

A review of dinosaur body fossils from British Columbia, Canada

Since the 1900s, dinosaur fossils have been discovered from Jurassic to Cretaceous age strata, from all across the prairie provinces of Canada and the Western United States, yet little material is known from the outer provinces and territories. In British Columbia, fossils have long been uncovered from the prevalent mid-Cambrian Burgess Shale, but few deposits date from the Mesozoic, and few of these are dinosaurian. The purpose of this paper is to review the history of dinosaurian body fossils in British Columbia. The following dinosaur groups are represented: ankylosaurians, hadrosaurids, pachycephalosaurids, ornithomimosaurians, dromaeosaurids and tyrannosaurids.

A review of dinosaur body fossils from British Columbia, Canada

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Abstract Since the 1900s, dinosaur fossils have been discovered from Jurassic to Cretaceous age strata, from all across the prairie provinces of Canada and the Western United States, yet little material is known from the outer provinces and territories. In British Columbia, fossils have long been uncovered from the prevalent mid-Cambrian Burgess Shale, but few deposits date from the Mesozoic, and few of these are dinosaurian. The purpose of this paper is to review the history of dinosaurian body fossils in British Columbia. The following dinosaur groups are represented: ankylosaurians, hadrosaurids, pachycephalosaurids, ornithomimosaurians, dromaeosaurids and tyrannosaurids.

Introduction

The first fossil excavations from British Columbia, Canada, were begun in 1909, when Charles Doolittle Walcott uncovered a deposit near the town of Field (Gould, 1989). This deposit, of Cambrian fauna, is located at Yoho National Park within the Canadian Rocky Mountain Parks, and was designated as a World Heritage Site in 1984 (Morris & Whittington, 1985). Though the Burgess Shale preserves many fossils of extinct organisms, the deposit predates dinosaurs by more than a quarter of a billion years, at about 508 million years old (Butterfield, 2006).

In British Columbia, there are many formations during the Mesozoic, nearly all of which preserve dinosaurian traces, such as footprints, with a few also preserving pterosaurian traces (McCrea et al., 2014). However, dinosaur bones were unheard of in British Columbia until 1971, when bones, including part of an arm and a leg from a derived ornithischian, were discovered in the north of the province (Arbour & Graves, 2008). However, dinosaur bones remained exceptionally rare until the early 2000s, when large deposits near the town of Tumbler Ridge were discovered (Arbour & Graves, 2008). Most recently, a nearly complete hadrosaur was discovered in the Tumbler Ridge deposits, which marks the most complete find in the province. Along with the hadrosaur are also the first potential tyrannosaur and dromeosaur teeth (IJR, pers. obs.).

This is different from other western regions of North America, especially Alberta, where many hundreds or thousands of specimens have been discovered in Jurassic and Cretaceous deposits, with only minimal track or other trace fossils.

The map illustrating the distribution of currently known dinosaur fossils in British Columbia (Figure 1) is based on https://commons.wikimedia.org/wiki/File:Canada_British_Columbia_location_map_2.svg by "Hanhil", which has a CC-BY-SA 3.0 license.

Institutional abbreviations: **RBCM**, Royal British Columbia Museum, Victoria, Vancouver Island, British Columbia, Canada; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **PRPRC**, Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia, Canada; **CM**, Courtenay Museum, Courtenay, Vancouver Island, British Columbia; **QBM**, Qualicum Beach Museum, Qualicum Beach, Vancouver Island, British Columbia.

RESULTS

Systematic Palaeontology

Clade Dinosauria (Owen, 1842)
 Order Ornithischia (Seeley, 1888)
 Clade Genasauria (Sereno, 1986)
 Clade Thyreophora (Nopcsa, 1915)
 Suborder Ankylosauria (Osborn, 1923)
 Ankylosauria *indet.* (McCrea & Buckley, 2004)

Material: PRPRC collections, a single ankylosaurian scute.

Location: Quality Creek canyon, Kaskapau Formation, Tumbler Ridge, British Columbia (~90 mya; Fig. 1a).

Discussion: Based on the presence of a single scute clearly from an ankylosaurian, there was at least one taxon of ankylosaurian present in the Tumbler Ridge area of northeastern B.C. (McCrea & Buckley, 2004).

As only a single scute is known, not much anatomical information can be identified beyond an ankylosaurian identity. Thus, while being noted in McCrea & Buckley (2004), it is unlikely any following publications will be made regarding this scute. However, based on the location and age of this scute, is it possible it belongs to a nodosaurid, as ankylosaurids were only present much later in nearby Alberta.

Clade Cerapoda (Sereno, 1986)
 Suborder Ornithopoda (Marsh, 1881)
 Family Hadrosauridae (Cope, 1869)
 Hadrosauridae *indet.* (McCrea & Buckley, 2004)

Material: PRPRC collections, an incomplete, mostly disarticulated skeleton comprising of five dorsal vertebrae, four ribs, a pedal phalanx, a fibula, an ischium and ossified tendons (Fig 2).

Location: Quality Creek canyon, Kaskapau Formation, Tumbler Ridge, British Columbia (~90 mya; Fig. 1a).

Discussion: While disarticulated, and spread throughout several blocks, the material of an ornithopod is relatively complete compared to other fossils found in the deposit. The phalanx was not specified to a limb by McCrea & Buckley (2004), but the presence of a nearby fibula would make it likely it was from the pes. In addition, the possible pelvic bone (McCrea & Buckley, 2004, fig. 5a), corresponds strongly with the ischium of other ornithischians. Among other features, the age and presence of ossified tendons point

strongly towards a hadrosaurid identity for the taxon, along with the presence of another highly complete hadrosaurid specimen in the same locality. This material is among the other Tumbler Ridge fossils currently undergoing preparation and description (Rylaarsdam *et al.*, 2006).

The ischium of this specimen appears to be unique among other hadrosaurids in general, as the pubic peduncle is strongly reduced, so that the pubis would be contributing to the entire ventral edge of the acetabulum, and the ischium would only participate in the posterior edge. A general reduction in the pubic peduncle can be seen throughout Hadrosauroidea, although no taxa yet have it as reduced in this specimen. The shaft of the ischium gently curves dorsally, as found in *Kundurosaurus* and *Edmontosaurus*. However, the distal end of the ischial shaft is not preserved, and thus it cannot be identified if the specimen possesses a ventral curve and expansion, characteristic of Lambeosaurinae.

Hadrosauridae nov. tax. (McCrea, pers. comm.)

Material: a partial skeleton lacking portions of the vertebral column, limbs and skull.

Location: Quality Creek canyon, Wapiti Formation, Tumbler Ridge, British Columbia (~73 mya; Fig. 1a).

Discussion: Not much will be said about this specimen, apart from it has been proposed to be a new taxon of lambeosaurine, for this specimen is currently under preparation and is to be studied on (McCrea, pers. comm.). The specimen has not been described or figured in published literature, and cannot be certainly assigned to either Hadrosaurinae or Lambeosaurinae at this moment.

Clade Marginocephalia (Serenó, 1986)

Family Pachycephalosauridae (Sternberg, 1945)

Subfamily Pachycephalosaurinae (Serenó, 2000)

Tribe Pachycephalosaurini (Sullivan, 2003)

Pachycephalosaurini nov. tax. (Arbour & Graves, 2008)

Material: RBCM.EH2006.019, a partial skeleton including a partial scapula, humerus, radius, ischium, tibia, fibula, astragalus and pedal digits III and IV (Fig. 3).

Location: Brothers Peak Formation, Sustut Basin, British Columbia (~72 mya; Fig. 1b).

Discussion: Arbour & Graves (2008) provided a description of RBCM.EH.2006.019 that does not need to be replicated here, however, there are some points that warrant reconsidering, and other important features, which are quoted here.

“Several bones recovered by Larsen cannot be identified at this time. One of these is an extremely thin and flat bone, 98 mm long and 33 mm wide, with thicknesses ranging from 6 to 15 mm (Arbour & Graves, 2008 Fig. 2G-H). It is strongly curved in several directions. Identification of this bone is difficult because it is broken on almost every edge, but, based on its thin, curved shape, this fragment may represent a bone from the skull (Arbour & Graves, 2008: pp. 459–460).”

This bone, while potentially belonging to the skull roof, clearly lacks the rugose texture in other pachycephalosaurids, and is only gently curved. Based on the shape, and thickening of the posterior edge, it aligns more closely with the proximal end of the scapula, with a thickened coracoid articulation, and an even thicker glenoid.

“A bone fragment 78 mm long, 32 mm wide, and 7 to 22 mm thick represents an unidentifiable element (Arbour & Graves, 2008 Fig. 2E-F). One end of the fragment has a triangular outline with a pronounced notch, whereas the other end is thin and flattened. The long axis of the fragment is bowed. This element may be a fragment of a rib, but if so, it probably does not belong to the same individual as the rest of the bones as it is much larger than would be expected (Arbour & Graves, 2008: p. 460).”

While being proposed as the rib of a separate individual, this bone also appears similar to the distal blade of an ischium. The slight curvature is likely facing medially, and a slight anterior expansion is present. Also, if interpreted as an ischium, it fits within the size expected for RBCM.EH.2006.019, and as all other material can be assigned to the same individual without major issues, this ischium would follow suit.

The most important feature of this specimen is the presence of an anteroposterior bowing of the distal end of the tibia (Arbour & Graves, 2008 Fig. 2R). This feature is not present in any other ornithischians, with the closest comparison a mediolateral bowing in the tibia of *Zalmoxes* (Arbour & Graves, 2008). This feature, not being attributable to post-mortem crushing, is thus autapomorphic of the specimen, and potentially warrants a new taxon. However, as no cranial material is known, it cannot readily be distinguished from other pachycephalosaurids in Alberta, such as *Sphaerotholus* and *Pachycephalosaurius*, or *Alaskacephale*, from northern Alaska, which are also known from a similar region and age.

Order Saurischian (Seeley, 1888)
Suborder Theropoda (Marsh, 1881)
Clade Coelurosauria (Huene, 1914)
Superfamily Tyrannosauroidae (Osborn, 1906)
Family Tyrannosauridae (Osborn, 1906)
cf. *Albertosaurus* (Osborn, 1905)

Material: PRPRC collections, partial shed tooth crown.

Location: Quality Creek canyon, Wapiti Formation, Tumbler Ridge, British Columbia (~73 mya; Fig. 1a).

Discussion: A single large, but incomplete tooth was found in the same deposit as the nearly complete hadrosaur (McCrea, pers. comm.). Only the ventral third of the crown is preserved, but it has small and numerous carinae preserved along both edges. The tooth is not circular in cross section, instead being broadly D-shaped, which is also found in tyrannosaurids. The age and location of this tooth, being in the Wapiti Formation, matches with cf. *Albertosaurus*, which has also been found in the formation (Currie *et al.*, 2008). Both *Gorgosaurus* and *Albertosaurus* have very similar dentition, so the assignment of the PRPRC tooth to *Albertosaurus* is based on the age of the Wapiti Formation, the British Columbian deposits being 73 mya, closer to the

oldest fossils of *Albertosaurus* (70.5 mya sensu Larson *et al.*, 2010) then the youngest fossils of *Gorgosaurus* (75.1 mya sensu Arbour *et al.*, 2009). Regardless of the generic identity, this specimen provides reasonable evidence of a large tyrannosaur present in British Columbia during the early Maastrichtian.

Clade Maniraptoriformes (Holtz, 1995)
Clade Ornithomimosauria (Barsbold, 1976)
Ornithomimosauria *indet.* (Bullard, 1999)

Material: RBCM.EH.2010.001.0001, a single mid-distal caudal vertebra (Fig. 4).

Location: Cedar District Formation, Denman Island, British Columbia (~80 mya; Fig. 1c).

Discussion: The single caudal bone RBCM.EH.2010.001.0001 was originally collected and briefly described by Bullard in 1999, where he proposed it belonged to an ornithomimid (Bullard, 1999). However, only ornithomimids more derived than *Archaeornithomimus* share any truly distinct features in the region of the tail. Pending a complete description of the material in progress (Trask, pers. com.), it cannot be identified if the vertebrae is indeed from an ornithomimid.

Based purely on the locality and other vertebrates preserved, the deposit seems to be a deep-water marine turbidite, with aquatic birds and other invertebrates (Dyke *et al.*, 2011). However, the ornithomimosaur caudal was found a few km away from the deposit Dyke stated was deep-water, and as other deposits of this formation instead preserve a shallow marine deposit (Peacock & Sidar, 2015), it may be possible that the caudal was from a skeleton deposited upstream, in a fluvial plain, before being swept downstream and settling in a marine deposit of unknown depth.

Clade Maniraptora (Gauthier, 1986)
Clade Paraves (Sereno, 1997)
Family Dromaeosauridae (Matthew & Brown, 1922)
Subfamily Velociraptorinae (Barsbold, 1983)
cf. *Boreonykus certekorum* (Bell & Currie, 2015)

Material: PRPRC collections, a single shed tooth crown.

Location: Quality Creek canyon, Wapiti Formation, Tumbler Ridge, British Columbia (~73 mya; Fig. 1a).

Discussion: A single small theropod tooth was found along with the cf. *Albertosaurus* and nearly complete hadrosaur skeleton. This tooth was assigned to a small theropod by McCrea & Buckley (2004), and later to *Saurornitholestes* (McCrea, online). However, in light of recent analyses of the theropods of the Wapiti Formation, the theropod *Boreonykus certekorum* was named for material previously associated with *Saurornitholestes* (Bell & Currie, 2015). While the PRPRC tooth was not among the material reassigned, several other shed teeth were. These teeth are not strongly posteriorly inclined, unlike those of *Saurornitholestes* (Bell & Currie, 2015), which is a feature also shared with the PRPRC tooth. However, while the shed teeth of *Boreonykus* are much taller than wide (Bell & Currie, 2015), this shows that the PRPRC

tooth would have been placed anteriorly in the sequence, likely in the premaxilla (Pers. obs.), with the assigned teeth of *Boreonykus* falling into the distal maxilla, or dentary (Bell & Currie, 2015).

DISCUSSION

Phylogenetic analysis

A phylogenetic analysis was conducted using PAUP*4.0a149 (Swofford, 1998) to test the systematics of Pachycephalosauridae and RBCM.EH.2006.019. The matrix consisted of 24 in-group taxa coded for 103 characters, with *Thescelosaurus neglectus* selected as the outgroup. Characters and codings for the matrix were primarily taken from Longrich *et al.* (2010), the most complete analysis to date, with the addition of 4 new cranial and 9 new addendicular characters, as well as codings for *Acrotholus* (Evans *et al.*, 2013); *Amtocephale* (Watabe *et al.*, 2011); *Stegoceras novomexicanum* (Jasinski & Sullivan, 2011); and the Sandy Site Pachycephalosaurine, with codings taken from their respective descriptions and a combination of published photographs (Horner & Goodwin, 2009) and personal observations for the Sandy Site specimen.

The results of this analysis (Fig. 4) show that Pachycephalosauria and Pachycephalosauridae can be considered distinct, with *Wannanosaurus* being the only non-pachycephalosaurid pachycephalosaurian. In addition, the most basal pachycephalosaurids are a clade including both *Stegoceras* species, *Gravitholus*, *Colepiocephale* and *Texacephale*, here named Stegocerotinae Clade Nov. and defined as “all pachycephalosaurids closer to *Stegoceras validum* than *Pachycephalosaurus wyomingensis*” (Table 1). Next more derived is *Hanssuesia*, then *Amtocephale*, both of which are excluded from any other clades, unlike in their original descriptions (Sullivan, 2003; Watabe *et al.*, 2011; respectively). Further up the tree is a clade of all *Sphaerolitholus* species, with the exception of *Sphaerolitholus? brevis*, which supports the hypothesis that *Sphaerolitholus* is a distinct and monophyletic taxon (Evans *et al.*, 2013). *Sphaerolitholus? brevis* places as the next most derived taxon after *Sphaerolitholus* proper, and places as a distinct taxon unique from both *Sphaerolitholus* and *Prenocephale*, supporting it as a new taxon (“Foraminacephale” sensu Schott & Evans, in review).

Following “Foraminacephale”, there is a clade of Homalocephalidae and Pachycephalosaurinae, Goyocephalia as defined here (Table 1.). Homalocephalidae was originally named as Homalocephaleridae by Dong (1978), and then corrected by Perle *et al.* (1982). The family was originally used to house all flat-headed pachycephalosaurs with open supra temporal fenestrae, *Homalocephale*, *Yaverlandia*, *Micropachycephalosaurus* and *Wannanosaurus* (Dong, 1978), and then *Goyocephale* was added (Perle *et al.*, 1982) However, it was never defined, and thus the first definition of the clade it proposed here (Table 1). Homalocephalidae includes all asian pachycephalosaurids with the exception of *Amtocephale*, although it included north american *Acrotholus*. In this clade, *Homalocephale* and *Goyocephale* group as the most derived, followed by *Tylocephale*, *Acrotholus* and *Prenocephale* respectively. This

shows a gradual trend toward a flatter head, with each more derived taxon having a more reduced dome, until both *Homalocephale* and *Goyocephale* fully lack a dome.

Pachycephalosaurinae includes *Alaskacephale*, *Pachycephalosaurus*, RBCM.EH. 2006.019, the Sandy Site Pachycephalosaurine, *Stygomoloch* and *Dracorex*, with each taxon being respectively more derived, and each taxon (known from cranial material) also having a more reduced dome, conversantly similar to Homalocephalinae. This reduction has been cited as evidence supporting a growth pattern in *Pachycephalosaurus* (Horner & Goodwin, 2009), but here the taxa are retained as separate, following Longrich *et al.* (2011) and Watabe *et al.* (2011), as an in-depth discussion of pachycephalosaurid ontogeny is out of the scope of this paper. *Alaskacephale* is recovered as the only non-pachycephalosaurin pachycephalosaurine, with only a single character, the angle of the parieto-squamosal suture in posterior view, separating it from *Pachycephalosaurus* and more derived pachycephalosaurines.

Putative dinosaur fossils

Several putative dinosaur fossils have also been found in British Columbia. One of these is a tooth that was described in Ludvigsen (1996), where he decided it belonged to a theropod. This tooth was found by amateur fossil hunters along the Trent River, being one of few fossils from the south-west of British Columbia. However, in pers. com. with Pat Trask, curator of the CM, he informed me that the tooth of a “theropod” was instead most certainly from the mosasaur *Kourisodon puntledgensis*, also found in the same region of the Comox Formation. Personal observations of casts of *Kourisodon* material show that both taxa share vertical ridges along the teeth, lack obvious denticles, and have a similar labio-lingual compression. Several of these features are also shared with theropods; the labio-lingual compression is similar to Troodontidae; the lack of denticles can be found in several scattered taxa (eg. *Byronosaurus*, *Paronychodon*, *Dilophosaurus*, some specimens of *Albertosaurus* and *Tyrannosaurus*); however, the ridges on the teeth are nearly uniquely shared with aquatic predators, like teleosaurids, plesiosaurs and mosasaurs. Thus, it seems most likely that the tooth belongs to *Kourisodon*, and thus is not a dinosaur.

Specimen was noted in Sampson & Currie (1996) as belonging to a dinosaur, a single manual phalanx of an ornithischian. This specimen was said to come from a coal deposit near Fernie, the age of that deposit being from Late Jurassic to Late Cretaceous. I attempted to locate this phalanx, and pers. com. with Pat Trask (CM) and Graham Beard (QBM) lead me to presume that this specimen was confused for a phalanx found by Graham Beard’s daughter near Mount Benson, Nanaimo, from the Haslam Formation. This phalanx was apparently brought to the attention of Currie, and the Haslam Formation is a black shale deposit, which makes it seem suitable that this was the phalanx described by Sampson & Currie (1996; Beard, pers. com.). The formation is a marine deposit, and comfortably underlies the Comox Formation. In the Comox Formation have been found a mosasaur (*Kourisodon*) as well as an unnamed plesiosaur. Both these groups have specialized limbs, and the manual and pedal phalanges are of a similar morphology to the Mt. Benson “ornithischian” phalanx.

While the above specimens do not come from a dinosaur, and the absolute numbers of dinosaur fossils is very low in British Columbia, the number of discoveries is steadily increasing in the province, signifying that over the same amount of time since the earliest discoveries, British Columbia could rival or even surpass every province but Alberta in fossil discoveries, as discoveries are equally uncommon in Yukon, Northwest Territories, Nunavut, Saskatchewan and Manitoba. However, the Dinosaur Park region of Alberta is very prolific for discoveries, one of the most prolific in the world.

CONCLUSIONS

Few dinosaur fossils have been found in British Columbia, especially when compared to the abundant fossils uncovered in adjacent Alberta, however, the number of fossil discoveries has been steadily increasing, including the first true bonebed, from where fossils of four different and distinct dinosaur clades have been found. Among these is the first over half-complete skeleton, which, while currently in preparation and undescribed, marks a milestone in the history of the discoveries in the province. The northernmost fossil includes the first ever dinosaur discovery, which was analyzed phylogenetically, and placed as a basal pachycephalosaurine. From the Tumbler Ridge bonebed have come *Boreonykus*, a velociraptorine dromaeosaurid, *Albertosaurus*, a basal tyrannosaurid, two intermediate or undescribed hadrosaurids, and a single ankylosaur scute of unknown assignment. The only other verifiable dinosaur fossil comes from an ornithomimosaurian, from the southwest coastal islands.

ACKNOWLEDGEMENTS

I would like to acknowledge the help of Mike Taylor, who provided suggestions and comments on the initial draft of this manuscript, as well as Victoria Arbour and an unnamed reviewer, who provided a critical review of a much earlier draft of this manuscript. Other suggestions were provided by Brad McFeeters, who led me to the description of the ornithomimosaurian caudal. Pat Trask of the Courtenay Museum and Graham Beard in the Qualicum Beach Museum, who held email conversations with me about potential dinosaur fossils, as well as Richard McCrea of the Peace Region Dinosaur Research Center.

REFERENCES

- Arbour, V. M.; Burns, M. E.; & Sissons, R. L. (2009). "A redescription of the ankylosaurid dinosaur *Dyoplosaurus acutosquameus* Parks, 1924 (Ornithischia: Ankylosauria) and a revision of the genus." *Journal of Vertebrate Paleontology* **29** (4): 1117–1135. doi: 10.1671/039.029.0405.
- Arbour, V.M., & Graves, M.C. (2008). "An ornithischian dinosaur from the Sustut Basin, north-central British Columbia, Canada." *Canadian Journal of Earth Sciences*, **45**(4): 457–463. doi: 10.1139/E08-009.

Bell, P. R. & P. J. Currie. (2015). "A high-latitude dromaeosaurid, *Boreonykus certekorum*, gen. et sp. nov. (Theropoda), from the upper Campanian Wapiti Formation, west-central Alberta." *Journal of Vertebrate Paleontology*, **36**(1): e1034359. doi: 10.1080/02724634.2015.1034359.

Bullard, T. (1999). "A dinosaur from the Nanaimo Group." *British Columbia Palaeontological Alliance Newsletter*, **22**: 11.

Butterfield, N.J. (2006). "Hooking some stem-group worms: fossil lophotrochozoans in the Burgess Shale." *BioEssays*, **28**(12): 1161–1166. doi: 10.1002/bies.20507.

Currie, P.J., Langston, W., & Tanke, D.H. (2008). "A new species of *Pachyrhinosaurus* (Dinosauria, Ceratopsidae) from the Upper Cretaceous of Alberta, Canada." pp. 1–108. In: Currie, P.J., Langston, W., and Tanke, D.H. A New Horned Dinosaur from an Upper Cretaceous Bone Bed in Alberta. *NRC Research Press*, Ottawa. ISBN: 0-660-19819-4.

Dong. 1978. [A new genus of Pachycephalosauria from Laiyang, Shantung]. *Vertebrata PalAsiatica* **16**(4): 225–228.

Dyke, G., Wang, X., & Kaiser, G. (2011). "Large fossil birds from a Late Cretaceous marine turbidite sequence on Hornby Island (British Columbia)." *Canadian Journal of Earth Sciences*, **48**: 1489-1496. doi: 10.1139/e11-050.

Evans, D. C.; Schott, R. K.; Larson, D. W.; Brown, C. M. & Ryan, M. J. (2013). "The oldest North American pachycephalosaurid and the hidden diversity of small-bodied ornithischian dinosaurs". *Nature Communications* **4**: 1828. doi: 10.1038/ncomms2749.

Gould, S.J. (1989). "Wonderful Life: Burgess Shale and the Nature of History." *W.W. Norton & Co*, pp. 2. ISBN: 0-393-02705-8.

Horner J.R. & Goodwin, M.B. (2009). "Extreme cranial ontogeny in the Upper Cretaceous Dinosaur *Pachycephalosaur*." *PLoS ONE*, **4**(10): e7626. doi: 10.1371/journal.pone.0007626.

Jasinski, S.E. & Sullivan, R.M. (2011). "Re-evaluation of pachycephalosaurids from the Fruitland-Kirtland transition (Kirtlandian, late Campanian), San Juan Basin, New Mexico, with a description of a new species of *Stegoceras* and a reassessment of *Texascephale langstoni*." *Fossil Record 3. New Mexico Museum of Natural History and Science, Bulletin* **53**: 202–215.

Larson, Derek W.; Brinkman, Donald B.; & Bell, Phil R. (2010). "Faunal assemblages from the upper Horseshoe Canyon Formation, an early Maastrichtian cool-climate assemblage from Alberta, with special reference to the *Albertosaurus sarcophagus* bonebed." *Canadian Journal of Earth Sciences* **47**: 1159–1181. doi: 10.1139/e10-005.

Longrich, N.R., Sankey, J., & Tanke, D. (2010). “*Texacephale langstoni*, a new genus of pachycephalosaurid (Dinosauria: Ornithischia) from the upper Campanian Aguja Formation, southern Texas, USA.” *Cretaceous Research* **31**(2): 274–284. doi: 10.1016/j.cretres.2009.12.002.

Ludvigsen, R. (1996). “Ancient saurians: Cretaceous reptiles of Vancouver Island.” In: Ludvigsen, R. Life in stone: a natural history of British Columbia’s fossils. *UBC Press, Vancouver*, pp. 156–166. ISBN: 0-7748-0577-3.

Maryańska, T.; Chapman, R.E. & Weishampel, D.B. (2004). “Pachycephalosauria”. pp. 464–477. In: Weishampel, D.B.; Dodson, P. & Osmólska, H. The Dinosauria (2nd ed.). *University of California Press, Berkeley*. ISBN: 0-520-24209-2.

Maryanska, T. & Osmolska, H. (1974). “Pachycephalosauria, a new suborder of ornithischian dinosaurs.” *Palaeontologica Polonica*, **5**: 45–101.

McCrea, R.T., & Buckley, L.G. (2004). “Excavating British Columbia's first dinosaurs and other palaeontological projects in the Tumbler Ridge area.” *Alberta Palaeontological Society, Abstracts for 8th Annual Symposium*. pp. 24–33.

McCrea, R.T., Buckley, L.G., Plint, A.G., Currie, P.J., Haggart, J.W., Helm, C.W., & Pemberton, S.G. (2014). “A review of vertebrate track-bearing formations from the Mesozoic and earliest Cenozoic of western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus.” pp. 5–93 In: Lockley, M.G. & Lucas, S.G. Fossil footprints of western North America. *New Mexico Museum of Natural History and Sciences Bulletin*, **62**.

Morris, C.S. & Whittington, H.B. (1985). “Fossils of the Burgess Shale: A National Treasure in Yoho National Park, British Columbia.” *Geological Survey of Canada*, pp. 28 ISBN: 0-660-11901-3.

Peacock, B.R. & Sidor, C.A. (2015). “The First Dinosaur from Washington State and a Review of Pacific Coast Dinosaurs from North America.” *PLoS ONE* **10**(5): e0127792. doi: 10.1371/journal.pone.0127792.

Perle, A.; Maryańska, T.; Osmólska, H. (1982). “*Goyocephale lattimorei* gen. et sp. n., a new flat-headed pachycephalosaur (Ornithischia, Dinosauria) from the Upper Cretaceous of Mongolia.” *Acta Palaeontologica Polonica* **27** (1–4): 115–127.

Rylaarsdam, J.R., Varban, B.L., Plint, A.G., Buckley, L.G., & McCrea, R.T. (2006). “Middle Turonian dinosaur paleoenvironments in the Upper Cretaceous Kaskapau Formation, northeast British Columbia.” *Canadian Journal of Earth Sciences*, **43**: 631–652. doi: 10.1139/E06-014.

Sampson, S.D. & Currie, P.J. (1996). "On the Trail of Cretaceous Dinosaurs." In: Ludvisgen, R. Life in stone: a natural history of British Columbia's fossils. *UBC Press*, Vancouver, pp. 143–155. ISBN: 0-7748-0577-3.

Schott, R. & D. C. Evans. (In review) "Cranial Anatomy and Ontogeny of "Prenocephale" *brevis* gen. nov. (Ornithischia: Cerapoda), and the systematics of Pachycephalosauridae from the Belly River Group (Campanian) of Alberta." *Zoological Journal of the Linnean Society*.

Sereno, P.C. (1986). "Phylogeny of the bird-hipped dinosaurs (order Ornithischia)." *National Geographic Research* **2**(2): 234–256.

Sereno, P.C. (1997). "The Origin and Evolution of Dinosaurs." *Annual Review of Earth and Planetary Sciences*, **25**: 435–489. doi: 10.1146/annurev.earth.25.1.435.

Sereno, P.C. (2005) "Stem Archosauria—*TaxonSearch* <http://www.taxonsearch.org/Archive/stem-archosauria-1.0.php>" Accessed July 24, 2016

Sternberg, C.M. (1945). "Pachycephalosauridae Proposed for Dome-Headed Dinosaurs, *Stegoceras lambei*, n. sp., Described." *Journal of Paleontology* **19**(5): 534–538.

Sullivan, R.M. (2003). "Revision of the dinosaur *Stegoceras* Lambe (Ornithischia, Pachycephalosauridae)." *Journal of Vertebrate Paleontology* **23** (1): 181–207. doi: 10.1671/0272-4634(2003)23[181:ROTDLS]2.0.CO;2.

Swofford, D. L. (1998). "PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4." *Sinauer Associates*, Sunderland.

Watabe, M.; Tsogtbaatar, K. & Sullivan, R.M. (2011). "A new pachycephalosaurid from the Baynshire Formation (Cenomanian-late Santonian), Gobi Desert, Mongolia." *Fossil Record 3. New Mexico Museum of Natural History and Science, Bulletin* **53**: 489–497.



Figure 1. Map of British Columbia showing locations of non-avian dinosaur body fossils. A - Tumbler Ridge; B - Sustut Basin; C - Denman Island. Inset showing location of British Columbia within Canada.

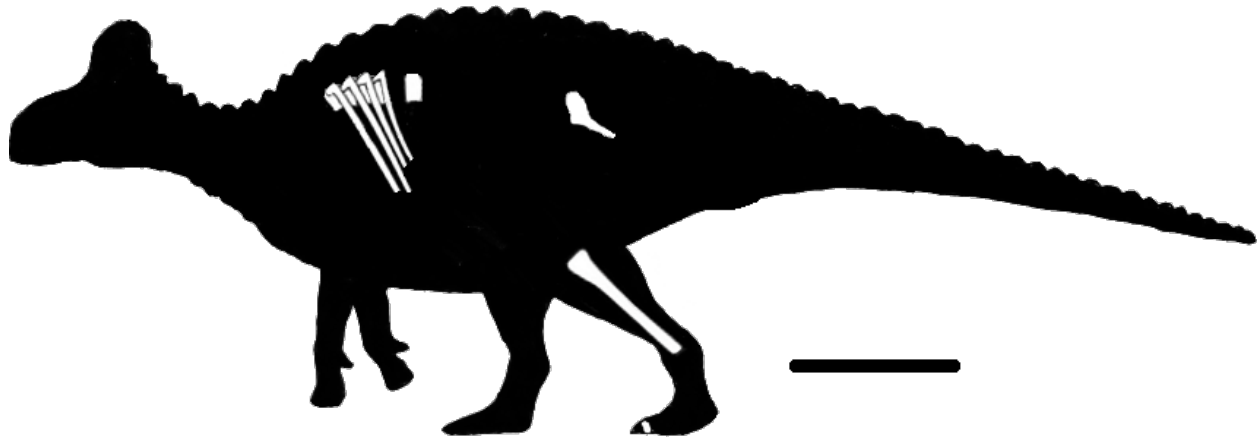


Figure 2. Reconstructed skeleton of PRPRC Hadrosauridae *indet.*, showing known material. *Edmontosaurus regalis* silhouette by Pete Buchholz from Phylopic, CC-BY-SA 3.0 license. Scale bar = 1 meter.

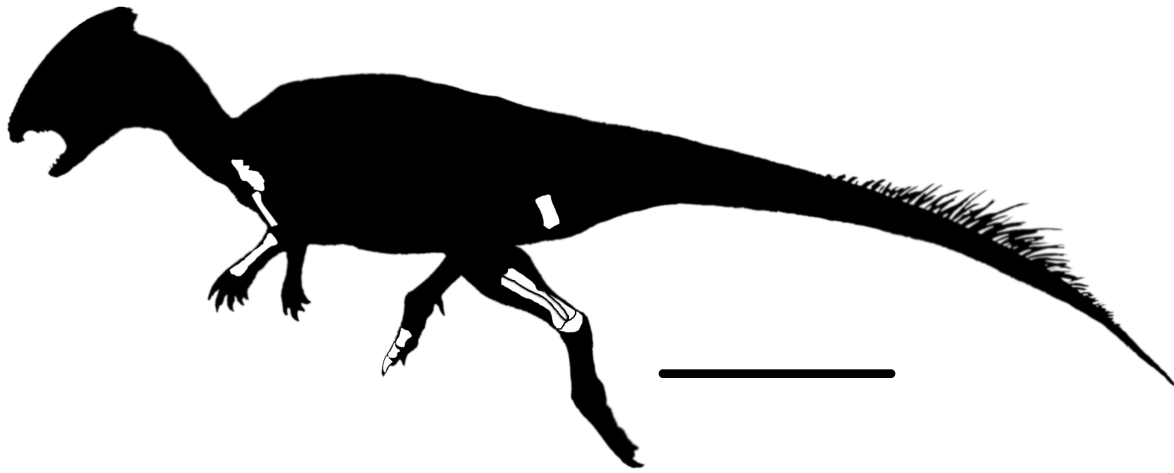


Figure 3. Reconstructed skeleton of RBCM.EH.2006.019 Pachycephalosaurini nov. tax., showing known material. *Homalocephale calathocercas* silhouette by “FunkMonk” from Phylopic, CC-BY 3.0 license. Scale bar = 0.5 meters.

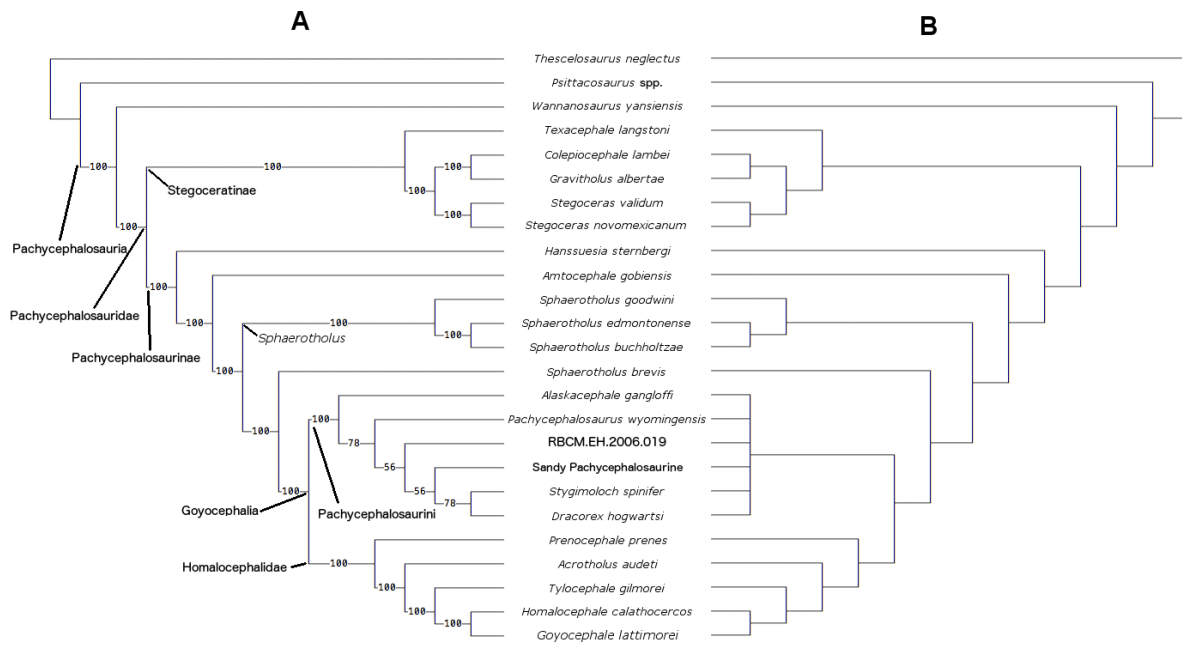


Figure 4. Phylogenetic analysis of Pachycephalosauridae. A - Majority Rules 50% consensus; B - Strict Consensus tree. Clades labelled based on new definitions proposed here (Table 1).

Clade	Definition	Reference	First usage of term
Pachycephalosauria	All the taxa more closely related to <i>Pachycephalosaurus wyomingensis</i> than to <i>Triceratops horridus</i> , <i>Thescelosaurus neglectus</i> or <i>Hypsilophodon foxi</i>	This study	Maryanska & Osmolska, 1974
Pachycephalosauridae	The least common ancestor of <i>Pachycephalosaurus wyomingensis</i> and <i>Stegoceras validum</i> , <i>Colepiocephale lambei</i> and all its descendants	This study	Sternberg, 1945
Stegoceratinae	All pachycephalosaurids closer to <i>Stegoceras validum</i> than to <i>Pachycephalosaurus wyomingensis</i>	This study	This study
Pachycephalosaurinae	All pachycephalosaurids closer to <i>Pachycephalosaurus</i> than to <i>Stegoceras validum</i>	This study, emended from Sereno (1998)	Sereno, 1997
Goyocephalia	The least common ancestor of <i>Pachycephalosaurus wyomingensis</i> and <i>Goyocephale lattimorei</i> , and all its descendants.	This study, emended from Maryanska <i>et al.</i> , 2004	Sereno, 1986
Homalocephalidae	All pachycephalosaurids closer to <i>Homalocephale calathocercos</i> than to <i>Stegoceras validum</i> or <i>Pachycephalosaurus wyomingensis</i>	This study	Dong, 1978
Pachycephalosaurini	The least common ancestor of <i>Pachycephalosaurus wyomingensis</i> and <i>Alaskacephale gangloffii</i> , and all its descendants	This study	Sullivan, 2003

Table 1. List of clades and definitions used in this work. For reasons for novel definitions, as well as clade synonyms, see supplementary information.