggests that fundamental changes in the organization of the brain occurred in the transition from more primitive ischyromyids to early squirrels, with an increase in neocortex size, the appearance of a sylvian fossa, and a more complex cerebellar structure including an increase in the relative size of the paraflocculi. These neurological modifications could potentially be related to the process of becoming arboreal in rodents, forming a contrast with Primates in which key changes postdated the origin of arboreality. Ultimately, this research provides a better understanding of the process of brain evolution for Euarchontoglires by studying another order in this group aside from Primates.

Literature Cited

- Bertrand, O.C., and M.T. Silcox. 2016. First virtual endocasts of a fossil rodent: *Ischyromys typus* (Ischyromyidae) and brain evolution in rodents. *Journal of Vertebrate Paleontology* 36(3):1–19
- Bertrand, O.C., F. Amador-Mughal, and M.T. Silcox. 2016. Virtual endocasts of Eocene *Paramys* (Paramyinae): oldest endocranial record for Rodentia and early brain evolution in Euarchontoglires. *Proceedings of the Royal Society B: Biological Sciences* 283:20152316.
- Pilleri, G., M. Gühr, and C. Kraus. 1984. Cephalization in rodents with particular reference to the Canadian beaver (*Castor canadensis*; pp. 11–102 in G. Pilleri (ed.), *Investigations on Beavers*. Brain Anatomy Institute, Berne, Switzerland.
- Silcox, M.T., A.E. Benham, and J.I. Bloch. 2010. Endocasts of *Microsyops* (Microsyopidae, Primates) and the evolution of the brain in primitive primates. *Journal of Human Evolution* 58:505–521.
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Locomotor reconstructions from semicircular canals in fossil rodents: the evolution of arboreality in squirrels

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Reconstructing locomotor behaviour from fossil specimens can be challenging, especially when postcranial material is not available. The size of the semicircular canals has been shown to be effective for reconstructing some aspects of the locomotor repertoire. In general, animals with faster, jerkier locomotion have larger semicircular canals for their body mass than slower moving forms with less jerky locomotion (Spoor et al. 2007). Since the petrosal is frequently preserved, semicircular canal dimensions provide a broadly applicable source of data for adding to our knowledge of the locomotion in fossil species.

The current study considers semicircular canal dimensions in early representatives of Rodentia from the families Ischyromyidae and Scuriidae. There is little consensus on the locomotor modes for ischyromyids, with authors suggesting varying degrees of arboreality vs. terrestriality (Szalay 1985; Korth 1994; Rose and Chinnery 2004). Although primitive squirrels have been inferred to likely be arboreal (Emry and Thorington 1982), not all species are known from postcranial material.

Semicircular canal dimensions were calculated for five species: *Paramys copei* from the early Eocene, *Paramys delicatus* and *Reithroparamys delicatissimus* from the middle Eocene, and *Ischyromys typus* and *Cedromus wilsoni* from the early Oligocene. Agility scores were calculated on a scale ranging from 1 (very slow) to 6 (very fast) following Spoor and colleagues (2007). Based on average semicircular canal radius, three of the ischyromyids had agility scores in the medium-slow to medium range: *Paramys copei* = 3.6; *P. delicatus* = 3.4; *Ischyromys typus* = 3.8. In contrast, *Reithroparamys delicatissimus* was found to have a higher agility score (4.4), well into the medium-fast range. The highest agility scores were calculated for *Cedromus wilsoni* (5.5), which can be reconstructed as a fast-moving form with very jerky locomotion. These values are in keeping with suggestions that *Paramys* and *Ischyromys* were more terrestrially adapted, with possibly some semi-fossorial adaptations in the latter case. *Reithroparamys* has been identified as a possible relative of living squirrels, and its higher agility score could signal a move towards a more active, possibly arboreal locomotor repertoire. *Cedromus* is considered a primitive member of Scuriidae. Although unknown from postcranial material, preliminary endocranial data found intriguing specializations in the brain that foreshadow adaptations of modern squirrels, which could relate to an increasing use of three dimensional space in an arboreal milieu. The very high inferred agility of this early fossil squirrel, within the range for modern arboreal squirrels, is in keeping with this inference. Overall, semicircular canal dimensions provide an independent means for testing ideas about locomotion in fossil rodents, speaking particularly to the transition to greater degrees of agility, and therefore likely arboreality, in the evolution of squirrels.

Literature Cited

- Emry, R.J., and R.W. Thorington. 1982. Descriptive comparative osteology of the oldest fossil squirrel, *Protosciurius* (Rodentia: Scuriidae). Washington, DC: Smithsonian Institution Press.
- Korth, W.W. 1994. The Tertiary record of rodents in North America. *Topics in Geobiology* 12:799-801.
- Rose, K.D., and B.J. Chinnery. 2004. The postcranial skeleton of early Eocene rodents. *Bulletin of the Carnegie Museum of Natural History* 36:211-244.
- Spoor, F., T. Garland Jr, G. Krovitz, T.M. Ryan, M.T. Silcox and A. Walker. 2007. The primate semicircular canal system and locomotion. *Proceedings of the National Academy of Sciences* 104:10808-10812.
- Szalay, F.S. 1985. Rodent and lagomorph morphotype adaptations, origins, and relationships: some postcranial attributes analyzed. In *Evolutionary Relationships among Rodents*, eds. W.P. Luckett, J.-L. Hartenberge, pp. 83-132. Springer US.

First occurrence of *Dimetrodon* (Synapsida: Sphenacodontidae) at the Early Permian Richards Spur locality, Oklahoma

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The Early Permian Richards Spur locality is well known for preserving a diverse paleoassemblage of small- to medium-sized terrestrial vertebrates (MacDougall and Reisz 2012). The locality is unique among most Early Permian localities of the USA in that it lacks evidence of the most abundant large-bodied sphenacodontid known from the early Permian, *Dimetrodon*. Here we report on the occurrence of neural spine material from the Richards Spur locality that can be attributed to *Dimetrodon* on the basis of its unique figure-8 cross sectional outline. A piece of the neural spine was sectioned histologically to determine the bone type and a possible age for the specimen. Results show that the neural spine is composed of laminar bone, which is typical of sphenacodontids (Huttenlocker et al. 2010), but the somatic age of the specimen could not be determined. Furthermore, teeth attributed to sphenacodontids from the locality (Evans et al. 2009) were re-examined histologically given the recent understanding of the diversity of tooth morphologies and the species-specific nature of the teeth (Brink et al. 2014; Brink and Reisz 2014). The teeth bear true denticles (ziphodonty) and lack plicidentine, both of which are features of derived species of *Dimetrodon* (Brink et al. 2014; Brink and Reisz 2014). The combination of ziphodont teeth lacking plicidentine and a figure-8 shaped neural spine suggest the presence of either a small-bodied, derived species of *Dimetrodon* or a juvenile of *Dimetrodon grandis* at Dolese. Given that the only other productive upland locality known also produces a small-bodied species of *Dimetrodon* (Berman et al. 2001), it is possible that the *Dimetrodon* at Richards Spur is a new species. Considering that recent dating methods obtained for Richards Spur places the age of the locality in the Artinskian (Woodhead et al. 2010), the presence of a derived species of *Dimetrodon* similar to those known only from the later Kungurian is unexpected. At this time it is not possible to differentiate between three alternative interpretations of these findings: a) the upland nature of Richards Spur has resulted in the preservation of numerous endemic taxa that do not occur in contemporaneous lowland paleoassemblages; b) there is a preservational bias that is affecting both upland and lowland paleoassemblages; or c) a combination of both factors.

Literature Cited

- Berman, D.S., R.R. Reisz, T. Martens, and A.C. Henrici. 2001. A new species of *Dimetrodon* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany records first occurrence of genus outside North America. *Canadian Journal of Earth Science* 38:803–812.
- Brink, K.S., A.R.H. LeBlanc, and R.R. Reisz. 2014. First record of plicidentine in Synapsida and patterns of tooth root shape change in Early Permian sphenacodontians. *Naturwissenschaften* 101:883–892.
- Brink, K.S., and R.R. Reisz. 2014. Hidden dental diversity in the oldest terrestrial apex predator *Dimetrodon*. *Nature Communications* 5:10.1038/ncomms4269.
- Evans, D.C., H.C. Maddin, and R.R. Reisz. 2009. A re-evaluation of sphenacodontid synapsid material from the Lower Permian fissure fills near Richards Spur, Oklahoma. *Palaeontology* 52:219–227.
- Huttenlocker, A., E. Rega, and S. Sumida. 2010. Comparative anatomy and osteohistology of hyperelongate neural spines in the sphenacodontids *Sphenacodon* and *Dimetrodon* (Amniota: Synapsida). *Journal of Morphology* 271:1407–1421.
- MacDougall, M.J., and R.R. Reisz. 2012. A new parareptile (Parareptilia, Lanthanosuchoidea) from the Early Permian of Oklahoma. *Journal of Vertebrate Paleontology* 32:1018–1026.
- Woodhead, J., R.R. Reisz, D. Fox, R. Drysdale, J. Hellstrom, R. Maas, H. Cheng, and R. L. Edwards. 2010. Speleothem climate records from deep time? Exploring the potential with an example from the Permian. *Geology* 38:455–458.

A late Campanian euselachian assemblage from the Upper Campanian Bearpaw Formation of southern Alberta, Canada

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A euselachian (shark and ray) assemblage was collected from the Upper Campanian Bearpaw Formation in southern Alberta, Canada. During this time, the province was situated along the western margin of the Western Interior Seaway. Previous prospecting of the Bearpaw exposure has produced numerous vertebrate remains, including several well-preserved large marine reptile specimens (e.g., Konishi et al. 2011). Konishi et al. (2014), in their description of *Mosasaurus missouriensis*, noted the likely scavenging of its carcass by an indeterminate lamniform and *Squalicorax*. Surprisingly, very little else is known about the euselachian diversity in this part of the seaway during this time.

Herein, we report multiple euselachian species belonging to five orders, six families, and at least nine genera. The occurrence of several of these species is the first documented report from Canada and significantly extends their palaeobiogeographical ranges to the north. Conspicuously absent from this assemblage are small orectolobid species and batoids that are reported from slightly older regional deposits (e.g., Beavan and Russell 1999) and from contemporaneous assemblages located at lower palaeolatitudes (Case 1978, 1987; Cappetta and Case 1999). The lack of benthic taxa may suggest an adverse bottom water palaeoenvironment in this region of the seaway during this time.

Literature Cited

- Beavan, N.R., and A.P. Russell. 1999. An elasmobranch assemblage from the terrestrial-marine transitional Lethbridge Coal Zone (Dinosaur Park Formation: Upper Campanian), Alberta, Canada. *Journal of Paleontology*, 73:494–503.
- Cappetta, H., and G.R. Case. 1999. Additions aux faunes de sélaciens du Crétacé du Texas (Albien supérieur-Campanien). *Palaeo Ichthyologica*, 9:5–111.
- Case, G.R. 1978. A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica, Abt. A*, 160: 176–205.
- Case, G.R. 1987. A new selachian fauna from the Late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). *Palaeontographica, Abt. A*, 197:1–37.
- Konishi, T., D. Brinkman, J.A. Massare, and M.W. Caldwell. 2011. New exceptional specimens of *Prognathodon overtoni* (Squamata, Mosasauridae) from the upper Campanian of Alberta, Canada, and the systematics and ecology of the genus. *Journal of Vertebrate Paleontology* 31:1026–1046.
- Konishi, T., M. Newbrey, and M.W. Caldwell. 2014. A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, Western Canada, and the first stomach contents for the genus. *Journal of Vertebrate Paleontology* 34:802–819.

Computed tomography (CT) analysis of *Champsosaurus lindoei* (Diapsida: Choristodera) and evidence for the neomorphic bone

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Braincase characters have been shown to retain reliable phylogenetic signals at the species level in many groups of tetrapods. The choristoderan *Champsosaurus* represents a clade whose classification is well established. However, classifications based on cranial material to date have been limited to externally visible characters and braincase characters exposed in broken specimen. Additionally some characters such as the neomorphic braincase bone have historically been in contention both within and outside *Champsosaurus*. In this study we examine computed tomography (CT) data of *CMN 8920, *Champsosaurus lindoei* to provide a complete description of the mature braincase bones. Related cranial material is also described and the braincase of *Champsosaurus lindoei* is compared with modern analogues of Reptilia in an iguana (*Iguana iguana*) and a juvenile alligator (*Alligator mississippiensis*). Additionally this study provides further evidence for the presence of the neomorph as a distinct ossification within Neochoristodera.

*CMN = Canadian Museum of Nature

The vertebrate assemblage of the Madsen bonebed, north-central Montana, Judith River Formation (Campanian)

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The Judith River Formation is a relatively poorly sampled geologic unit in comparison to other formations deposited in the Campanian (72.1–83.6 Ma) of North America. The Judith River Formation is chronostratigraphically and lithostratigraphically equivalent to the uppermost Foremost and Oldman Formation in Alberta. The lower half of the Judith River Formation, the McClelland Ferry Member, was deposited during a regressive phase in the Judith River Wedge and as such records the transition from marine to non-marine environments. The fauna of this unit is particularly poorly known. Here we report on the vertebrate assemblage of a recently excavated bonebed in the upper, sandy interval of the McClelland Ferry Member located near Malta, Montana. Approximately 70 vertebrate fossils were collected from the multi-taxic bone bed that originate from a diverse set of terrestrial and freshwater species species that died in the area millions of years ago. The majority of the fossils collected from the Madsen bonebed are ≥ 5 cm and the site represents a mixture of microfossils and larger elements. The bones were identified to the lowest taxonomic level and an illustrated faunal list has been compiled. The site is dominated by reptiles. Of the bones excavated, 38% belong to hadrosaurian dinosaurs, 15% belong to saurischian dinosaurs, 8% belong to Testudines, and 10% belong to crocodylians. This assemblage also includes the first record of some taxa in the Judith River Formation, including the turtle *Boremys* sp. The site is in strata that are equivalent to the Comrey Sandstone zone of the Oldman Formation, allowing comparison of this fauna with sites in Alberta, which are located over 100 km further west. The single sampled microsite from the Comrey zone in the Manyberries region of Alberta has a greater relative abundance of fish and salamanders, with hadrosaurs being the most abundant reptile. However, the difference in fossil size distribution of these two sites may account for some of the differences in faunal composition. The analysis of this assemblage provides insight into the paleoecology of the region.

Re-evaluation of *Medusaceratops lokii* as a centrosaurine ceratopsid

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Medusaceratops lokii was originally described as the oldest known member of Chasmosaurinae, and therefore, important to understanding the evolution of the clade. To date, all known *Medusaceratops* materials are derived from the Mansfield bonebed in the Campanian Judith River Formation in Montana. The bonebed horizon occurs in beds that correlate to the lower unit of the Oldman Formation in Alberta that yield the basal centrosaurines *Albertaceratops* (Ryan 2007) and *Wendiceratops* (Evans and Ryan 2015). The holotype of *Medusaceratops* is a right lateral parietal ramus with three epiparietal processes; from medial to lateral these are a large, laterally-directed and rostrally-curved, hook-like process, a smaller process resembling the large process, and a small, unmodified, triangular process. The holotype parietal of *Medusaceratops* was originally referred to *Albertaceratops* due to the similar morphology of what was interpreted as the posterolateralmost epiparietal process (a large hook) (Ryan 2007). Ryan et al. (2010) redescribed *Medusaceratops* as a basal member of Chasmosaurinae based on the fact that the holotype of *Medusaceratops* has only three epiparietals, which is the typical number for chasmosaurines.

Here we describe two new parietals from the Mansfield bonebed that help refine the taxonomic status of *Medusaceratops*. The first parietal preserves the medial portion of the left posterior ramus and the posterior portion of a broad midline ramus, the latter of which is a synapomorphy of centrosaurines (Evans and Ryan 2015). Importantly, this specimen preserves a small epiparietal near the midline on the dorsal surface. This epiparietal was not originally recognized in the holotype, but reassessment indicates the likely presence of the same feature in the same position, medial to the largest epiparietal. The second parietal that consists of a lateral ramus with three epiparietals indicates that *Medusaceratops* has an additional unmodified triangular epiparietal very close to the squamosal contact, which is not preserved in the holotype of *Medusaceratops*, probably because it was unfused at the time of death. The recognition of these two additional epiparietals thus allows for a reinterpretation of the parietal of *Medusaceratops* as having five epiparietals and a broad midline bar, similar to the contemporaneous centrosaurines, *Albertaceratops* and *Wendiceratops*, but differing from them in the presence of the apomorphic, medially positioned, and diminutive epiparietal. These characters cannot be accounted for by ontogenetic change.

The new parietals of *Medusaceratops* indicate that this species is a taxonomically distinct basal centrosaurine, rather than a chasmosaurine. Additional undescribed material from the bonebed is under study to clarify phylogenetic position of *M. lokii* within Centrosaurinae

Literature Cited

- Evans, D.C., and M.J. Ryan. 2015. Cranial anatomy of *Wendiceratops pinhornensis* gen. et sp. nov., a centrosaurine ceratopsid (Dinosauria: Ornithischia) from the Oldman Formation (Campanian), Alberta, Canada, and the evolution of ceratopsid nasal ornamentation. PLoS ONE 10: e0130007.
- Ryan, M.J. 2007. A new basal centrosaurine ceratopsid from the Oldman Formation, southeastern Alberta. Journal of Paleontology 81: 376–396.
- Ryan, M.J., A.P. Russell, and S. Hartman. 2010. A new chasmosaurine ceratopsid from the Judith River Formation, Montana; pp. 181–188 in M. J. Ryan, B. J. Chinnery-Allgeier, and D. A. Eberth (eds.), New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium. Indiana University Press, Bloomington, IN.

Report on the first Canadian dinosaur finds

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Between 1880 and 1889, members of the Geological Survey of Canada (GSC) led various expeditions to Western Canada to do resource reconnaissance and exploration. Nearly 80 vertebrate fossils were collected during this time, including the first known dinosaurs from Canada, most of which are currently at the Canadian Museum of Nature (CMN) in Ottawa. Although much has been written about the early expeditions of the GSC, relatively little is known about the fossils they collected. Examination of these collections reveals that the early surveyors (G. M. Dawson, R. G. McConnell, J. Macoun, T. C. Weston, and J. B. Tyrrell) collected approximately 45% hadrosaur, 27% tyrannosaur, 9% ornithomimid, 5% miscellaneous small theropod, and 9% each for ceratopsid and unknown dinosaur material from the Milk River, Foremost, Dinosaur Park, St. Mary River, and Edmonton formations. Comparison to presently known fossil faunas from the surveyed areas demonstrates that initial sampling by the GSC was not comprehensive. About half of the known dinosaur families were sampled from the Dinosaur Park and Foremost formations, while only about one seventh of presently known dinosaur families were sampled from the St. Mary River and Milk River formations. The long oversight of these fossils meant that the presence of many of these dinosaur families was not recognized in their respective formations until years after their initial collection. For example, Ornithomimidae was not reported within the Dinosaur Park Formation until 22 years after initial collection by Macoun in 1880. Similarly, McConnell's 1883 collection of a ceratopsid centrum in the Dinosaur Park Formation predates the first described occurrence of this family from these strata by 18 years.

Literature Cited

- Dawson, G.M. 1884. Preliminary Report on the Bow and Belly River Region N.W.T. with Special Reference to the Coal Deposits. Geol. and Nat. Hist. Surv. Canada, Rept. of Progress for 1888-1889. Montreal: Dawson Brothers.
- Dawson, G.M., and Phil Jenkins. 2007. *Beneath my Feet: the Memoirs of George Mercer Dawson*. Toronto: McClelland and Stewart.
- Johnson, Hope. 2009. *Guide to Common Vertebrate Fossils from the Cretaceous of Alberta*. Alberta Palaeontological Society. Calgary: Alberta.
- Osborn, H.F., and L.M. Lambe. 1902. On Vertebrata of the Mid-Cretaceous of the North West Territory. *Contributions to Canadian Palaeontology* 3.2.
- Russell, L.S. 1930. Cretaceous non-marine faunas of northwestern North America. *Proceedings of the American Philisophical Society* 69.1: 133-59.
- Russell, L.S. 1966. Dinosaur Hunting in Western Canada. *Life Sciences* 70.
- Selwyn, A.R.C. 1881. Summary Reports of the Operations of the Geological Corps to 31st December 1879, and to 31st December, 1880. Geol. and Nat. Hist. Surv. Canada, Rept. of Progress for 1879-1880. Montreal: Dawson Brothers.
- Selwyn, A.R.C. 1882. Summary Reports of the Operations of the Geological Corps to 31st December 1880, and to 31st December, 1882. Geol. and Nat. Hist. Surv. Canada, Rept. of Progress for 1880-1882. Montreal: Dawson Brothers.
- Weston, T.C. 1899. *Reminiscences among the Rocks: in Connection with the Geological Survey of Canada*. Toronto: Warwick Bro's & Rutter.

The Bukwa fossil locality: Implications for faunal change and palaeoenvironments in the East African early Miocene

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Several early Miocene fossil localities in East Africa document the early evolution of apes and cercopithecoid monkeys. One of the least known localities is Bukwa, a fossil outcrop located on the slopes of Mount Elgon in eastern Uganda (Walker 1969; Brock and MacDonald 1969). K-Ar radiometric dating from the 1960s indicated that Bukwa was 22 Ma (Bishop et al. 1969), making it the oldest of the East African complex of Miocene sites. This made the site of some interest, despite the fact that only two fragmentary teeth of the catarrhine *Limnopithecus legetet* were found in these early excavations (Harrison 1988). Subsequent research on the non-primate mammalian assemblage indicated that Bukwa sampled a diverse fauna, with broad similarities to localities that are several million years younger (Pickford 1981).

As part of a larger research program on the Ugandan early Miocene, we have collected new fossils at Bukwa and re-dated the deposits. We conducted 2-3 step heating ⁴⁰Ar/³⁹Ar dating that yielded ages of 18.99 +/- 0.17 Ma and 19.27 +/- 0.20 (average 19.11 ± 0.13 Ma) from a lava overlying the fossil deposits, and 19.5 +/- 0.3 Ma from the base of the section (MacLatchy et al. 2006).

Our age estimate for Bukwa of 19.5–19.1 Ma is roughly 3 Ma younger than the original estimate, and indicates that Bukwa is located stratigraphically in between other more fossiliferous localities in the region, such as the sequences at Tinderet (~20 Ma), Napak (20 Ma) and Kisingiri (~18 Ma). This result is further corroborated by our analysis of the mammalian fossil remains. Despite claims that the Bukwa fauna may be as young as 17 Ma (Pickford 2002), our results show that the Bukwa assemblage robustly supports the radiometric date of 19–19.5 Ma. It samples species common at Kisingiri, including lagomorphs (Winkler et al. 2005), sanitheres, and large bodied ruminants, which are absent from older localities. At the same time, Bukwa samples taxa found only at the ~ 20 Ma localities, including species bathyergid and cricetid rodents (Cote 2008). These differences appear to be robust to the effects of incomplete sampling.

These faunal differences between Bukwa (19–19.5 Ma) and both older and younger localities in the region could potentially be the result of habitat differences, however preliminary paleoenvironmental reconstructions for Bukwa, including analyses of vegetation (Jacobs et al. 2010), terrestrial, and aquatic faunas, do not support this hypothesis. Alternatively, our results could suggest that a significant faunal turnover took place in this region approximately 20–19.5 Ma, a hypothesis that can be tested once other localities in the region are re-dated using modern techniques. Further age refinements for the entire East African early Miocene sequence may demonstrate that these fossil sites form a relatively continuous temporal sequence documenting the early evolution of cercopithecoid and hominoid primates.

Literature Cited

- Bishop, W.W., J. A. Miller, and F. J. Fitch. 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *American Journal of Science* 267:669-699.
- Brock, P.W.G., and R. Macdonald. 1969. Geological environment of the Bukwa mammalian fossil locality, eastern Uganda. *Nature* 223:593-596.
- Cote, S. 2008. Sampling and ecology in three early Miocene catarrhine assemblages from East Africa. Ph.D. Dissertation, Harvard University.
- Harrison, T. 1988. A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatologica* 50:59-108.
- Jacobs, B., A. Pan, and C. Scotese. 2010. A review of the Cenozoic vegetation history of Africa. In: Werdelin, L., Sanders, B. (eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 57-72.
- MacLatchy, L., A. Deino, and J. Kingston. 2006. An updated chronology for the early Miocene of NE Uganda. *Journal of Vertebrate Paleontology* 26(Supplement to 3):93A.
- Pickford, M. 1981. Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution* 10:73-97.
- Pickford, M. 2002. Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palévol* 1:213-219.
- Walker, A. 1969. Fossil mammal locality on Mount Elgon, eastern Uganda. *Nature* 223:591-593.
- Winkler, A.J., L. MacLatchy, and M. Mafabi. 2005. Small rodents and a lagomorph from the early Miocene Bukwa locality, eastern Uganda. *Palaeontologia Electronica* 8:24A.
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A large gavialoid (Crocodylia: Eusuchia) from the Upper Cretaceous Hell Creek Formation of South Dakota, U.S.A.

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The uppermost Cretaceous (Maastrichtian) strata of the Hell Creek Formation have been intensely sampled due to interest in understanding the K/Pg extinction event. Crocodylians reported from this formation include the genera *Borealosuchus*, *Brachychampsa*, and *Thoracosaurus*. Of these taxa, *Borealosuchus* and *Brachychampsa* are known from largely complete and diagnostic material that has been described in detail by Brochu (1997) and Norell et al. (1994), respectively. Conversely, *Thoracosaurus* was first reported by Pearson et al. (2002), who noted its rarity relative to other crocodylians in the formation. However, the material referred to this taxon was never illustrated or described, and the presence of a gavialoid in the formation has never been confirmed; all subsequent papers noting the presence of *Thoracosaurus* in the Hell Creek Formation have simply referenced Pearson et al. (2002). Here, we describe the first known associated skeleton of a large gavialoid consistent with the morphology of *Thoracosaurus* from the Hell Creek Formation. The specimen was discovered in Perkins County, South Dakota and includes a partial splenial, one cervical vertebra, a cervical neural arch, a partial cervical centrum, and one dorsal vertebra. The splenial and dorsal vertebra are very well preserved. The splenial has a long mid-line symphysis, indicating the characteristic “Y shape” as found in gavialoids (Brochu 2004), and unlike the coeval crocodylians *Borealosuchus* and *Brachychampsa*. The vertebrae are procoelous, a characteristic of eusuchian crocodylians (Buscalioni et al. 2001), and they closely resemble the morphology of vertebrae assigned to *Thoracosaurus* from the latest Maastrichtian of New Jersey and Holland (Mulder 1997). The dimensions of the vertebrae indicate a substantially larger body size than the other crocodylians in the Hell Creek Formation, but are similar in size to *Thoracosaurus*. Although identification of the new Hell Creek material to the genus level is not possible, it does confirm the presence of a large member of Gavialoidae in this unit. Additionally, it expands the body size range of crocodylians in the Hell Creek Formation, and gives us better understanding of vertebrate diversity in this well-studied formation.

Literature Cited

- Brochu, C. A. 1997. A review of “*Leidyosuchus*” (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. *Journal of Vertebrate Paleontology* 17:679-697.
- Brochu, C.A. 2004. A new Late Cretaceous gavialoid crocodylian from eastern North America and the phylogenetic relationships of thoracosaurus. *Journal of Vertebrate Paleontology* 24:610-633
- Buscalioni, D. A., F. Ortega, D. B. Weishampel, and C. M. Jianu. 2001. A revision of the crocodyliform *Allodaposuchus presidens* from the Upper Cretaceous of Hateg Basin, Romania. Its relevance in the phylogeny of Eusuchia. *Journal of Vertebrate Paleontology* 21:74-86.
- Mulder, E. W. A., 1997. Thoracosaurine vertebrae (Crocodylia: Crocodylidae) from Maastrichtian type area. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B.* 100:161-170.
- Norrell, M. A., J. M. Clark, and J. H. Hutchison. 1994. The Late Cretaceous alligatoroid *Brachychampsa montana* (Crocodylia): new material and putative relationships. *American Museum of Natural History Novitates* 3116:1-126.
- Pearson, D. A., T. Schaefer, K. R. Johnson, D. J. Nichols, and J. P. Hunter. 2002. Vertebrate biostratigraphy of the Hell Creek Formation in southwestern North Dakota and northwestern South Dakota. In Hartman, J. H., Johnson, K. R., and Nichols, D. J. (eds.) *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains. An Integrated Continental Record of the End of the Cretaceous.* Geological Society of America Special Paper 361:145-167.

The influence of environmental drivers on vertebrate faunal assemblages in the late Cretaceous of Alberta, Canada

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Vertebrate microfossil sites play an important role in the current understanding of community palaeoecology in the heavily sampled Belly River Group (BRG) from the late Cretaceous of Alberta. The degree to which environmental (e.g., depositional, altitudinal, latitudinal) or other factors (e.g., time as related to natural population/community changes) influence the structure of these assemblages is not fully understood, but has been hypothesized to be linked to palaeoenvironment (inland vs coastal) and latitude (Brinkman 1990; Brinkman et al. 1998; Beavan and Russell 1999; Brinkman et al. 2004). However, these factors have been tested only in a stratigraphically restricted framework. Here, I assembled a comprehensive relative abundance dataset of microsites sampled from the entire Belly River Group and performed a series of analyses to test the influence of environmental factors on site and taxon clustering, and test the stability of faunal assemblages both temporally and spatially.

The effect of environmental factors on site clustering was tested using Redundancy Analysis (RDA), in which palaeoenvironment was found to be strongly associated with distinct site clustering, with depositional setting, stratigraphy, and paleogeography more weakly associated. In both depositional setting and stratigraphic position, apparent clustering was related to categories that are closely linked to marine palaeoenvironment, such as shoreface deposits or the lowermost and uppermost units of the BRG, the Foremost Formation and the Lethbridge Coal Zone (LCZ). Palaeogeography (latitude) appears to have a clustering effect independent of other palaeoenvironmental factors, in which distinct clustering exists in the time-equivalent section of the Oldman and Dinosaur Park formations for sites sampled from Dinosaur Provincial Park (DPP) and the Milk River region, respectively. This analysis confirms that depositional setting has little effect on faunal assemblage composition, with marine-terrestrial transitions driving temporal faunal dynamics within the BRG.

The time-equivalent portions of the Oldman (OM) and Dinosaur Park (DPF) formations are of particular interest in these comparisons, as they have been characterized as representing differing environments: a drier inland fluvial system, and an estuarine coastal plain, respectively (Eberth and Hamblin 1993; Brinkman et al. 2004; Eberth 2005). Dinosaur faunal composition has been proposed to be sensitive to such regional environmental variation (Horner et al. 1992; Lehman 2001; Gates et al. 2010), though recent work on ceratopsians has suggested that this sensitivity may be overstated (Chiba et al. 2015). To test the putative altitudinal sensitivity of dinosaurs in the time-equivalent sections of the Oldman and pre-LCZ Dinosaur Park formations of each sampling area, faunal assemblage proportions and pair-wise site similarities were compared, and were found to be mostly stable through this interval. The similarity of the dinosaur faunal assemblages, and vertebrate assemblages as a whole, between the time-equivalent portions of the DPF and OM suggests one of two scenarios: the environments are more similar than often characterized, and/or the dinosaurs are less sensitive to variation in the regional palaeoenvironment that previously suggested.

Literature Cited

- Beavan, N.R., and A.P. Russell. 1999. An elasmobranch assemblage from the terrestrial-marine transitional Lethbridge Coal Zone (Dinosaur Park Formation: Upper Campanian), Alberta, Canada. *Journal of Paleontology* 73:494-503.
- Brinkman, D. B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: Evidence from vertebrate microfossil localities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 78:37-54.

- Brinkman, D.B., A.P. Russell, D.A. Eberth, and J.H. Peng. 2004. Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213:295-313.
- Brinkman, D.B., M.J. Ryan, and D.A. Eberth. 1998. The paleogeographic and stratigraphic distribution of ceratopsids (Ornithischia) in the Upper Judith River Group of Western Canada. *Palaios* 13:160-169.
- Chiba, K., M.J. Ryan, D.R. Braman, D.A. Eberth, E.E. Scott, C.M. Brown, Y. Kobayashi, and D.C. Evans. 2015. Taphonomy of a monodominant *Centrosaurus apertus* (Dinosauria: Ceratopsia) bonebed from the upper Oldman Formation of southeastern Alberta. *Palaios* 30:655-667.
- Eberth, D.A. 2005. The Geology. Pages 54-82 in P. J. Currie and E. B. Koppelhus (eds). *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*. Indiana University Press, Bloomington, Indiana.
- Eberth, D.A., and A.P. Hamblin. 1993. Tectonic, stratigraphic, and sedimentologic significance of a regional discontinuity in the upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. *Canadian Journal of Earth Sciences* 30:174-200.
- Gates, T.A., S.D. Sampson, L.E. Zanno, E.M. Roberts, J.G. Eaton, R.L. Nydam, J.H. Hutchison, J.A. Smith, M.A. Loewen, and M.A. Getty. 2010. Biogeography of terrestrial and freshwater vertebrates from the late Cretaceous (Campanian) Western Interior of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291:371-387.
- Horner, J., D.J. Varricchio, and M.B. Goodwin. 1992. Marine transgressions and the evolution of Cretaceous dinosaurs. *Nature* 358:59-61.
- Lehman, T.M. 2001. Late Cretaceous dinosaur provinciality. Pages 310-328 in D. Tanke and K. Carpenter (eds). *Mesozoic Vertebrate Life*. NRC Research Press.
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New insights on the anatomy of *Captorhinus magnus* from the Lower Permian of Oklahoma with a note on captorhinid taxonomy

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The Richards Spur locality has yielded a treasure trove of vertebrate fossil material including an exhaustive collection of captorhinids (Fox and Bowman 1966; Modesto 1998). In 2002, Kissel et al. described a new Richards Spur species, *Captorhinus magnus*, on the basis of three diagnostic features including: (1) large size (1.5 to 2.3 times larger than *C. aguti*); (2) presence of a single row of ogival teeth (multiple rows in *C. aguti*); and (3) presence of a concave proximal articular surface on the head of the femur. Of these three characters, only the femoral morphology appears to be autapomorphic for this taxon. However, deBraga (2003) described a virtually identical condition in a large specimen of a procolophonid that was absent in smaller procolophonids and which is difficult to confirm in smaller presumably immature specimens of *C. magnus*. Therefore, the possibility that the femoral morphology, described for the type of *C. magnus*, might be reflective of its degree of maturity cannot be discounted. Nevertheless, additional preparation of the type material of *C. magnus* along with newly assigned material has yielded two new characters: (4) the presence of a single row of teeth along the medial margin of the anterior process of the pterygoid; and (5) a diagonal suture formed by the anterolateral border of the frontal and the corresponding posteromedial boundary of the nasal (OMNH* 56820) forming an angle of approximately 45°, when measured relative to the midline of the skull.

The nature of the pterygoid dentition is problematic as details of the pterygoid tooth morphology and the exact arrangement of the tooth rows have not been properly described in the majority of captorhinid taxa. Heaton (1979) described the presence of sharp teeth in the medial margin of the anterior pterygoid process but the figured material displays a scattered arrangement of teeth which differ from the prominent single row found in *C. magnus*. Regarding the sutural contact between the frontal and nasal, there appears to be a significant amount of variability in specimens of *C. aguti* examined for this study. Some *C. aguti* specimens differ from *C. magnus* in having a nearly straight suture that is effectively perpendicular to the long axis of the skull, whereas other specimens present a diagonal suture that is similar to the condition exemplified by *C. magnus*. Furthermore, in at least one specimen of *C. laticeps* (OMNH 15022), the morphology approaches the 45° angle found in *C. magnus*, whereas paradoxically the holotype, figured by Heaton (1979), displays a straight suture.

Aside from expanding the diagnosis of *C. magnus*, this re-examination of Richards Spur captorhinids has revealed a number of confounding factors that presently impact on the diagnosis of captorhinid species including: (1) the questionable taxonomic position and the validity of *C. laticeps* and (2) the curious interspecific variability demonstrated by *C. aguti*. Both of these taxonomic issues must be resolved in order to clarify any uncertainty within the family Captorhinidae and provide a clearer picture of early reptilian evolution.

*OMNH = Oklahoma Museum of Natural History

Literatures Cited

- deBraga, M. 2003. The postcranial skeleton, phylogenetic position, and probable lifestyle of the Early Triassic reptile *Procolophon trigoniceps*. *Canadian Journal of Earth Sciences*, 40(4):527-556.
- Fox, R.C., and M.C. Bowman. 1966. Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). *The University of Kansas Paleontological Contributions, Vertebrata*, 11:1-79.

Heaton, M.J. 1979. Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian of Oklahoma and Texas. *Bulletin of the Oklahoma Geological Survey*, 127:1–84.

Kissel, R.A., D.W. Dilkes, and R.R. Reisz. 2002. *Captorhinus magnus*, a new captorhinid (Amniota: Eureptilia) from the Lower Permian of Oklahoma, with new evidence on the homology of the astragalus. *Canadian Journal of Earth Sciences*, 39(9):1363–1372.

Modesto, S.P. 1998. New information of the skull of the Early Permian reptile *Captorhinus aguti*. *PaleoBios*, 18:21–35.

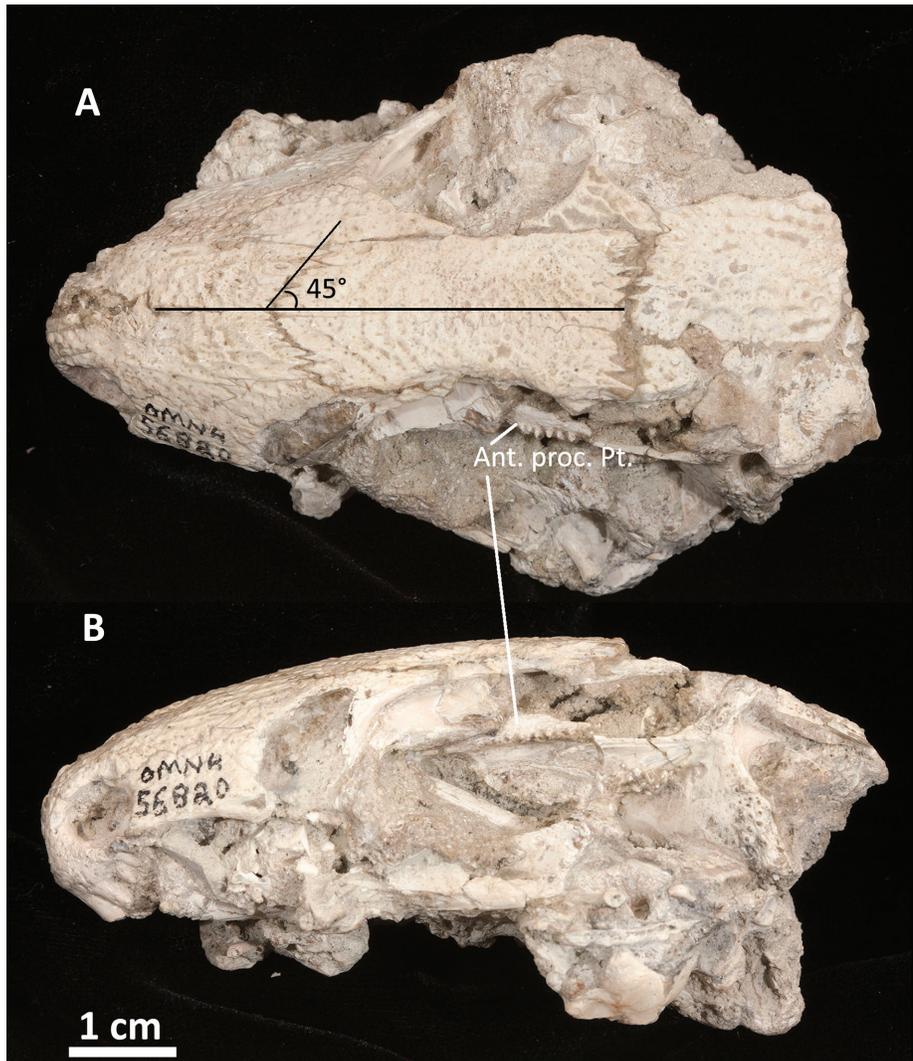


Figure 1. *Captorhinus magnus* (OMNH 56820) in dorsal view (A) and left lateral view (B). Angle on figure refers to arrangement of frontal/nasal suture. Ant. proc. Pt. (anterior process of pterygoid showing single row of teeth).

Up, up and away: an analysis of terrestrial launching in theropods

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Over the past three decades the study of the non-avian to avian theropod transition has been greatly enhanced by the discovery of numerous small maniraptorans detailing the evolution of many flight related characters (Makovicky and Zanno 2011). As some of these possess well-developed feathered forelimbs, some significant questions arise such as when does powered flight appear in this lineage and did it appear more than once within Maniraptora? Here we use a first principals modeling approach to explore these questions and attempt to determine in which taxa was take off and powered flight possible. This was done based on a dataset of 51 specimens encapsulating 37 non-avian and early avian genera whose wing length was either calculable directly from the fossils or reconstructed based on closely related taxa. We also assigned behavioural parameters such as flap angle to be at near the maximum possible value given the construction of the shoulder girdle in non-avians (Turner et al. 2012), with flapping frequency and the coefficient of lift to be similar to extant avian values (Tobalske and Dial 2000; Jackson 2009; Usherwood 2009) to ensure that our reconstructions were capturing all possible taxa that could succeed in take-off. We refined our dataset to only those specimens with sufficiently large wings to show wing loading values of less than 2.5 g/cm² (Meunier 1951) and specific lift values above 9.8 (Marden 1994) as both of these parameters have been shown to be reliable predictors of the flightless threshold in extant avians (Guillemette and Ouellet 2005). This reduced our dataset to only 18 specimens representing 4 non-avian and 5 avian genera. We then calculated the required minimum take off speed based on avian generated flapping frequencies. All avians generated sufficient velocity during leaping or running to take off, while only *Microraptor* and *Rahonavis* among the non-avians achieved take off velocity through leaping or running at speeds of less than 5 m/s. We re-ran our analysis factoring in some life history changes that alter the flight capability in extant avians (egg retention and molting) to determine how they would influence take off capacity. Egg mass, using either an avian or an squamate egg mass estimator, does not significantly alter the capability of avian or non-avian theropods to achieve take-off. In contrast molting, using parameters based on extant avian values, does have an effect and may have reduced the take-off ability in *Microraptor* such that leaping based methods would have been difficult, though not impossible. Our data suggests that due to the level of wing development in some non-avian and all basal avians, they had sufficiently lift potential to achieve powered take off from the ground, eliminating the need for gravity assisted launching. When these results are coupled with work detailing the lack of arboreal features among non-avian maniraptorans and early birds (Dececchi and Larsson 2011, Bell and Chiappe 2011) they support the hypothesis that bird achieved flight without a gliding intermediary step, something unique among volant tetrapod clades.

Literature Cited

- Bell, A., and L.M. Chiappe. 2011. Statistical approach for inferring ecology of Mesozoic birds. *Journal of Systematic Palaeontology* 9:119–133.
- Dececchi, T.A., and H.C.E. Larsson. 2011. Assessing arboreal adaptations of bird antecedents: testing the ecological setting of the origin of the avian flight stroke. *PLoS One* 6:e22292.
- Guillemette, M. And J.F. Ouellet. 2005. Temporary flightlessness in pre-laying Common Eiders *Somateria mollissima*: are

females constrained by excessive wing-loading or by minimal flight muscle ratio? *Ibis* 147:293-300.

Jackson, B.E. 2009. The allometry of bird flight performance. PhD Thesis etd.lib.umt.edu.

Makovicky, P.J., and L.E. Zanno. 2011. Theropod diversity and the refinement of avian characteristics. *Living dinosaurs: the evolutionary history of modern birds* 9–29.

Marden, J.H. 1994. From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *American Journal of Physiology* 266: 1077–1084.

Meunier, K. 1951. Korrelation und Umkonstruktion in den Grössenbeziehungen zwischen Vogelflügel und Vogelkörper. *Biologia Generalis* 19: 403–443.

Tobalske, B.W., and K. P. Dial. 2000. Effects of body size on take-off flight performance in the Phasianidae (Aves). *Journal of Experimental Biology* 203:3319–3332.

Turner, A.H., P.J. Makovicky, and M. A. Norell. 2012. A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* 371:1–206.

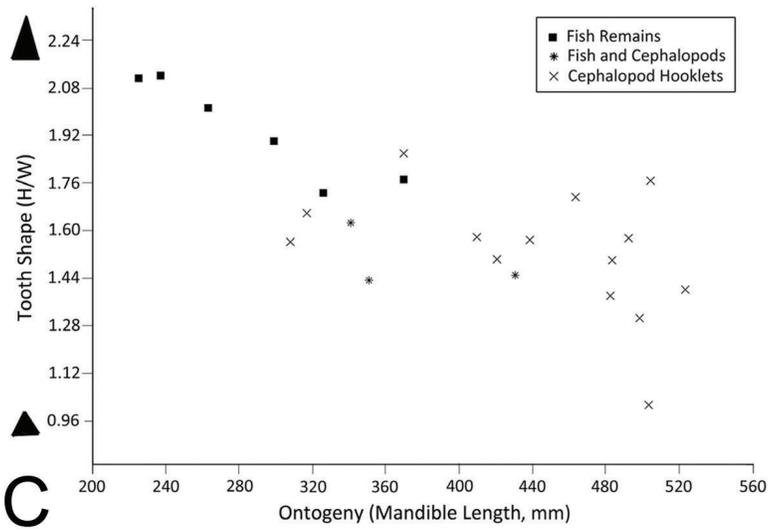
Usherwood, J.R. 2009. The aerodynamic forces and pressure distribution of a revolving pigeon wing. *Experiments in Fluids* 46:991–1003.

Dental developmental evolution and niche ontogeny of *Stenopterygius quadriscissus* (Reptilia: Ichthyosauria)

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With an exceptional fossil record containing nearly complete ontogenetic sequences, fossils of the ichthyosaur *Stenopterygius quadriscissus* from southern Germany's Posidonia Shale (early Toarcian) provide a unique opportunity for understanding the paleobiology and paleoecology of ichthyosaurs. Past researchers have noted the presence of dental reduction to the point of functional tooth loss in many specimens of this species (McGowan 1979). Reduction is most evident in the largest individuals, suggesting the possibility of an ontogenetic pattern of tooth reduction. Despite this, the potential for taphonomic bias and a lack of a clear definition of what constitutes "tooth reduction" have prevented a clear understanding of the evolution and ecological consequences of this unusual developmental pattern (Sander et al. 2011). To test this proposed ontogenetic trend and to explore underlying developmental and ecological aspects, I examined $n = 107$ specimens covering the three known species of *Stenopterygius*: *S. quadriscissus*, *S. triscissus*, and *S. uniter* (Maisch 2008). Controls were included to reduce the possibility of taphonomic bias. Dental morphology through ontogeny was examined by comparing enamel crown height, width, and shape (calculated as per Massare 1987) with mandible length and tooth row length (proxies of body size and presumed ontogenetic age). An inventory of preserved gut contents, identified to the least inclusive taxonomic level, was collected and integrated into the dental shape data to test the possibility of a concomitant ontogenetic niche shift. The histological structure of the reduced teeth of *S. quadriscissus* was compared statistically with the presumed ancestral condition (represented by *Mixosaurus*), with findings from contemporary developmental literature integrated to examine the possible causes of the observed ontogenetic trend. Results suggest that *S. quadriscissus* did undergo ontogenetic tooth reduction, with teeth decreasing not only in relative height, but also changing in shape and corresponding dental feeding guild (Dick and Maxwell 2015). Following a negative allometric growth trend, the teeth of *S. quadriscissus* become increasingly short and robust, corresponding to a shift from the Pierce II guild to the Smash guild (sensu Massare 1987) (Dick and Maxwell 2015). This pattern predicts a shift in resource use, and the results of the gut contents analysis support this. Specifically, a distinct niche shift was observed, with a transition from a diet focused on small burst-swimming fish during early post-natal ontogeny to a diet focused on fast-moving cephalopods following sexual maturity (Dick et al. 2016). Visual and metric comparison of the histological structure of the reduced teeth of *Stenopterygius* showed no evidence of an altered amelogenic pathway (predicted based on Plikus et al. 2005). While alteration of the Bmp4 or Fgf8 pathways in the odontogenic mesenchyme can produce teeth that are reduced in size, such a developmental change includes tissue-level changes, which were not observed (Plikus et al. 2005). Given this, tooth reduction in *Stenopterygius* does not appear to have occurred via the pathways observed to produce tooth reduction in cetaceans (Armfield et al. 2013), birds (Louchart and Viriot 2011), or turtles (Tokita et al. 2012), instead occurring due to reduced tooth bud size and negative allometry.



< Figure 1. A) Juvenile *Stenopterygius quadriscissus* (SMNS 54026) showing well developed, relatively large teeth. B) Adult *S. quadriscissus* (SMNS 53001) showing the highly reduced teeth characteristic of this species (red box). C) Graph showing the relationship between tooth shape, mandible length, and gut contents, to illustrate the proposed ontogenetic niche shift. D) Mid-crown histological section of the reduced tooth of an adult *S. quadriscissus*, showing well-developed and consistent enamel. Dental reduction via alteration of the *Bmp4* pathway causes inconsistent or halted enamel production (Plikus et al. 2005). An absence of these issues (and a lack of a statistically significant difference in size- and shape-standardized enamel thickness when compared to the ancestral condition in *Mixosaurus* [One-way ANCOVA, test for homogeneity of slope $p = 0.62$, test for equal means, adjusted for covariate $p = 0.95$]) suggests tooth reduction in *S. quadriscissus* occurs due to a smaller overall tooth bud, rather than an interruption of ordinary developmental processes. Scale bars: A = 1 cm, B = 5 cm, D = 500 μm . Modified from Dick and Maxwell 2015 and Dick et al. 2016.

Literature Cited

- Armfield, B., Z. Zheng, S. Bajpai, C. Vinyard, and J. Thewissen. 2013. Development and evolution of the unique cetacean dentition. *PeerJ* 1:e24. doi: 10.7717/peerj.24
- Dick, D.G. and E.E. Maxwell. 2015. Ontogenetic tooth reduction in *Stenopterygius quadriscissus* (Reptilia: Ichthyosauria): negative allometry, changes in growth rate, and early senescence of the dental lamina. *PLOS ONE* 10(11):e0141904. doi: 10.1371/journal.pone.0141904
- Dick, D.G., E.E. Maxwell, and G. Schweigert. 2016. Trophic niche ontogeny and palaeoecology of Early Toarcian *Stenopterygius* (Reptilia: Ichthyosauria). *Palaeontology* (Online Early View). doi: 10.1111/pala.12232
- Louchart, A, and L. Viriot. 2011. From snout to beak: the loss of teeth in birds. *Trends in Ecology and Evolution*. 26(12):663–673. doi: 10.1016/j.tree.2011.09.004
- Maisch, M. 2008. Revision der Gattung *Stenopterygius* Jaekel, 1904 emend. von Huene, 1922 (Reptilia: Ichthyosauria) aus dem unteren Jura Westeuropas. *Palaeodiversity* 1:227–271.
- McGowan, C. 1979. A revision of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. *Palaeontographica Abteilung A*. 166(4–6):93–135.
- Plikus, M., M. Zeichner-David, J. Mayer, J. Reyna, P. Bringas, J. Thewissen, M. Snead, Y. Chai, and C. Chuong. 2005. Morphoregulation of teeth: modulating the number, size, shape and differentiation by tuning *Bmp* activity. *Evolution and Development* 7(5):440–457. doi: 10.1111/j.1525-142X.2005.05048.x
- Tokita, M., W. Chaeychomsri, and J. Siruntawintei. 2012. Developmental basis of toothlessness in turtles: insight into convergent evolution of vertebrate morphology. *Evolution* 67(1):260–273. doi: 10.1111/j.1558-5646.2012.01752.x

North America's oldest softshell turtle: A new plastomenine (Testudines: Trionychidae) from Milk River Formation of Alberta (Late Cretaceous: Santonian)

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The pre-Campanian trionychid fossil record in North America is comprised of heavily fragmentary specimens, which can often only be identified as Trionychidae indet. (Russell 1935; Gardner et al. 1995; Fiorillo 1999; Brinkman 2003; Jasinski 2013). Here, I describe a new species of plastomenine soft shell turtle from the Santonian-aged Milk River Formation of southern Alberta, dated at ~84 MYA, based on an incomplete shell (*ROM 56647). Plastomeninae, a trionychid clade known only from the fossil record, is classically distinguished by the complete suturing of its plastral bones along the midline, a crescent-shaped entoplastron, and enlarged eighth costals (Hay 1908). ROM 56647 has a unique variety of plastomenine and more basal trionychid characteristics, in addition to key autapomorphies that suggest it is a novel species. It is characterized by the following: completely fused and relatively slender hyo-hypoplastral bridge, a bow-shaped nuchal, a distinctly straight pygal notch, a domed carapace, extensive plastral callosities and sculpturing, a posteriorly notched xiphiplastron, and enlarged tubercles with smaller intermittent shallow pits across the dorsal carapace. Phylogenetic analysis places it in a polytomy with *Gilmoremys*, *Plastomenus*, and a clade of *Hutchemys* spp within Plastomeninae. The morphological distinctiveness, together with its age, support the recognition of ROM 56647 a new species. As the oldest trionychid that can be described to the species level in North America, ROM 56647 provides new insights into the early evolution and dispersal of Trionychidae from Asia into North America, and the biodiversity of its locality, Milk River Formation, during the Late Cretaceous.

*ROM = Royal Ontario Museum

Literature Cited

- Brinkman, D. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. *Canadian Journal of Earth Sciences* 40:557-571.
- Fiorillo, A.R. 1999. Non-mammalian microvertebrate remains from the Robison Egghell Site, Cedar Mountain Formation (Lower Cretaceous) Emery County, Utah. Pp. 259–268 in D.D. Gillette (ed.). *Vertebrate Paleontology in Utah*. Utah Geological Survey: Salt Lake City, Utah.
- Gardner, J., A. Russell, and D. Brinkman. 1995. Systematics and taxonomy of soft-shelled turtles (Family Trionychidae) from the Judith River Group (mid-Campanian) of North America. *Canadian Journal of Earth Sciences* 32:631-643.
- Hay, O.P. 1908. *The Fossil Turtles of North America*. Washington, DC: Carnegie Institution of Washington.
- Jasinski, S. 2013. Review of the fossil Trionychidae (Testudines) from Alabama, including the oldest record of trionychid turtles from Eastern North America. *Bulletin Alabama Museum of Natural History* 31:46-59.
- Russell, L.S. 1935. Fauna of the Upper Milk River beds, Southern Alberta. *Transactions of the Royal Society of Canada Section 4* 29:115-128.
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A new peirosaurid crocodyliform (Mesoeucrocodylia: Peirosauridae) from the Late Cretaceous of Sudan, North Africa

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The Late Cretaceous Wadi Milk Formation (?Cenomanian) of northern Sudan has yielded a rich assemblage of fossil crocodyliforms, most of which have yet to be formally described. Recent fieldwork in this region has recovered material of a new peirosaurid from this unit, which is a rare record of this clade of terrestrial predators from the Cretaceous of eastern Africa. The new material consists of a complete dentary symphysis including splenial fragments and an almost complete fused frontal complex collected in close proximity to each other from a dense bonebed. The dentary differs from other peirosaurids in that the maximum diameter of the enlarged first dentary alveolus exceeds that at the fourth position, and hosted an anteriorly directed tooth. Phylogenetic analysis suggests that the new Sudanese taxon forms a close relationship to *Hamadasuchus*, *Rukwasuchus* and *Stolokrosuchus*, suggesting a north African radiation of this clade in the middle Cretaceous. The new taxon is notable for its large size compared to most Cretaceous peirosaurids. The estimated size of the skull is approximately 70 cm, with an estimated total body length of approximately 5 m. Peirosaurids are presumed to be terrestrial predators due to their tall snouts, forwardly directed nares and laterally directed orbits. Theropod dinosaur material from the Wadi Milk Formation is rare, and is typically from modestly sized taxa. The large size of the Sudan peirosaur suggests that may have occupied an upper tier terrestrial mesopredator role in its ecosystem.

Dental histology of *Coelophysis bauri* and the evolution of early dinosaurian periodontal tissues

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Studies of dinosaur dentition usually focus on crown morphology and shed teeth for studies of disparity, dietary preference, and relative abundance (Buffetaut et al. 1986; Fiorillo and Gangloff 2001; Hwang 2005). These studies typically do not describe the histological details of dinosaur teeth or are concerned with the crown tissues enamel and dentine. As such, the full suite of tissues that attach teeth to the jaws are poorly documented across Dinosauria. Tooth attachment tissues are a fundamental part of the tooth and vital to a more complete understanding of dinosaurian dental anatomy, function, development, and evolution. More recent work has examined these tissues in greater detail in derived, Cretaceous members of Dinosauria, such as titanosaurs, ceratopsids, and hadrosaurids (Garcia and Cerda 2010; Erickson et al. 2012; Erickson and Zelenitsky 2014; Erickson et al. 2015; Garcia and Zurriaguz 2015), but they remain undocumented in early dinosaurs. To better understand the nature of the tooth attachment tissues in dinosaurs, we must examine more basal members to establish the ancestral condition. As one of the most basal and oldest dinosaurs, the Triassic theropod *Coelophysis bauri* can provide important information on the ancestral dental condition in Dinosauria. Here histological thin sections were prepared from a partial skull of a *C. bauri* from the Whitaker Quarry, New Mexico, USA. The skull includes most of the maxilla and dentary and contains in situ teeth that preserve all of the periodontal tissues, which are cementum, periodontal ligaments and alveolar bone. In all, five tissue types were identifiable: enamel, dentine, cementum, periodontal ligament, and alveolar bone. The three-part periodontium identified in *C. bauri* is similar to that of crocodylians, mammals, titanosaurs, ceratopsids and hadrosaurids, indicating that it is representative of the plesiomorphic condition in dinosaurs. This adds to a growing number of studies indicating that a three-part periodontium is plesiomorphic for all amniote clades. *Coelophysis bauri* was also found to possess a thecodont gomphosis, whereby the tooth is attached via periodontal ligaments in a socket, similar to that of crocodylians and mammals and suggests an as yet unidentified functional significance. Finally, a tooth development sequence was also reconstructed and allowed for the tracking of tissue development timing and periodontal tissue growth directions. Taken together, our results provide a new comparative baseline for future work on dinosaurian dental histology, development and replacement.

Literature Cited

- Buffetaut, E., Y. Dauphin, J. J. Jaeger, M. Martin, J. M. Mazin, and H. Tong. 1986. Prismatic dental enamel in theropod dinosaurs. *Naturwissenschaften* 73:326–327.
- Erickson, G. M., B. A. Krick, M. Hamilton, G. R. Bourne, M. A. Norell, E. Lilleodden, and W. G. Sawyer. 2012. Complex dental structure and wear biomechanics in hadrosaurid dinosaurs. *Science* 338:98–101.
- Erickson, G. M., and D. K. Zelenitsky. 2014. Osteohistology and occlusal morphology of *Hypacrosaurus stebingeri* teeth throughout ontogeny with comments on wear-induced form and function. *Hadrosaurs*. p 422–432.
- Erickson, G. M., M. A. Sidebottom, D. I. Kay, K. T. Turner, N. Ip, M. A. Norell, W. G. Sawyer, and B. A. Krick. 2015. Wear biomechanics in the slicing dentition of the giant horned dinosaur *Triceratops*. *Science Advances* 1:e1500055–e1500055.
- Fiorillo, A. R., and R. A. Gangloff. 2001. Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on arctic dinosaur paleoecology. *Journal of Vertebrate Paleontology* 20:675–682.
- Garcia, R. A., and I. A. Cerda. 2010. Dentición de titanosaurios (Dinosauria, Sauropoda) del Cretácico Superior de la provincia de Río Negro, Argentina: morfología, inserción y reemplazo. *Ameghiniana* 47: 45–60.
- García, R. A., and V. Zurriaguz. 2015. Histology of teeth and tooth attachment in titanosaurs (Dinosauria; Sauropoda). *Cretaceous Research* 57:248–256.
- Hwang, S. H. 2005. Phylogenetic patterns of enamel microstructure in dinosaur teeth. *Journal of Morphology* 266:208–240.

A High Palaeolatitudinal Ancient Shark Assemblage from the Late Albian Western Interior Seaway

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A rare elasmobranch (shark and ray) assemblage was recently collected from Albian rock strata (ca. 100 Ma) of northern Alberta, Canada. During this time, the Western Interior Seaway was in the earliest stages of development and stretched from the present-day Arctic Ocean to the Gulf of Mexico. Very little is known about the marine vertebrates in the seaway at this time, particularly from the cooler waters at high palaeolatitude.

The recovered assemblage is dominated by hybodonts and lamniform sharks. Of the five taxa identified from the site, *Meristodonoides*, *Polyacrodus*, *Scapanorhynchus*, and *Cretalamna* appear to have a cosmopolitan distribution that included both temperate and subtropical waters. Conversely, fossilized remains of *Archaeolamna* have not been recovered from productive lower palaeolatitudinal assemblages, suggesting this taxon may have had an anti-tropical distribution.

A bonebed of *Avimimus* from the Late Cretaceous of Mongolia: insights into social behaviour in oviraptorosaurs

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A monodominant bonebed of *Avimimus* from the Nemegt Formation of Mongolia is the first oviraptorosaur bonebed described and the only recorded maniraptoran bonebed from the Late Cretaceous. Sedimentological data suggests that the assemblage represents a reworked deposit of skeletal material. Remains of at least 18 individuals are present, composed mostly of hindlimbs but also including parts of the skull and mandible. Cranial elements recovered from the bonebed provide insights on the anatomy of the facial region, which was formerly unknown in *Avimimus*. Both adult and subadult material was recovered from the bonebed, but no small juvenile material is present. Combined with the taphonomic evidence, this suggests that *Avimimus* engaged in social behaviour in which adults and subadults grouped to the exclusion of smaller individuals. This social aggregation may be explained either as lekking behaviour or, more likely, as flocking for predator avoidance. Therefore, the association of *Avimimus* specimens in the bonebed may be interpreted as the first evidence of birdlike flocking behaviour in a maniraptoran. Gregarious behaviour in ornithomimids and oviraptorosaurs may be an adaptation for predator avoidance to compensate for ontogenetic constraints on locomotion.

Description of a juvenile specimen of *Delorhynchus* based on a partially articulated skull and mandible from the Richards Spur locality, Oklahoma

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The Richards Spur locality of Oklahoma is well known for preserving a large assemblage of early Permian terrestrial tetrapod taxa (MacDougall and Reisz 2012). Among these taxa are numerous representatives of the clade Parareptilia, with new parareptilian material being described on a regular basis. Herein we describe the latest parareptile material from the Richards Spur locality, a new specimen of the genus *Delorhynchus*, which consists of a partially articulated skull and mandible. This new specimen exhibits ornamentation composed of an abundance of small circular pits, this ornamentation pattern is present on all elements of the skull roof but does not extend to the mandible, this is consistent with the ornamentation described in subadult individuals (Reisz et al. 2014). Also present are slightly recurved homodont teeth, and the specimen exhibits a tooth count similar to that in previously described specimens (Reisz et al. 2014). These aforementioned characteristics are associated with *Delorhynchus* and therefore we assign this new specimen as belonging to the genus. There are four major features that identify this specimen as ontogenetically young. The first is the dermal tuberosities that ornament the dorsal side and lateral edges of the skull, these tuberosities are hallmarks of the previously described *Delorhynchus* specimens (Reisz et al. 2014), these dermal tuberosities are absent from every aspect of the skull belonging to the new specimen, this indicates that this specimen can be placed earlier on in ontogeny. The second feature that supports the age of this specimen is that the temporal fenestra is proportionally larger in this specimen when compared to other specimens of *Delorhynchus*, which are more robust in bone structure and presumably more mature. The third feature is the incomplete fusion of some sutural contacts, most notably along the frontal and nasal, as well as the maxilla and lacrimal. Lastly, there is a lack of two distinct lateral exposures of the lacrimal in this specimen, this is likely due to a uniform edge of the maxilla, which extends across the lacrimal to meet with the prefrontal, only leaving one continuous lateral lacrimal exposure which is unlike the larger specimens described previously (Reisz et al. 2014). The description of this new specimen of *Delorhynchus* will aid in the overall examination of parareptiles by providing a more complete ontogenetic series for the growth of *Delorhynchus*. Which in turn contributes important information to our understanding of the development of parareptiles at the Richard Spur locality.

Literature Cited

- MacDougall, M.J., and R.R. Reisz. 2012. A new parareptile (Parareptilia, Lanthanosuchoidea) from the Early Permian of Oklahoma. *Journal of Vertebrate Paleontology* 32:1018–1026.
- Reisz, R.R., M.J. MacDougall, and S.P. Modesto. 2014. A new species of the parareptile genus *Delorhynchus*, based on articulated skeletal remains from Richards Spur, lower Permian of Oklahoma. *Journal of Vertebrate Palaeontology* 34:1033-1043.
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Crouzeliinae tribal warfare: taxonomic and evolutionary concepts in Pliopithecoidea (Order: Primates)

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In the description and differential diagnosis of *Barberapithecus huezeleri* Alba and Moyá-Solá (2012) argue that Crouzeliinae (Family: Pliopithecoidea) can be divided into two tribes: Anapithecini, composed of four distinct monotypic genera: *Anapithecus hernyaki*, *Barberapithecus huezeleri*, *Egarapithecus narcisoi*, and *Laccopithecus robustus*; and Crouzelinni, composed of a single genus with four species: *Plesiopliopithecus lockeri*, *P. auscitanensis*, *P. rhodanica*, *P. priensis*. A review of the fossil taxa that compose these tribes suggest such an arrangement would be paraphyletic. The extremely small fossil sample of *Plesiopliopithecus*, and the limited characters used to distinguish each species, suggest Crouzeliini can be collapsed into a single taxon, *P. lockeri*. Phylogenetic analysis of the Crouzeliinae (Moyá-Solá et al. 2001) has also shown that the precise phylogenetic status of *P. lockeri* cannot be successfully resolved. Tribal distinctions are intended as means to organize taxonomy and patterns of descent. Crouzeliini and Anapithecini do nothing to clarify Crouzeliinae or Pliopithecoidea systematics. These newly found tribes should therefore be abandoned, at least until additional fossil material enables a more robust and consistent systematic analysis.

Literature Cited

- Alba, D.M., and S. Moyá-Solá, S. 2012. A new pliopithecoidea genus (Primates: Pliopithecoidea) from Castell de Barberà (Vallès-Penedès Basin, Catalonia, Spain). *American Journal of Physical Anthropology* 147: 88-112.
- Moyá-Solá, S., M. Köhler, and D.M. Alba. 2012. *Egarapithecus narcisoi*, a new genus of Pliopithecidae (Primates, Catarrhini) from the late Miocene of Spain. *American Journal of Physical Anthropology* 114: 312-324.
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Evolution and development of avian tympanic sinuses: homologies and convergences of the amniote middle ear

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The middle ear is one of the major transformations in tetrapods. In spite of the many similar morphologies between the synapsid and sauropsid impedance-matching ears, the two are convergent. The tympanic middle ear in extant mammals and reptiles evolved independently and have drastically different topologies. We provide a comprehensive developmental pattern of the tympanic sinus in a model bird, Japanese quail (*Coturnix coturnix japonica*), with an emphasis on the development and topologies of its ventral portions, to examine potential homologies of the proximal extensions of the tympanic sinus between mammals and birds. We also describe the adult tympanic sinus morphology in phylogenetically distant model species, Japanese quail and zebra finch (*Taeniopygia guttata*), to help establish its ground state and variation within birds. The highly reticulating adult tympanic sinus is discovered to develop via a hierarchical, tree-like pattern. This pattern is discussed in light of what is known of tympanic sinus evolution in avian antecedents. The marginal sinus and siphoneal diverticulum develop independently at an early embryonic stage and the latter transforms into its mature morphology with stellate and ciliated epithelia prior to their confluence to each other in a latest stage. We present the first observation of cilia in an archosaur siphoneal diverticulum (quail and Alligator) may indicate that cilia are likely function to clear debris, similar to cilia present in ventral portions of the mammalian tympanic sinus. Pneumatization of the quadrate supports an association of angiogenesis and ossification of the bones in which the pneumatic extension extends. Furthermore it is revealed that the quadrate pneumatic foramen shifts dorsally following the ossification, with blood cell fronts of the pneumatic epithelia. Comparative data of the development of mouse and quail embryos suggest that only the proximal portions of the Eustachian tube which form the tympanic sinus during later stages are homologous based on their topological positions of the tympanic sinus and equivalent muscles between the taxa. This supports the long known non-homology between the mammalian and reptilian ear but further clarifies what topologies are shared and what are convergent between these clades.

Heterochrony and the evolution of mammalian tooth attachment

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Mammalian dentitions have evolved to maintain precise occlusion, which has resulted in changes to the shapes of the teeth, patterns and frequency of tooth replacement, and the composition of the dental tissues. Whereas dental occlusion (Kemp 1982) and the origin of diphyodonty (Edmund 1960; Hopson 1964; Osborn 1974) have been focal points in mammalian dental research, virtually nothing is known about the origin of the mammalian tooth attachment system (periodontium), a vital component of any dentition. The long-held consensus has been that mammals are unique among amniotes in possessing a periodontium consisting of three tissues: root cementum, alveolar (socket) bone, and periodontal ligament (Osborn 1984; Gaengler 2000). This ligamentous attachment system, also called a gomphosis, consists of suspended teeth within a socket, allowing them to resist the forces of occlusion and thus prolong the life of each tooth. By comparison, non-mammalian amniotes were thought to possess a single-tissue attachment system in which teeth were fused to the jaw by “bone of attachment” (Luan et al. 2009). Despite numerous attempts to reconstruct the evolution of the three-part periodontium in mammals from “bone of attachment” in a hypothetical ancestor (Osborn 1984; Gaengler 2000; Luan et al. 2009) no study has presented histological data for the numerous clades of non-mammalian synapsids. As such, the evolution of the mammalian periodontium and its origins are unknown.

Here we provide the first tissue-level comparison of tooth attachment across Synapsida, from early Permian “pelycosaur” to Triassic non-mammalian cynodonts, and track the evolution and development of the mammalian periodontium. We identify tissue-level homology across the “pelycosaur”-to-mammal transition and show that the mammalian periodontium is not a product of the evolution of new dental tissues. Instead, all synapsids possessed cementum, alveolar bone, and periodontal ligament. In synapsid taxa with teeth that are fused to the jaws the periodontal ligament was present, but it was completely calcified in older teeth, with a soft ligament attaching teeth to the socket in teeth preserved in intermediate stages. Furthermore, using data from multiple samples for several taxa, it was possible to reconstruct the relative timing of the formation of the tooth attachment tissues in several synapsid clades. Within a phylogenetic context, these results show that the evolution of the mammalian periodontium is the result of heterochrony, namely, a delay in the calcification of the ligament that holds teeth within their sockets. This heterochronic delay allowed the periodontal ligament to become an active component in the mammalian periodontium, providing a compliant attachment that permits fine-scale movement of a tooth within its socket. These histological comparisons also show for the first time that gomphosis actually evolved multiple times in non-mammalian synapsids and is not restricted to mammals, further supporting a growing consensus that cementum, periodontal ligament, and alveolar bone are deeply conserved across Amniota and have evolved to suit a particular function in any given taxon.

Literature Cited

Edmund, A.G. 1960. Tooth replacement phenomena in the lower vertebrates. Royal Ontario Museum, Life Sciences Division, Contribution 52:1–190.

- Gaengler, P. 2000. Evolution of tooth attachment in lower vertebrates to tetrapods. Pp. 173–185 in M.F. Teaford, M.M. Smith, and M.W.J. Ferguson (eds.), *Development, Function and Evolution of Teeth*. Cambridge, United Kingdom: Cambridge University Press.
- Hopson, J.A. 1964. Tooth replacement in cynodont, dicynodont and therocephalian reptiles. *Proceedings of the Zoological Society of London* 142:625–654.
- Kemp, T. S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. London, United Kingdom: Academic Press Inc.
- Luan, X., C. Walker, S. Dangaria, Y. Ito, R. Druzinsky, K. Jarosius, H. Lesot, and O. Rieppel. 2009. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontium. *Evolution & Development* 11:247–259.
- Osborn, J.W. 1974. On tooth succession in *Diademodon*. *Evolution* 28:141–157.
- Osborn, J.W. 1984. From reptile to mammal: evolutionary considerations of the dentition with emphasis on tooth attachment. *Symposium of the Zoological Society of London* 52:549–574.
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Paromomyids: early primates who like the cold?

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Plesiadapiforms represent the first adaptive radiation of primates, appearing near the Cretaceous–Paleogene boundary. Eleven families of plesiadapiforms are recognized, including the Paromomyidae, which are known from North America (Silcox and Gunnell 2008; Silcox et al. 2008), Europe (Russell et al. 1967; Marigó et al. 2012), and Asia (Tong and Wang 1998). Paromomyids represent the longest lived group of plesiadapiforms appearing in the early Paleocene (Clemens and Wilson 2009) and lasting until the late Eocene (Kihm and Tornow 2014).

The ultimate objective of this work is to understand the evolutionary relationships among species of paromomyids. To do that, it is necessary to determine if all the reported species of paromomyids are actually members of this family. Two species of particular interest are among the latest occurring members: *Phenacolemur shifrae* and *Ignacius mcgrewi*, which have atypical characteristics for a paromomyid (e.g. a strong paraconid on the third lower molar). Also of central interest is the problem of the taxonomy and relationships of the less well-known paromomyids from Europe, which bear closely on the biogeographic history of the group.

We find previously reported late middle Eocene paromomyids from California and Wyoming to pertain to a new genus of omomyoid eupriate. The new genus forms a monophyletic clade with “*Phenacolemur*” *shifrae* and “*Ignacius*” *mcgrewi*, forms a monophyletic clade and clusters with the omomyid *Trogolemur*. Purported European records of paromomyids later than the earliest middle Eocene are reconsidered and found to be non-diagnostic. Reassessment of these late middle Eocene primates demonstrates that trogolemurid omomyoids are more diverse and geographically widespread in North America than previously recognized. Conversely, this reassessment leads to the conclusion that paromomyids are known from only a single tooth after the early middle Eocene and that the group suffered near-extinction much earlier than previously supposed, possibly correlated with the early Eocene Climatic Optimum (López-Torres et al. in prep). This conclusion forms part of a growing understanding of the differential response of primate taxa to climate change, with paromomyids seeming to be better suited to colder climates. This preference for cooler temperatures may partially explain why paromomyids are known from the furthest north (Ellesmere Island) of any non-human primate taxa (West and Dawson 1977).

In terms of the question of how paromomyids got to Europe, the monophyly of the European paromomyids suggests it happened once, shortly before the start of the Eocene. Two of the most primitive forms from Europe

are found in Great Britain and northern France. This reinforces previous inferences (Marandat et al. 2012) about the pathway from North America to continental Europe being through Greenland and the British Isles, which would have been facilitated by the cold adaptations of the group. However, one of the oldest records of European paromomyid comes from the western Iberian Peninsula. This could suggest a rapid dispersal of early Eocene paromomyids throughout Europe and Iberia (then separated by a strait). In sum, a greater understanding of the phylogeny of paromomyids fosters a better understanding of all aspects of the biology of the group.

Literature Cited

- Clemens, W.A., and G.P. Wilson. 2009. Early Torrejonian mammalian local fauna from northeastern Montana, U.S.A. In: L.B. Albright III, editor. *Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne*. Museum of Northern Arizona Bulletin 65:111-158.
- Kihm, A.J., and M.A. Tornow. 2014. First occurrence of plesiadapiform primates from the Chadronian (latest Eocene). *Paludicola* 9:176-182.
- López-Torres, S., M.T. Silcox, and P.A. Holroyd. In prep. New omomyoid (Euprimates, Mammalia) from the late Uintan of Southern California and the question of the extinction of the Paromomyidae (Plesiadapiformes, Primates). *American Journal of Physical Anthropology*.
- Marandat, B., S. Adnet, L. Marivaux, A. Martinez, M. Vianey-Liaud, and R. Tabuce. 2012. A new mammalian fauna from the earliest Eocene (Ilerdian) of the Corbières (southern France): palaeobiological implications. *Swiss Journal of Geosciences* 105:417-434.
- Marigó, J., R. Minwer-Barakat, S. Moyà-Solà, and S. López-Torres. 2012. First record of Plesiadapiformes (Primates, Mammalia) from Spain. *Journal of Human Evolution* 62:429-433.
- Russell, D.E., P. Louis, and D.E. Savage. 1967. *Primates of the French early Eocene*. University of California Publications in Geological Sciences 73:1-46.
- Silcox, M.T., and G.F. Gunnell. 2008. Plesiadapiformes. In: C.M. Janis, G.F. Gunnell, M.D. Uhen, editors. *Evolution of Tertiary Mammals of North America*. Cambridge University Press. p 207-238.
- Silcox, M.T., K.D. Rose, and T.M. Bown. 2008. Early Eocene Paromomyidae (Mammalia, Primates) from the southern Bighorn Basin, Wyoming: systematics and evolution. *Journal of Paleontology* 82:1074-1113.
- Tong Y., and J. Wang. 1998. A preliminary report on the early Eocene mammals of the Wutu fauna, Shangdong Province, China. In: K.C. Beard, M.R. Dawson, editors. *Dawn of the Age of Mammals in Asia*. *Bulletin of the Carnegie Museum of Natural History* 34:186-193.
- West, R.M., and M.R. Dawson. 1977. Mammals from the Paleogene of the Eureka Sound Formation: Ellesmere Island, Arctic Canada. *Géobios Mémoire Spécial* 1:107-124.
-

Cranial variation in *Gryposaurus* (Dinosauria: Hadrosauridae) from the Dinosaur Park Formation of Southern Alberta, Canada

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The Dinosaur Park Formation (Campanian, Alberta, Canada) contains one of the most diverse assemblages of hadrosaurid dinosaurs (Ryan and Evans 2005). Despite a good fossil sample, the systematics of species within the genus *Gryposaurus* is unresolved. Historically, two *Gryposaurus* species have been recognized from the Dinosaur Park Formation: *G. notabilis* and *G. incurvimanus* (Gates and Sampson 2007). The two have recently been suggested to either represent two valid taxa, intraspecific variation within *G. notabilis* (e.g., ontogeny or sexual dimorphism), or anagenesis within an evolving *Gryposaurus* population (Prieto-Marquez 2010). However, these alternative hypotheses have never been tested via detailed morphological comparisons and biostratigraphy. In this study, I describe the cranial anatomy of *TMP 80.22.01, which represents the most complete specimen unequivocally assigned to *G. incurvimanus* to date. Most notably, TMP 80.22.01 possesses a much shallower nasal arch than any other known *Gryposaurus* skull, and this arch occurs far more anteriorly, in relation to the frontal bone, than those assigned to *G. notabilis*. A morphometric analysis of *Gryposaurus* and other hadrosaurine skulls from the Dinosaur Park Formation is performed to assess the influence of ontogeny (i.e., skull size) on skull morphology. Stratigraphic data is then used to map this morphology through time, to evaluate whether these morphological differences are correlated with their chronological order, suggesting that anagenetic evolution has occurred.

Independent of size, the specimens assigned to *G. incurvimanus* are found to be more similar to each other than to those of *G. notabilis*, with little overlap in a landmark-based morphospace. However, their biostratigraphy shows considerable chronological overlap, indicating that these species lived during similar time periods, and over a short period (< 0.5 mya). The anagenesis hypothesis is therefore rejected. Additionally, the nasal crest seems to retract posteriorly in larger-sized skulls, indicating that skull morphology may change throughout ontogeny. This type of ontogenetic nasal retraction is commonly seen in other hadrosaurids, such as *Brachylophosaurus* and lambeosaurines (Freedman, Fowler, and Horner 2015). Therefore, I do not reject the hypothesis that *G. incurvimanus* and *G. notabilis* represent different ontogenetic stages within a single species. Ultimately, this study aims to determine the range of individual variation within a single hadrosaurid species, assess the validity of other named species, and enrich the existing knowledge on dinosaur diversity in North America during the Late Cretaceous period.

*TMP = Royal Tyrrell Museum of Palaeontology

Literature Cited

- Freedman Fowler, E., and J. Horner. 2015. A new brachylophosaurin hadrosaur (Dinosauria: Ornithischia) with an intermediate nasal crest from the Campanian Judith River Formation of northcentral Montana. PLoS ONE 10: e0141304. doi:10.1371/journal.pone.0141304.
- Gates, T.A., and S.D. Sampson. 2007. A new species of *Gryposaurus* (Dinosauria: Hadrosauridae) from the late Campanian Kaiparowits Formation, southern Utah, USA. Zoological Journal of the Linnean Society 151:351-376.
- Prieto-Marquez, A. 2010. The braincase and skull roof of *Gryposaurus notabilis* (Dinosauria, Hadrosauridae) with a taxonomic revision of the genus. Journal of Vertebrate Paleontology 30:838-854.
- Ryan, M. J., and D.C. Evans. 2005. Ornithischian Dinosaurs. In P.J. Currie, and E.B. Koppelhus (eds), Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed (pp. 312-348). Bloomington, Indiana: Indiana University Press.

The parareptile fauna of the Early Permian (Cisuralian) Richards Spur locality of Oklahoma, and the early evolution and diversity of the clade

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The earliest members of Parareptilia first appear in the fossil record during the Late Carboniferous (Modesto et al. 2015). The clade continued to diversify into the Permian, eventually obtaining a cosmopolitan distribution and becoming a common component of Middle and Late Permian terrestrial vertebrate faunas. In contrast to their diversity during the middle and Late Permian, Early Permian parareptiles were historically rare and exhibited much lower taxonomic diversity (Tsuji et al. 2010), with eureptiles and synapsids being the most common carnivores and herbivores. However, the upland cave deposits found at the Richards Spur locality of Oklahoma have yielded an exceptionally diverse fauna of parareptiles since the description of *Colobomycter pholeter* (Vaughn 1958; Modesto 1999), the first parareptile to be found at the locality. Richards Spur represents a unique faunal assemblage in which numerous small- to medium-sized taxa are exceptionally preserved and in abundance. As a result of extensive study of the vertebrate assemblage at Richards Spur, several new parareptile taxa have been described (Tsuji et al. 2010; MacDougall and Reisz 2012; 2014; Reisz et al. 2014; MacDougall et al. in press), which has drastically increased the knowledge of parareptile evolution from the Early Permian.

Here we discuss the importance of the Richards Spur parareptile fauna and how it grants us understanding of the Early Permian that was not previously available. Currently, eight of the 15 Early Permian parareptile species known are found from Richards Spur. Furthermore, the species present at Richards Spur represent some of the earliest members of most major Early Permian parareptilian clades, the sole exception being the absence of the Gondwanan-restricted Mesosauridae. These factors indicate that Richards Spur was clearly an important location for the early evolution and diversification of parareptiles, given that it has produced the earliest known representatives of several major clades. The species-level/taxonomic diversity of Early Permian parareptiles now closely matches that of contemporaneous eureptiles, which is unsurprising given that the two clades both first appear in the fossil record during the Late Carboniferous. The Richards Spur assemblage provides a rare glimpse into the initial diversification of Parareptilia and highlights the importance of Laurasia as the center of a radiation of small, predatory parareptiles, as exemplified by the Lanthanosuchoids.

Literature Cited

- MacDougall, M.J. and R.R. Reisz. 2012. A new parareptile (Parareptilia, Lanthanosuchoidea) from the Early Permian of Oklahoma. *Journal of Vertebrate Paleontology* 32:1018–1026.
- MacDougall, M.J. and R.R. Reisz. 2014. The first record of a nyctiphruetid parareptile from the Early Permian of North America, with a discussion of parareptilian temporal fenestration. *Zoological Journal of the Linnean Society* 172:616–630.
- MacDougall, M.J., S.P. Modesto, and R.R. Reisz. In press. A new reptile from the Richards Spur locality, Oklahoma, USA, and patterns of Early Permian parareptile diversification. *Journal of Vertebrate Paleontology*.
- Modesto, S.P. 1999. *Colobomycter pholeter* from the Lower Permian of Oklahoma: A parareptile, not a protorothyrid. *Journal of Vertebrate Palaeontology* 19:466–472.
- Modesto, S.P., D.M. Scott, M.J. MacDougall, H.-D. Sues, D.C. Evans, and R.R. Reisz. 2015. The oldest parareptile and the early diversification of reptiles. *Proceedings of the Royal Society B* 282:20141912.

Reisz, R.R., M.J. MacDougall, and S.P. Modesto. 2014. A new species of the parareptile genus *Delorhynchus*, based on articulated skeletal remains from Richards Spur, Lower Permian of Oklahoma. *Journal of Vertebrate Paleontology* 34:1033–1043.

Tsuji, L.A., J. Müller, and R.R. Reisz. 2010. *Microleter mckinzieorum* gen. et sp. nov. from the Lower Permian of Oklahoma: the basalmost parareptile from Laurasia. *Journal of Systematic Palaeontology* 8:245–255.

Vaughn, P.P. 1958. On a new pelycosaur from the Lower Permian of Oklahoma, and on the origin of the family Caseidae. *Journal of Paleontology* 32:981–991.

A bodacious new ceratopsid (Dinosauria: Ornithischia) from the Judith River Formation (Upper Cretaceous: Campanian) of Montana, U.S.A.

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This study reports on a new species of ceratopsid from the lower Coal Ridge Member of the Judith River Formation in Montana, which dates to approximately 76 Ma (Upper Campanian). The species is distinguished by rugose dorsal contacts on the premaxillae for the nasals, laterally projecting postorbital horncores, fully fused and anteriorly curled epiparietals at loci P1 and P2, and a posteriorly projecting P3 epiparietal. The holotype specimen is also notable for its pathological left squamosal and humerus, which show varied signs of osteomyelitis and osteoarthritis. Although the postorbital horncores of the new species closely resemble those of the contemporaneous ‘*Ceratops*’, the horncores of both species are nevertheless indistinguishable from those of some other horned dinosaurs, including *Albertaceratops* and *Kosmoceratops*; ‘*Ceratops*’ is therefore maintained as a nomen dubium. Cladistic analysis recovers the new species as the sister taxon to the clade *Vagaceratops* + *Kosmoceratops*, and appears transitional in the morphology of its epiparietals. This new discovery serves to highlight the taxonomically distinctive and temporally dynamic nature of the dinosaur assemblage from the Judith River Formation in Montana.

A re-description of *Amphibamus grandiceps* (Temnospondyli: Dissorophoidea) from the Francis Creek shale, Mazon Creek, Illinois.

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The Carboniferous temnospondyl *Amphibamus grandiceps* (Cope 1865) is one of the oldest known members of Amphibamidae from the Middle Pennsylvanian aged (309 Mya) Mazon Creek deposits in Grundy County, Illinois, USA. *Amphibamus* was once considered a pivotal taxon in the debate over the origins of modern amphibians. It has since been usurped by the closely related amphibamids *Doleserpeton* and *Gerobatrachus* (Anderson et al. 2008). Despite this, several features, including the presence of small pedicellate bicuspid teeth, an abbreviated skull table, reduced ribs, a pectoral girdle incorporating a small interclavicle and bar like clavicles, link *Amphibamus* to modern amphibians. Taxonomic revision of *Amphibamus* has been hindered by the loss of the original type specimen in a fire, and a lack of subsequent descriptive papers on significant specimens, including the near complete neotype *YPM 799 (Moodie 1912). In addition, many specimens from Mazon Creek have since been reassigned to *Amphibamus*, including *Micrerpeton caudatum* (Moodie 1909), *Miobatrachus romeri* (Watson 1940), *Mazonerpeton longicaudatum* (Moodie 1912), as well as a variety of larval specimens (Milner 1982). Many of these specimens vary in their morphology and their ontogenetic stages have not been assessed. Anatomical features including the shape of the skull and cranial elements, morphology of the terminal phalanges, length of the limbs, and number of caudal vertebrae (tail length) all remain unclear. Here we re-describe the neotype of *Amphibamus* and include a discussion of new anatomical and ontogenetic data from reassigned specimens. Exceptional preservation of soft tissues found in Mazon Creek nodules also allows for a new analysis of labile structures including the integument (scale impressions), and structures of the eye (scleral ossicles). A phylogenetic analysis including YPM 799 was performed for the first time, recovering it as the sister taxon to *Amphibamus*.

*YPM = Yale Peabody Museum

Literature Cited

- Anderson, J.S., R.R. Reisz, D. Scott, N.B. Fröbisch, and S.S. Sumida. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* 453: 515–518.
- Cope, E.D. 1865. On *Amphibamus grandiceps*, a new batrachian from the Coal Measures. *Proceedings of the Academy of Natural Sciences of Philadelphia* 134–137.
- Milner, A.R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology* 25: 635–664.
- Moodie, R.L. 1909. A contribution to a monograph of the extinct Amphibia of North America, New forms from the Carboniferous. *The Journal of Geology* 17: 38–8.
- Moodie, R.L. 1912. The Pennsylvanian Amphibia of the Mazon Creek, Illinois, Shales. University of Kansas.
- Watson, D.M.S. 1940. VII.—The Origin of Frogs. *Transactions of the Royal Society of Edinburgh* 60: 195–231.

Palaeobiogeographic implications of new ornithomimid material from Alberta sharing unexpected characters with non-Canadian taxa

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Ornithomimid dinosaurs are best known from Upper Cretaceous deposits in the western interior of Canada and the United States, and the Gobi of northern China and Mongolia. Two recently named taxa extend the geographic range of definitive ornithomimid occurrences: *Qiupalong henanensis* from central China (Xu et al. 2011), and *Tototlmimus packardensis* from northwestern Mexico (Serrano-Brañas et al. 2016). Here we report on previously undescribed ornithomimid material from the Belly River Group (middle-upper Campanian) of Alberta sharing unexpected characters with these new taxa. These include some characters originally considered autapomorphic, adding new evidence to discussions of ornithomimid palaeobiogeography and systematics. An isolated ornithomimid ankle, *UALVP 53595, from the Dinosaur Park Formation resembles *Q. henanensis* in the presence of a distinct pit at the contact between the astragalus and calcaneum. The partial skeleton **CMN 8902, previously referred to *Struthiomimus altus* (Russell 1972), resembles *Q. henanensis* and differs from other specimens of *Struthiomimus* and other Laramidian ornithomimids in having a very short anterior extension of the pubic boot. Distal caudal vertebrae of CMN 8902 are similar to *Struthiomimus*, lacking derived characters of *Ornithomimus*/*Dromiceiomimus*. The coracoid of CMN 8902 also differs from the holotype of “*D.*” *samuelyi* in having only a shallow depression for the origin of *M. coracobrachialis brevis*, without a vertical crest. An isolated pedal ungual, ***TMP 2011.053.0060, from the lower Oldman Formation resembles *T. packardensis* in possessing very strong asymmetry in dorsal/ventral view, very shallow medial and lateral grooves towards the proximal end, and ventral edges not strongly pinched inwards proximal to the ventral spurs. TMP 2011.053.0006, a pedal phalanx II-2 from the same level, resembles both *Q. henanensis* and *T. packardensis*, but differs from better-known Laramidian ornithomimids in having the ventromedial corner form a distinctly expanded lobe in proximal view. This material suggests that derived ornithomimids evolved high morphological diversity in Laramidia prior to the geographic divergence of endemic lineages. The distinctive shape of the proximal end of the second metatarsal is a potential synapomorphy uniting *Qiupalong* and *Ornithomimus* to the exclusion of other ornithomimids, and *Qiupalong* may have been a Laramidian migrant to Asia rather than a native Asian outgroup to North American ornithomimids. The hypothesis that *Tototlmimus* is more closely related to *Ornithomimus* than to *Struthiomimus* was based on miscoded characters of the pedal unguis. Isolated ornithomimid pedal unguis from the Belly River Group are highly variable, but at least some pedal ungual characters may be morphologically continuous or homoplastic in the observed sample.

*UALVP = University of Alberta Laboratory for Vertebrate Palaeontology; **CMN = Canadian Museum of Nature; ***TMP = Royal Tyrrell Museum of Palaeontology

Literature Cited

Russell, D. A. 1972. Ostrich dinosaurs from the Late Cretaceous of western Canada. *Canadian Journal of Earth Sciences* 9:375–402.

-
- Serrano-Brañas, C.I., E. Torres-Rodríguez, P.C. Reyes-Luna, I. González-Ramírez, and C. González-León. 2016. A new ornithomimid dinosaur from the Upper Cretaceous Packard Shale formation (Cabullona Group) Sonora, México. *Cretaceous Research* 58:49–62.
- Xu, L., Y. Kobayashi, J. Lü, Y.N. Lee, Y. Liu, K. Tanaka, X. Zhang, S. Jia, and J. Zhang. 2011. A new ornithomimid dinosaur with North American affinities from the Late Cretaceous Qiupa Formation in Henan Province of China. *Cretaceous Research* 32:213–222.
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Late Cretaceous fishes of the northern Western Interior Seaway

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In the mid to Late Cretaceous, from the Albian through to the end of the Maastrichtian, the west-central area of North America was variously covered by shallow marine waters, known as the Western Interior Seaway (WIS). At its greatest extent, this seaway stretched all the way from the Gulf of Mexico in the south, to reach the Arctic Ocean in the north. This great expanse of shallow, continental seaway provided habitat for a diverse array of marine organisms, and formed important connections with the Western Tethys (modern Gulf of Mexico area) and the Boreal Sea (Arctic Ocean). A north-western branch of the seaway, named the Hudson Arm, was probably present during at least some of this time, forming a connection to the east and the Eastern Tethys (Mediterranean) region.

Shallow seaways were productive habitats for the evolution of a number of fish taxa. The water depth, expanded coastal areas, and palaeoenvironments provided many niches for smaller fishes to inhabit and in which to diversify. Many ichthyofaunas have previously been reported from the middle area of the WIS (U. S. A.) and a number of new fishes have recently been documented from the southernmost part of the WIS (modern Mexico). However, the more northerly areas have, until recently, been less well documented. New research from the last decade, and still ongoing, is providing much new information on fishes from throughout the Canadian WIS, from southern Alberta and Saskatchewan to the Northwest Territories. We here provide an overview of the ichthyofaunas from the northern Western Interior Seaway of Canada, from the Albian/Cenomanian through to the end of the Maastrichtian.

Potential Lagerstätte-type beds in the Upper Cretaceous of the Salento Peninsula (Apulia, Italy)

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The recovery of an exceptionally well preserved pythonomorph lizard from the Apulian Platform (southern Italy), together with other well-preserved and undescribed vertebrate remains in the collections of the Natural History Museum of Verona from the same deposits, led to an investigation of some interesting but so far understudied fossil localities in southern Italy.

The deposits of interest outcrop on the Salento Peninsula (Apulia) and are Upper Cretaceous in age. They are particularly famous for the abundance of a well-preserved and characteristic ichthyofauna. Other well-preserved vertebrates have been recovered from the same localities, but are still undescribed. The geology of this area has been poorly investigated and the resolution of the geological datum on a regional scale is untrustworthy; the stratigraphic age of these fossil-rich horizons is dated as Campanian-Maastrichtian according to the biostratigraphy (nanoplankton, rudists), or Santonian-Coniacian based on isotopes. In order to improve our knowledge of the geology of the area, we carried out sedimentological studies (facies analysis and composition) intended to identify the most fossiliferous beds.

The new pythonomorph lizard was recovered from a small outcrop outside the town of Nardò (Lecce, Apulia), is the first complete basal pythonomorph (Squamata, Dolichosauridae) from southern Italy, and is particularly important since both mineralized scales and muscles are preserved together with the skeleton. The fossil is extremely important also for stratigraphic and palaeogeographical reasons: it significantly extends the temporal range of dolichosaurs from the Cenomanian-Turonian boundary to possibly the Coniacian-Santonian, or even as young as the Campanian-Maastrichtian. This new specimen fills the palaeogeographical gap in the fossil record of basal pythonomorphs of the Tethyan realm – described material since now was from the Mediterranean of Africa (Lebanon), the Dalmatian Domain (Croatia, Slovenia), and southeast England.

This project aims to understand the stratigraphic relationships and palaeoenvironmental conditions characterizing these vertebrate-rich deposits, very likely with important repercussions on both the palaeogeography and geodynamics of the Mediterranean portion of the Tethys. An improvement in the resolution of the palaeogeographic arrangement of the Apulian Platform during the Upper Cretaceous will also allow better understanding of the radiation and distribution of basal pythonomorphs (e.g., dolichosaurs), which seems to be restricted to the Western Tethys.

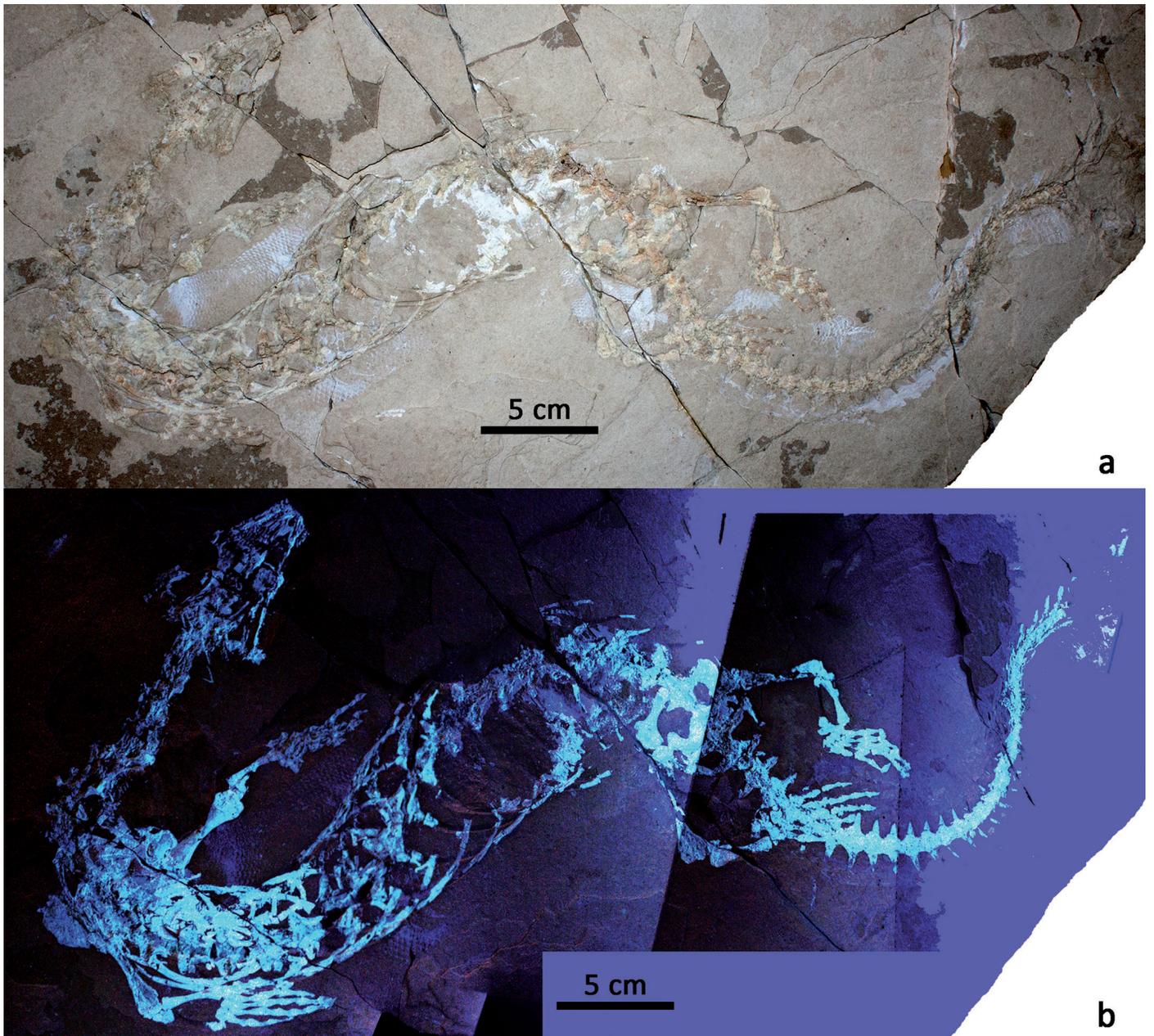


Figure 1. Overview of the new pythonomorph lizard from the Apulian Platform, showing preservation of soft tissues (permineralized scales and muscles). The specimen, housed at the Museum of Paleontology of the University of Rome 'Sapienza' (MPUR NS unnumbered), is figured at both normal light (a) and UV-light (b). When exposed to ultraviolet radiations, the bony elements (cartilage and bone) are emphasized in a bright white colour, while skin and muscles are coloured in different shades of purple (pink to dark pink for the muscles, purple to dark purple for the scales).

A complete description and phylogenetic analysis of *Puijila darwini*, a transitional pinniped

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Whereas the land-to-sea transition is well-documented in many secondarily aquatic mammals, the fossil record of stem pinnipeds is relatively sparse, offering few well-preserved transitional fossils. Due to this paucity of transitional pinniped forms, it remains unclear how such divergent locomotory modes and associated morphologies evolved within pinnipeds. In 2009, Rybczynski et al. reported the discovery of *Puijila darwini*, a putative stem pinniped from the Miocene of Canada's high arctic. A brief description of *Puijila* was complemented with a preliminary phylogenetic analysis that united *Puijila* in a clade with *Enaliarctos* (previously the oldest known stem pinniped), *Potamotherium* (an arctoid of unresolved phylogenetic position) and *Amphicticeps* (a terrestrial carnivoran from the Oligocene of Eurasia). The present study offers a complete description of *Puijila*, and further identifications of new potentially taxonomically informative traits shared by *Puijila* and other proposed stem pinnipeds. Such traits include reduced, lingually-located upper and lower second molars, posteriorly expanded and moderately excavated basioccipitals, presence of a fossa muscularis anteromedially to the enlarged circular infraorbital foramen, presence of a nasolabialis fossa, reduction of the post-glenoid foramen, the presence of a secondary scapular spine, and presence of a sharp keel continuous with an expansive process on the centrum of the axis. A phylogenetic analysis, modified from Rybczynski et al. (2009), aligns additional fossil arctoids, including *Kolponomos*, with the aforementioned group of stem pinnipeds. *Kolponomos* has previously been hypothesized as a possible pinniped ancestor (Tedford 1994). To make inferences on the locomotor habits of *Puijila*, a PCA was performed, following Gingerich (2003), to determine how various linear skeletal measurements interact with body size and ecological variables. PC scores for PC2 (level of aquatic adaptation) and PC3 (preference for forelimb- or hindlimb-powered propulsion) were calculated for *Puijila*, which plots out as well-adapted to aquatic environments (PC2) and as a forelimb-dominated swimmer (PC3).

Literature Cited

- Gingerich, P. D. 2003. Land-to-sea transition in early whales: evolution of Eocene Archaeoceti (Cetacea) in relation to skeletal proportions and locomotion of living semiaquatic mammals. *Paleobiology* 29: 429-454.
- Rybczynski, N., M.R. Dawson, and R.H. Tedford. 2009. A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature* 458:1021-1024.
- Tedford, R.H., L.G. Barnes, and C.E. Ray. 1994. The early Miocene littoral ursoid carnivoran *Kolponomos*: systematics and mode of life. In: *Proceedings of the San Diego Society of Natural History*. 29:11-32.
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Utilizing fossil shark teeth as a biostratigraphical tool to date the Karabogaz Formation in SE Turkey

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Marine fossils were recently collected from the Karabogaz Formation situated on the Arabian Platform, in SE Turkey. The deposit produced abundant invertebrate fragments and fish remains, including numerous shark teeth. Biostratigraphical analysis of recovered nannofossils from the deposit indicates an age range spanning the late Coniacian to late Santonian, a difference of 3 million years. Recovered elasmobranch material included dentition from *Squalicorax lindstromi*, *Pseudocorax* cf. *P. granti*, *Scapanorhynchus* cf. *S. lewisii*, and *Ctenopristis jordanicus*. Herein, we provide a more accurate age determination of the deposit by comparing the morphology of the recovered shark teeth with those retrieved from other well-dated shark assemblages from Europe and North America.

Dental anatomy and skull length to tooth size ratios support the hypothesis that theropod dinosaurs had lips

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Two competing hypotheses, whether the large teeth of theropod dinosaurs were exposed or covered by peri-oral tissues or lips when the mouth was closed, are tested using phylogenetic bracketing, dental anatomy and development, and regression analyses using skull length to tooth size ratios.

Two different anatomical patterns can be discerned in reptiles. In crocodiles, the closest extant, toothed relatives of theropod dinosaurs, about ¼ of the tooth is covered by gingiva, but there are no lips, and the crowns are exposed permanently. In contrast, in extant squamates, a more distant reptilian relative to dinosaurs, teeth are covered by lips when the mouth is closed, and there is extensive gingiva. Phylogenetic bracketing, in the absence of evidence from birds and from fossils would tend to support the hypothesis that the large teeth of theropod dinosaurs would be exposed when the mouth is closed, although there is little reason to suggest that the same was the case for the small teeth of other dinosaurs, like the cheek teeth of ornithischians.

Dental anatomy and development offer a different perspective. As the hardest vertebrate tissue, enamel has a low water content (Zheng et al. 2013), and is hydrated and maintained by glandular secretions in the mouth.

We propose that this requirement of hydration is not possible to maintain if the tooth is exposed permanently. We tested this by examining the exposed teeth of terrestrial mammals (tusks), modified teeth that evolved independently in several mammal clades. Histological thin sections show that tusks in mammals do not have enamel. At the initial stages of development, some enamel may be formed, but soon after eruption the enamel is worn away, and may be replaced by cementum. This suggests that the large teeth of theropod dinosaurs, all known to have well preserved and maintained enamel, even with specialized ziphodonty (Brink et al. 2015), were not exposed permanently, but covered by reptilian lips similar to those found in squamates.

Similarly, ordinary least squares regression analyses of skull lengths to tooth sizes in varanid lizards and theropod dinosaurs of various sizes indicate that the teeth of theropod dinosaurs conform to the same pattern as varanid lizards. This provides strong added support to the hypothesis that theropod dinosaurs had lip-covered teeth, as teeth in theropod dinosaurs are no larger than would be expected in a similarly sized varanid lizard. This conclusion has wider implications, suggesting that this may be the primitive condition for all terrestrial vertebrates, allowing us to test whether the large, tusk-like structures of some basal ornithischians (Weishampel and Witmer 1990), or the large canine-like teeth of terrestrial vertebrates (Brink et al. 2015) were exposed or not.

Finally, we propose that the lip-covered dental pattern is primitive for terrestrial vertebrates, and that of crocodylians is a derived condition related to their secondary aquatic or semiaquatic adaptations. It should be noted that terrestrial stem crocodylians (Clark et al. 2001) have a dental anatomy very similar to that of theropod dinosaurs, and likely had lips too.

Literature cited

- Brink, K.S., R.R. Reisz, A.R.H. LeBlanc, R.S. Chang, Y.C. Lee, C.C. Chiang, T. Huang, and D.C. Evans. 2015. Developmental and evolutionary novelty in the serrated teeth of theropod dinosaurs. *Scientific reports*, 5.
- Brink, K. S., H. C. Maddin, D. C. Evans, R. R. Reisz. 2015. Re-evaluation of the historic Canadian fossil *Bathynathus borealis* from the Early Permian of Prince Edward Island. *Canadian Journal of Earth Sciences*, 52(12): 1109-1120.
- Clark JM, HD, Sues, DS Berman. 2001. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. *Journal of Vertebrate Paleontology*. 20(4):683-704.
- Weishampel, D. B., L. M. Witmer.1990. "Heterodontosauridae". In Weishampel, D. B.; Dodson, P; Osmólska, Halszka. *The Dinosauria*. Berkeley: University of California Press. pp. 486–497. ISBN 0-520-06727-4.
- Zheng, J., L.Q. Weng, M.Y. Shi, J. Zhou, L.C. Hua, L.M. Qian, and Z.R. Zhou. 2013. Effect of water content on the nano-mechanical properties and microtribological behaviour of human tooth enamel. *Wear*, 301(1):316-323.
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Long bone histology of *Smilodon fatalis* (Carnivora: Felidae) from Talara, Peru

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Palaeohistology can reveal important aspects of the growth and life history of extinct organisms (Cooper et al. 2008; Köhler and Moyà-Solà 2009; Lee et al. 2013; Martinez-Maza et al. 2014; Kolb et al. 2015a). However, most studies have focused on dinosaurs; comparatively less research has been conducted on fossil mammals, and most studies have been conducted on herbivorous species (Kolb, 2015b). The palaeohistology of carnivorans is virtually unknown. While typically carnivores are rare in the fossil record, they can be found in abundance in tar seep deposits, which appear to have functioned as carnivore traps. Here, we describe the histology of *Smilodon fatalis* limb bones from the South American Talara locality (Pleistocene; Peru).

Transverse, diaphyseal sections were taken of a femur, humerus, and tibia. Prior to sectioning, age classes were assigned based on degree of epiphyseal fusion. The primary bone tissue of the femur, which is from either a sub-adult or small adult, appears to be a fibrolamellar complex consisting primarily of woven-fibred bone inset with primary osteons. The vascularity is largely longitudinal with some anastomosing canals, although some circumferential vascular canals can be seen towards the outer cortex on the posteromedial side. The inner and outer cortices are composed of lamellar bone. Although interrupted at times by secondary osteons, which can be found scattered throughout the cortex, at least six lines of arrested growth (LAGs) can be seen in the outer cortex as well as one possible annulus. The large nutrient canal is observed about halfway through the cortex on the posterior side, with a thin area of lamellar bone skirting it on its posterior edge. The tibia, likely from an adult, shows extensive secondary remodelling throughout the cortex and well-developed inner circumferential layers. Secondary osteons have obliterated most of the primary tissue, but lamellar bone is present on the periosteal margin on the anterolateral side of the bone. Several LAGs can be seen on this anterolateral edge. The adult humerus, much like the tibia, is also heavily remodelled. This remodelling extends through the outer cortex in some regions, but lamellar bone occurs along much of the outer circumference, along with several LAGs. Inner circumferential layers are present and some exhibit secondary remodelling. The nutrient canal is again observed on the posterior side of the cortex.

This study represents the first multi-element histological analysis of a fossil felid. The majority of the primary bone tissue, at least in the femur, is fibrolamellar with longitudinal vascular canals. The inner circumferential layer is well-developed in all samples and lamellar bone with LAGs is preserved in the outer cortex. Extensive secondary remodelling is not necessarily surprising in adult individuals, as extant large felids are relatively long-lived species. Results suggest that the histology of *S. fatalis* is well-suited to further more detailed analyses of growth and life history.

Literature Cited

- Cooper, L. N., A. H. Lee, M. L. Taper, and J. R. Horner. 2008. Relative growth rates of predator and prey dinosaurs reflect effects of predation. *Proceedings of the Royal Society B: Biological Sciences* 275:2609–2615.
- Köhler, M., and S. Moyà-Solà. 2009. Physiological and life history strategies of a fossil large mammal in a resource-limited environment. *Proceedings of the National Academy of Sciences of the United States of America* 106:20354–20358.
- Kolb, C., T. M. Scheyer, A. M. Lister, C. Azorit, J. de Vos, M. Schlingemann, G. E. Rössner, N. T. Monaghan, and M. R. Sánchez-Villagra. 2015a. Growth in fossil and extant deer and implications for body size and life history evolution. *BMC Evolutionary Biology* 15:19.
- Kolb, C., T. M. Scheyer, K. Veitschegger, A. M. Forasiepi, E. Amson, A. Van Der Geer, and L. W. Van Den. 2015b. Mammalian bone palaeohistology: new data and a survey. *PeerJ* 3:e1358.

Lee, A.H., A. K. Huttenlocker, K. Padian, and H.N. Woodward. 2013. Analysis of growth rates. Pp. 217-251 in K. Padian and E.-T. Lamm (eds). *Bone Histology of Fossil Tetrapods: Advancing Methods, Analysis, and Interpretation*. Berkeley, California: University of California Press.

Martinez-Maza, C., M. T. Alberdi, M. Nieto-Diaz, and J. L. Prado. 2014. Life-history traits of the Miocene *Hipparion concudense* (Spain) inferred from bone histological structure. *PloS ONE* 9:e103708.

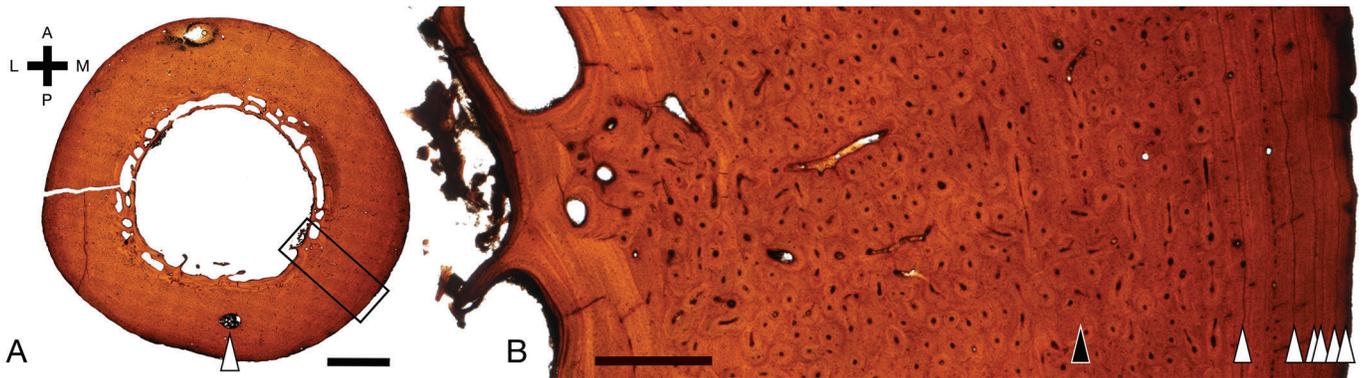


Figure 1. Bone histology of *Smilodon fatalis*. (A) Femur thin section with nutrient canal indicated by an arrow. Scale bar is 5 mm. (B) Posteromedial portion of this femur. Six LAGs are indicated with white arrows and a possible annulus is indicated with a black arrow. Scale bar is 1 mm.

The origin of feathers and avian flight, as seen in the Mesozoic record of northeast China

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Exceptionally preserved fossils from the Mesozoic of northeast China began to revolutionize scientific understanding of the origin of flight in the mid-1990s. The first wave of key discoveries came from the Early Cretaceous Jehol Biota (Zhou et al. 2003), but more recently specimens of comparable significance have also begun emerging from the Mid-Late Jurassic Yanliao (or Daohugou) Biota in the same region (Sullivan et al. 2014). Early discoveries from the Jehol Biota revealed that some non-avian theropods rather distant from birds, including compsognathids (Chen et al. 1998) and therizinosaurids (Xu et al. 1999), had filamentous feathers superficially more like mammalian hairs than the pennaceous flight feathers of modern birds. While unsuitable for flight, they could have provided insulation, and in some cases were colourful enough to have had a visual display function (Zhang et al. 2010). Filamentous feathers may have been ubiquitous among typical coelurosaurian theropods, and were even present in at least one very large (~1400 kg) tyrannosauroid (Xu et al. 2012). However, pennaceous feathers are restricted to the clade Pennaraptora, which includes the clearly flightless Oviraptorosauria. The function of the pennaceous feathers seen on the forelimbs and tails of basal Jehol oviraptorosaurs such as *Caudipteryx* is an enigma in the study of flight origins, with the main possibilities being display, brooding and production of small aerodynamic forces to aid terrestrial manoeuvrability.

Volancy (flapping flight and/or gliding) may have had a single origin near the base of Paraves, the clade containing birds and deinonychosaurs. However, recently discovered specimens from the Jehol and Yanliao Biotas suggest that the emergence of avian flight must have involved high levels of homoplasy and morphological experimentation. Many early birds and deinonychosaurs had large pennaceous feathers on their hindlimbs as well as their forelimbs, but the interpretation of these apparent hindwings is controversial. They may indicate that a four-winged, “tetrapterygian” mode of flight was the ancestral, transitory paravian condition (Zheng et al. 2013), but caution is warranted. Pennaceous hindlimb feathers occur in many extant birds without forming aerodynamic surfaces, and most fossil “hindwings” may actually represent feathers with other functions such as ornamentation (O’Connor and Chang 2015). Furthermore, mapping the likely distribution of aerodynamic forewings and hindwings onto current paravian cladograms, even with relatively generous assumptions, suggests that tetrapterygian locomotion probably appeared separately in multiple paravians.

Another striking example of short-lived morphological novelty is provided by *Yi*, a member of the enigmatic paravian or near-paravian clade Scansoriopterygidae. Although typical pennaceous feathers are lacking in scansoriopterygids, *Yi* appears to have moved through the air on a unique membranous wing supported by a rod-like bone extending from the wrist and an elongated outer manual digit (Xu et al. 2015). The similar hand proportions of the scansoriopterygid *Epidendrosaurus* (Zhang et al. 2002) hint that other scansoriopterygids perhaps shared this mode of volancy. The transition to birds clearly took place in the context of a rapid diversification of structures related to aerial locomotion, only a subset of which survived to be incorporated into the derived avian flight apparatus.

Literature Cited

- Chen, P.-J., Z.-M. Dong, and S.-N. Zhen. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* 391:147–152.
- O’Connor, J. K. and H. Chang. 2015. Hindlimb feathers in paravians: primarily “wings” or ornaments? *Biology Bulletin* 42:616–621.

- Sullivan, C., Y. Wang, D. W. E. Hone, Y. Wang, X. Xu, and F. Zhang. 2014. The vertebrates of the Jurassic Daohugou Biota of northeastern China. *Journal of Vertebrate Paleontology* 34:243–280.
- Xu, X., Z.-L. Tang, and X.-L. Wang. 1999. A therizinosauroid dinosaur with integumentary structures from China. *Nature* 399:350–354.
- Xu, X., K. Wang, K. Zhang, Q. Ma, L. Xing, C. Sullivan, D. Hu, S. Cheng, and S. Wang. 2012. A gigantic feathered dinosaur from the Lower Cretaceous of China. *Nature* 484:92–95.
- Xu, X., X. Zheng, C. Sullivan, X. Wang, L. Xing, Y. Wang, X. Zhang, J. K. O'Connor, F. Zhang, and Y. Pan. 2015. A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. *Nature* 521:70–73.
- Zhang, F., Z. Zhou, X. Xu, and X. Wang. 2002. A juvenile coelurosaurian theropod from China indicates arboreal habits. *Naturwissenschaften* 89:394–398.
- Zhang, F., S. L. Kearns, P. J. Orr, M. J. Benton, Z. Zhou, D. Johnson, X. Xu, and X. Wang. 2010. Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds. *Nature* 463:1075–1078.
- Zheng, X., Z. Zhou, X. Wang, F. Zhang, X. Zhang, Y. Wang, G. Wei, S. Wang, and X. Xu. 2013. Hind wings in basal birds and the evolution of leg feathers. *Science* 339:1309–1312.
- Zhou, Z., P. M. Barrett, and J. Hilton. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421:807–814.
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A saurolophine hadrosaur skeleton from the Foremost Formation of Southern Alberta and the origin of South American hadrosaurs.

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The Campanian Belly River Group (BRG) of Alberta is comprised of, in ascending order, the Foremost (FF), Oldman (OF), and Dinosaur Park (DPF) formations. The upper two units are composed of terrestrially derived sediments, and both, but especially the DPF, are known for having rich dinosaur faunas and spectacular abundances of vertebrate fossil remains (Mallon et al. 2012). The fauna of the FF is comparatively poorly known with only two taxa — the centrosaurine ceratopsid, *Xenoceratops foremostensis* (Ryan et al. 2012), and the pachycephalosaurid, *Colepiocephale lambei* (Schott et al. 2011) — being recognized from skeletal material not derived from vertebrate microfossil localities.

The FF comprises mostly marine sediments deposited during the transgression of the Claggett cycle, but is transitional between the underlying fully marine shales of the Pakowki Formation and the overlying fully non-marine OF (Eberth and Hamblin 1993). The FF is bounded below and above by the Mackay Coal and Taber Coal zones, respectively, and can be up to 83 m thick. The upper portion, including the 10–30 m of outcrop, exposes a near-shore terrestrial sequence that is capped by the Herronton sandstone (generally considered to mark the lowermost portion of the OF) (Eberth and Hamblin 1993). The FF is thus important for preserving the first terrestrial

faunas of the BRG, and the vertebrate material recovered from it will have important implications for understanding the evolutionary dynamics of the Late Cretaceous dinosaur fauna in Laramidia.

To date, several undescribed partial Hadrosauridae indet. skeletons have been collected from the FF. *WL 139 was collected by Wann Langston, Jr. in 1957 from near the village of Foremost and includes an associated ilium, pubis, and both ischia from one individual, and the hind foot of another individual. WL 139 can be identified as saurolophine (= hadrosaurine sensu Forster 1997) based on the long, narrow neck of the prepubic process of the pubis, a supra-acetabular process of the ilium with sub-rectangular lateral profile and relatively shallow ventral projection, and the lack of a terminal “boot” process of the ischial shaft (commonly seen in lambeosaurines). WL 139 is the oldest saurolophine identified from Canada based on the approximate age range of 80.5 Ma to 78 Ma (Freedman-Fowler and Horner 2015). This referral is supported by phylogenetic analyses based on the data sets of Wu and Godefroit (2012) and Prieto-Marquez et al. (2016) that recovers it as a derived hadrosauroid in a polytomous clade otherwise composed of hadrosaurids, or a saurolophine in the clade (Big Bend **UTEP 37+(WL 139+(*Secernosaurus*+*Willinaquake*))), respectively. This latter phylogenetic hypothesis indicates that WL 139 is the outgroup to the South American clade *Secernosaurus*+*Willinaquake*. This suggests that WL 139 is linked to the inferred dispersal event that also involved the Big Bend UTEP 37 OTU from the Aguja Formation of Big Bend National Park, Texas, that brought hadrosaurs, specifically of the clade Kritosaurini, to South America during the Campanian.

*WL = Wann Langston field numbers; housed in the Canadian Museum of Nature

**UTEP = University of Texas, El Paso; housed in the Texas Memorial Museum, Austin, Texas

Literature Cited

- Eberth, D.A., and A.P. Hamblin. 1993. Tectonic, stratigraphic, and sedimentological significance of a regional discontinuity in the upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. *Canadian Journal of Earth Sciences* 30:174-200.
- Freedman-Fowler, E.A., and J.R. Horner. 2015. A new brachylophosaurine hadrosaur (Dinosauria: Ornithischia) with an intermediate nasal crest from the Campanian Judith River Formation of northcentral Montana PLoS ONE 10:e0141304.
- Forster, C.A. 1997. Phylogeny of the Iguanodontia and Hadrosauridae. *Journal of Vertebrate Paleontology* 17 (Supplement to 3):47A.
- Mallon, J.C., D.C., Evans, M.J. Ryan, and J.S. Anderson. 2012. Megaherbivorous dinosaur turnover in the Dinosaur Park Formation (upper Campanian) of Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 350-352:124-138.
- Prieto-Marquez, A., M.E. Gregory, and J.A. Ebersole. 2016. A primitive hadrosaurid from southeastern North America and the origin and early evolution of ‘duck-billed’ dinosaurs. *Journal of Vertebrate Paleontology* 36:e1054495.
- Ryan, M.J., D.C. Evans, and K.M. Shepherd. 2012. A new ceratopsid from the Foremost Formation (middle Campanian) of Alberta. *Canadian Journal of Earth Sciences* 49:1251-1262.
- Schott, R.K., D.C. Evans, T.E. Williamson, T.D. Carr, and M.B. Goodwin. 2009. The Anatomy and systematics of *Colepiocephale lambei* (Dinosauria: Pachycephalosauridae). *Journal of Vertebrate Paleontology* 29:771-786.
- Wu, W., and P. Godefroit. 2012. Anatomy and relationships of *Bolong yixianensis*, an Early Cretaceous iguanodontid dinosaur from western Liaoning, China. *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*: 292-333.

The Cypress Hills Formation (late Eocene-Miocene), Saskatchewan: the non-mammal contingent and least cataloguable units

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Some of the earliest discoveries of vertebrate fossils in western Canada were of Paleogene mammals from the Cypress Hills region of Saskatchewan, from what is now known as the Cypress Hills Formation. Since the discovery of these primarily mammalian assemblages, collections of Cypress Hills Formation fossils have grown almost exponentially. Despite these vast collections, the palaeofauna of the Cypress Hills Formation was for decades considered to be comprised of a single biostratigraphic unit from the early Oligocene. John Storer, then with the Royal Saskatchewan Museum, was the first to recognize that many of the fossil assemblages within the Cypress Hills Formation represented distinct 'local faunas'. Storer went on to describe at least eleven 'local faunas' from the Cypress Hills Formation, covering a time period from the late Eocene to the Miocene. He emphasized the importance of considering Cypress Hills Formation assemblages locality by locality, particularly when it came to biochronology and biostratigraphy. Storer's 'local faunas' were defined solely on the mammalian contingent of the Cypress Hills Formation assemblages, and their correlation to other mammal faunas in the Great Plains Basin. Most of the historic work in the Cypress Hills Formation focused almost exclusively on mammals, but the significant collections of non-mammalian material is currently being studied at the Royal Saskatchewan Museum. The non-mammalian contingent of the assemblages, particularly the herpetological component, may hold critical information about the Eocene-Oligocene Transition in Canada that has not been previously recognized.

The Cypress Hills Formation faunas are critical in understanding the impact of climate change on biological systems near the end of the Eocene and into the early Oligocene, a period known as the Eocene-Oligocene Transition. Despite the significant advances that have been made in the past, there is still much work to be done in the Cypress Hills Formation. Future research can be divided up into three steps: First, to complete the processing and documentation of the non-mammal faunas throughout the Cypress Hills Formation. Second, to review previously catalogued fossil collections with an eye to establishing the Least Cataloguable Unit (LCU). The LCU is the smallest vertebrate element to be catalogued (i.e., a single tooth). Establishing a LCU can ensure uniformity when creating a referable collection of all fossils in an open database. Thirdly, to create a 'Cypress Hills Formation Working Group', involving researchers from multiple interested research institutions who, in conjunction with the Royal Saskatchewan Museum, can help to elucidate the vital importance the Cypress Hills Formation faunas play in the palaeohistory of the great plains of North America.



Figure 1. A crew from the Royal Saskatchewan Museum and Royal Ontario Museum processing microvertebrate material from the Cypress Hills Hunter Quarry, circa 1960.

The elusive ichthyosaurs of Saskatchewan

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The Campanian-early Maastrichtian Bearpaw Formation of Saskatchewan contains a wide diversity of marine reptiles from the Elasmosauridae (long-necked plesiosaurs), Polycotyliidae (short-necked plesiosaurs) and Mosasauridae families. Ichthyosaurs, the ‘fish-like’ marine reptiles, are notably absent from Saskatchewan’s fossil record, with the exception of a few enigmatic reports spread out over a century. The first report of ichthyosaur fossils from Saskatchewan dates back to the early 20th century, when local lore spoke of a giant ichthyosaur in southeastern Saskatchewan (King 1967). The specimen, if it existed, was never collected or figured, and these reports were never substantiated. There are modern-day reports of an ichthyosaur fossil in southeastern Saskatchewan, near Pinto. However, judging by photos posted of the ‘specimen’ online, it is almost certainly an ichthyosaur-shaped glacial erratic. In 1973, Christopher McGowan from the Royal Ontario Museum described a partial ichthyosaur coracoid from the upper Campanian Bearpaw Formation near Stewart Valley, SK, calling it the most recent ichthyosaur ever discovered (McGowan 1973). However, this specimen was re-identified as belonging to a plesiosaur in 1984 (Baird 1984). An articulated ichthyosaur skull was also discovered in a Saskatchewan art gallery’s collection (Fig. 1). However, the accompanying Wards label suggests the specimen came from the Jurassic of England.

Perhaps the most intriguing, and likely the most legitimate, ichthyosaur fossil from Saskatchewan came from a mine near Esterhazy in southeastern Saskatchewan. The specimen, an isolated rostra with teeth, was collected in the 1960s (no earlier than 1963) and is currently curated at the Canadian Museum of Nature. Corroborative materials from the locality suggest the specimen originated from the Ashville Formation (Cenomanian), a marine unit that paleogeographically places it in central – eastern edges of the Western Interior Seaway. This is a time period when ichthyosaurs were still present and diverse in North America (Fischer et al. 2016). The Esterhazy specimen is somewhat problematical in that nearly all the known Ashville sediments in Saskatchewan, including those that produced the hesperornithiform *Pasquiaornis*, contain rich and diverse vertebrate faunas, and yet have not produced any other ichthyosaur material. Could this be the result of a preservation artifact or an identification bias (i.e. have we been identifying ichthyosaur teeth as plesiosaur)? Or is this a paleogeographic disparity between the Esterhazy specimen and that of the more northern deposits? More research, and possibly a shifting search image when collecting and cataloguing, is needed to solve this enigma.

Literature Cited

- Baird, D. 1984. No ichthyosaurs in the Upper Cretaceous of New Jersey. . . or Saskatchewan. *The Mosasaur* 2:129-133.
- Fischer, V., N. Bardet, R.B.J. Benson, M.S. Arkhangelsky, and M. Friedman. 2016. Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. *Nature Communications* 7:10825.
- King, A. 1967. *Estavan – the Power Center*. Modern Press, Saskatoon, 203 pages.
- McGowan, C. 1973. A note on the most recent ichthyosaur known: an isolated coracoid from the Upper Campanian of Saskatchewan (Reptilia, Ichthyosauria). *Canadian Journal of Earth Sciences* 10:1346-1349.



Figure 1. An articulated ichthyosaur skull discovered in a Saskatchewan art gallery's collections. The specimen almost certainly comes from the Jurassic of England.

Modelling the effects of continental fragmentation on terrestrial vertebrate biodiversity through the Mesozoic

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Terrestrial regions went through a dramatic reorganization in the Mesozoic (252 to 66 million years ago [mya]), with major shifts in continental position, size, and connectivity. During the Triassic (252 to 201 mya), most of the terrestrial regions on Earth were joined into a single supercontinent called Pangaea. However, through the Jurassic (201 to 145 mya) and Cretaceous (145 to 66 mya), terrestrial regions had fragmented until, during the Late Cretaceous, total terrestrial area was both smaller as well as more disconnected than at any other time since the colonization of land by vertebrates. This reduction in land area and increase in fragmentation was primarily driven by two somewhat interrelated factors, namely the rifting apart of Pangaea via plate tectonism and the flooding of inland areas due to the rising eustatic sea level. While area is a strong predictor of biodiversity in modern terrestrial ecosystems, how terrestrial vertebrate biodiversity was affected by this fragmentation and large scale flooding of the earth's landmasses is uncertain. Using estimates of the inter-provincial Species-Area Relationship derived from modern surveys, and combined with georeferenced palaeo-coastline maps, terrestrial vertebrate biodiversity can be modelled through this interval. During the Mesozoic, terrestrial vertebrate biodiversity would be expected to nearly double due to continental fragmentation, despite a large decrease in total terrestrial area. Previous studies of terrestrial Mesozoic vertebrates have generally found increases in diversity towards the end of the era, though these increases are often attributed to intrinsic or climatic factors. Instead, continental fragmentation over this time may largely explain any observed increase in terrestrial biodiversity, and in contrast to the trend predicted by geographic area alone. This study demonstrates the importance that non-intrinsic effects can have on the taxonomic success of a group, and the importance of geography to understanding past biodiversity.

Diversity of the scute armour in the Ellimmichthyiformes (Teleostei: Clupeomorpha) with implications for the phylogeny reconstruction

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In clupeomorphs (herrings and allies), scutes are modified scales that form a keel along the ventral and/or dorsal margins of the body. Presence of at least one abdominal scute is regarded as a diagnostic character of the Clupeomorpha. Among the extant members of the order Clupeiformes, scute armour is mostly limited to the abdominal series, and predorsal scutes are present only in few species of the genera *Nematalosa*, *Hyperlophus*, *Ethmidium*, and *Clupanodon*. The fossil clupeomorphs of the order Ellimmichthyiformes, on the other hand, show a high degree of the scute armour development. These fishes are often referred to as ‘double-armored’ herrings for the presence of the dorsal series of scutes in addition to the abdominal scutes. These structures can have a very complex form with surface sculpturing as well as marginal spines and projections.

The most common condition among ellimmichthyiforms is the presence of a complete series of predorsal scutes from the occiput to the origin of the dorsal fin; however, there are modifications to this condition. In *Armigatus*, the predorsal series is incomplete, leaving an unscuted gap posterior to the back of the skull, and in *Triplomystus* the dorsal scute series continues behind the dorsal fin forming a postdorsal series of scutes that is unique to the members of this genus.

Ellimmichthyiforms also show variation in the dorsal scute shape, from subrectangular and subrhomboid to heart-shaped and ovoid. Moreover, recently described Early Cretaceous ellimmichthyiforms that lack dorsal scutes suggest even greater diversity of the scute armour within the Ellimmichthyiformes. Despite this variation, only presence or absence of subrectangular scutes has been used as a character in phylogenetic analyses; therefore, the need for the revision of this character has become apparent.

Herein, we present a revised phylogeny of the Ellimmichthyiformes with optimized character coding and newly added characters to better reflect the diversity of the scute armour in clupeomorph fishes. We also expand our analysis by adding newly described species as well as those fossil clupeomorph taxa that have not yet been included in the cladistic analysis.

The updated phylogenetic hypothesis reveals high degree of variation in the scute armour development within the early diverging lineages of both ellimmichthyiforms and clupeiforms. This suggests that the loss of the dorsal scutes has evolved multiple times within the Clupeomorpha and should not be regarded as a derived characteristic exclusive to the recent clupeiforms. Our findings raise questions of the possible causes and mechanisms underlying the disparity of the scute armour development between the later clupeiform and ellimmichthyiform lineages.

Examining the form of the plesiosaur caudal fin using the osteology of caudal fins and flukes in fossil and extant tetrapods

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Over the course of vertebrate evolutionary history, a number of groups have transitioned from a terrestrial lifestyle back to an aquatic or marine one. This transition is accompanied by a suite of anatomical changes, often including the development of a horizontal caudal fluke or vertical caudal fin. Among extant tetrapods, flukes are present in cetaceans and sirenians, while a vertical fin can be found in the sail-fin lizards of the genus *Hydrosaurus*. In fossil taxa, soft tissue and skeletal evidence indicates the presence of a caudal fin in ichthyosaurs, mosasaurs, and thalattosuchians. In plesiosaurs, the only possible soft-tissue evidence is no longer examinable due to further preparation of the specimen after its original description. Osteological evidence from a number of genera supports the presence of a caudal fin in this group. Here, the osteology of these extant and fossil taxa was examined in order to determine what features are correlated with the presence of a caudal fin or fluke. These features include changes in neural spine direction, increases in neural spine or transverse process length, reduction of zygapophyses, and ventral bending of the tail. The tail fin in plesiosaurs was examined by looking for these osteological correlates in specimens of plesiosaurs with complete or near complete caudal regions. These comparisons suggest the presence of a caudal fin in multiple clades of plesiosaurs and can help reconstruct the shape of this structure in the absence of soft-tissue evidence.

First occurrence of a nestling-sized *Edmontosaurus* skeleton (Ornithischia: Hadrosauridae) from the Hell Creek Formation (Maastrichtian), Montana, U.S.A.

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A recent fossil census of the Upper Cretaceous Hell Creek Formation (Maastrichtian) of northeastern Montana suggested that the horned dinosaur *Triceratops* was the most common dinosaur skeleton from this well-sampled unit, and *Tyrannosaurus* was equally as common as the duck-billed *Edmontosaurus* (Horner et al. 2011). Juveniles of all taxa are surprisingly rare, with only *Triceratops* known from multiple specimens spanning a wide ontogenetic range (Horner and Goodwin 2006). The hadrosaurid *Edmontosaurus* from the Hell Creek Formation is known primarily from specimens representing later ontogenetic stages (Campione and Evans 2011) with only one recognized juvenile specimen, *LACM 23504 (Prieto-Márquez 2014). This specimen is the smallest and presumably youngest described ontogimorph of *Edmontosaurus* with a femur length of 567 mm, approximately 40% of adult size (Prieto-Márquez 2014).

Here we describe a very small (~50 cm body length) articulated hadrosaurid skeleton, **UCMP 128181, discovered by Harley Garbani in Garfield County, Montana. It represents the earliest ontogenetic growth stage of *Edmontosaurus* and is recognized as a large nestling based, in part, on a femur length of 148 mm. This specimen preserves a partial scapula, rib cage, vertebral series from the shoulder to mid-tail, a large portion of the pelvic girdle, and both hind limbs through a combination of bone and/or natural impressions in the concretion. The prepubic process of the pubis is shallow with a relatively long proximal constriction of the pubic blade and a paddle-like subellipsoidal anterior end that expands more ventrally than dorsally. This supports our taxonomic assignment of UCMP 128181 to *Edmontosaurus* (Prieto-Márquez 2014). Although none of the autapomorphies of *E. annectens* are present due to the lack of cranial material, we refer the specimen to this taxon because it is the only *Edmontosaurus* species known from the Hell Creek Formation despite over a century of intense collecting (Campione and Evans 2011; Horner et al. 2011; Prieto-Márquez 2014). Across an ontogenetic perspective (UCMP 128181 – LACM 23504 – ***AMNH 5730), the proportions of the major hind limb elements remain isometrically conservative in this taxon.

Based on comparisons with other hadrosaurid taxa, UCMP 128181 is assignable to the Late Nestling stage (Horner et al. 2000). This is the first occurrence of a baby dinosaur skeleton from the Hell Creek Formation and greatly expands the known ontogenetic spectrum for *Edmontosaurus*.

*LACM = Los Angeles County Museum; **UCMP = University of California Museum of Paleontology;
***AMNH = American Museum of Natural History

Literature Cited

- Campione, N.E. and D.C. Evans. 2011. Cranial growth and variation in edmontosaurs (Dinosauria: Hadrosauridae): Implications for latest Cretaceous megaherbivore diversity in North America. PLoS ONE 6:e25186.
- Horner, J.R., A. de Ricqlès, and K. Padian. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: Growth dynamics and physiology based on an ontogenetic series of skeletal elements. Journal of Vertebrate Paleontology 20:115-129.
- Horner, J.R. and M.B. Goodwin. 2006. Major cranial changes during *Triceratops* ontogeny. Proceedings of the Royal Society B 273:2757-2761.
- Horner, J.R., M.B. Goodwin, and N. Myhrvold. 2011. Dinosaur census reveals abundant *Tyrannosaurus* and rare ontogenetic stages in the Upper Cretaceous Hell Creek Formation (Maastrichtian), Montana, USA. PLoS ONE 6:e16574.
- Prieto-Márquez, A. 2014. A juvenile *Edmontosaurus* from the late Maastrichtian (Cretaceous) of North America: Implications for ontogeny and phylogenetic inference in saurolophine dinosaurs. Cretaceous Research 50:282-303.