Cretaceous Bird Fossils of Alberta, Canada

by

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Abstract

Cretaceous birds of Alberta are poorly understood, as skeletal elements are rare and typically consist of fragmentary postcranial remains. A partial avian coracoid from the upper Campanian Dinosaur Park Formation of Alberta, Canada can be referred to the Ornithurae, and is referred to here as Ornithurine G. Its structure is similar to previously described ornithurine coracoids from Alberta and other localities in North America, including those belonging to the genus *Cimolopteryx*. A comparison of these elements indicates that the new coracoid is distinct; however, its preservation prevents complete diagnosis. A pneumatized coracoid is a defining trait of Neornithes, often associated with the presence of a pneumatic foramen. Ornithurine G does not preserve this feature. Also, CT and micro-CT scans of both pneumatic and apneumatic coracoids of modern birds show similar internal structures to Ornithine G, indicating that pneumaticity of the coracoid cannot be determined in the absence of an external pneumatic foramen. A phylogenetic analysis was unable to resolve unclear relationships between Ornithine G, Cimolopterygidae, and neornithine birds, and questions both the assignment of *Lamarqueavis* to the Cimolopterygidae, and the validity of the family as a whole.

Isolated teeth, previously identified as avian, are more common than other avian fossils from the Late Cretaceous of Alberta, although none are associated with skeletal material. A variety of specimens ranging from Late Santonian to Late Maastrichtian in age are described in detail and categorized into morphotypes based on qualitative assessment. Numerous characters are shared between birds, non-avian theropods, and crocodilians. In particular, the shape of the crown and surface enamel features of some putative avian teeth strongly resembles those found in the jaws of extant juvenile and some fossil crocodilians. However, whereas quantitative analysis (PCA ordination) was able to separate some putative avian morphotypes from non-avian theropods, and most crocodilian teeth, many of these clusters overlapped. Variation within this sample of teeth may reflect the heterodont dentition of crocodilians, rather than avian species diversity. Reassignment of many putative avian teeth to Crocodylia has important ramifications for the identification of small, isolated teeth, and for interpreting the evolutionary history of Cretaceous birds.

Dedication

This thesis is dedicated in loving memory to Dr. Calvin R. Evans, for his constant support, encouragement, and generosity. Every step I take, he will be there with me.

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Chapter 1. Introduction

The study of fossil birds is a continuously developing subject concerned with the evolution of early birds in the Late Jurassic and Early Cretaceous, the extinction of several archaic groups in the Late Cretaceous–including the Enantiornithes and basal members of Ornithurae–and the survival and radiation of crown birds past the KPg boundary. The period of time preceding the mass-extinction event is represented by Alberta's Upper Cretaceous sediments were laid down during the period of time preceding the mass-extinction event, spanning a stratigraphic range from the Upper Turonian to the Upper Maastrichtian. Although key to understanding avian species diversity and evolutionary trends leading up to the extinction event, Alberta's bird material is rare and typically fragmentary, and difficult to interpret and identify as a result. Here I provide an assessment of the best-preserved skeletal and dental elements, comment on the current consensus regarding Cretaceous bird fossils, and re-examine the evidence for referral of various fragmentary elements to Aves.

I provide an overview of the current state of the avian fossil record in Alberta, including comments on preservation, described taxa, and undescribed material, and a summary of the challenges of identifying fossil birds. I compare Alberta material with fossil taxa from other localities, and place material from Alberta in the larger context of Late Cretaceous North America. The following outline of the thesis will explain how this study attempts to rectify gaps in our understanding regarding fossil birds from Alberta.

1.2 Usage of the Term Ornithurae

The Ornithurae is a derived group of Cretaceous birds that are morphologically similar to crown birds, or Neornithes, and are also close phylogenetically. The definition of Ornithurae has undergone significant and frequent changes in the literature. However, regardless of definition, Neornithes is nested within Ornithurae. Thus, it should be noted that for the sake of this study, any following mention of Ornithurae refers only to basal Cretaceous members of the group to the exclusion of crown birds.

Ornithurae Haeckel, 1866, originally included birds with a short tail and fused pygostyle, rather than a long, bony tail, and thereby excluded *Archaeopteryx*. Gauthier and de Queiroz (2001) discussed various possible definitions, one of which comprised of those taxa with a modern bird-like tail and pygostyle, and included *Hesperornis*, *Ichthyornis*, and Aves (represented by *Vultur gryphus*). A number of studies have favored a more restrictive definition of Ornithurae encompassing *Hesperornis*, *Ichthyornis*, and crown birds (Neornithes), while others have used a much broader classification that includes a number of more basal taxa often referred to the Ornithuromorpha, such as the Early Cretaceous and semi-aquatic *Gansus yumenensis* (Padian et al., 1999; You et al., 2006; Wang et al., 2013). The original description of *Gansus yumenensis* considered it more derived than *Hesperornis*, and was referred to Ornithurae even under the stricter definition (You et al., 2006), although *Gansus* has also been placed within Ornithuromorpha (O’Connor and Zhou, 2012). Ornithurae was then expanded by the discovery of *Changzuiornis ahgmi*, in which the maxilla comprised a large portion of the facial margin at the base of a long rostrum (Huang et al., 2016). This feature was also reported in more derived Late Cretaceous ornithurines (also occasionally referred to as ornithurans) such as *Hesperornis* and *Ichthyornis*, whereas in crown birds, the premaxilla constitutes the main part of the rostrum and facial margin.

1.3 The Status of the Avian Fossil Record in Alberta

Skeletal remains of birds in the province of Alberta, Canada, are exceptionally rare and typically consist of single broken skeletal elements. As a result, they are difficult to definitively diagnose. Brown et al. (2013) found that taphonomic bias in the Dinosaur Park Formation tends to preserve larger-bodied taxa, such as non-avian dinosaurs, while the chances of smaller taxa being preserved are much reduced. Likewise, those processes acting in the coastal floodplain environment that produced the Dinosaur Park Formation may have been similar to other terrestrial systems in the Mesozoic of Alberta and elsewhere. This partially explains why bird fossils are uncommon and disarticulated in all Cretaceous formations in the province. In addition to small size, the hollow, pneumatic bones, and the overall fragile construction of the avian skeleton, further reduce the likelihood of preservation. This situation stands in stark contrast to Early Cretaceous localities in China known for very well preserved avian fossils that are often complete, articulated, and show soft-tissue preservation, largely as a result of low-energy depositional environments and volcanic tuffs that prevent decay by microorganisms (Zhou et al., 2003). The Jiufotang formation of the Jehol group contains a highly diverse assemblage of various avian groups, including basal avialians such as *Jeholornis prima*, basal members of Pygostylia such as *Confuciusornis sanctus*, and a large number of enantiornithines, as well as ornithuromorphs and basal ornithurines (O'Connor et al., 2012; Huang et al., 2016).

As a result, Late Cretaceous bird taxa in Alberta are likely highly under-sampled, resulting in an incomplete understanding of avian diversity from this time. Currently, a substantial portion of material referred to Aves in collections of the Royal Tyrrell Museum of Palaeontology and University of Alberta Laboratory of Vertebrate Paleontology are difficult to interpret, and remain undescribed. Isolated unguals and limb fragments are among the most common elements, whereas portions of the skull, vertebrae, and pectoral and pelvic girdles are rare (Chapter 2). Several sets of avian footprints from the Early and Late Cretaceous of Alberta, British Columbia, and other localities in western North America have been described, pointing to diversity of bird taxa (McCrea et al., 2014). However, this thesis focuses only on skeletal material.

A significant number of the previously described avian fossils from Alberta and other localities in North America are partial coracoids. A recent review of these elements indicates that birds occupied a range of body sizes, although very small (<20 g) and very large (>10 kg) species were either absent from the fauna, or subject to preservational biases and rarely fossilized as a result (Longrich, 2009; Longrich et al., 2011). These studies show as many as seventeen species can be identified in the avifauna of the Late Cretaceous of North America. The known avifauna was seemingly dominated by ornithurine birds.

1.3.1 Ornithurae in the Late Cretaceous of Alberta and Canada

While bird material is comparatively scarce in Alberta, other assemblages in North America hint at what may have been present throughout the Late Cretaceous of the province. Among the best preserved North American fossil members of the Ornithurae are the flightless, diving bird *Hesperornis regalis* and the volant, gull-like *Ichthyornis dispar* (Marsh, 1892). Members of Hesperornithes are perhaps the most common bird fossils in the Cretacous of western North America, with Canadian representatives including *Baptornis*, *Brodavis*, *Canadaga*, *Hesperornis*, and *Pasquianornis* (Fox, 1974; Tokaryk and Harington, 1992; Tokaryk, 1997; Hou, 1999; Aotsuko and Sato, 2016). Aotsuko and Sato (2016) expanded the known diversity of southern Manitoba's Campanian Pierre Shale include the following taxa: *Hesperornis chowi*, *Hesperornis macdonaldi*, *Hesperornis mengeli*, *Hesperornis lumgairi*, *Hesperornis rossicus*, and *Hesperornis sp*., as well as *Brodavis sp*., Hesperornithidae indet., and Hesperornithiformes indet. A number of isolated possible hesperornithine elements are currently housed in the Royal Tyrrell Museum of Palaeontology collections, including cervical vertebrae and partial tarsometatarsi from the Foremost and Oldman Formations. A single well-preserved humerus from the Turonian–Coniacian Kaskapau Formation was referred to *Ichthyornis* (Fox, 1984). A partial presacral vertebra resembling that of *Ichthyornis* in size and structure was also recovered from the Vermillion River Formation in Manitoba (Martin, 1982). The large fossil bird *Palintropus retusus* has been recovered from the Dinosaur Park Formation. It was originally identified as a charadriiform (Hope, 2002), and was more recently recovered as an archaic ornithurine closely related to the Campanian fossil bird from Mongolia, *Apsaravis ukhaana* (Longrich, 2009; Longrich et al., 2011).

Birds from other Canadian localities include the new Turonian ornithurine *Tingmiatornis arctica* found in the Arctic and described from two humeri and an ulna (Bono et al., 2016). Other unnamed ornithurine specimens include a distal portion of an ulna, complete tarsometatarsus, partial tarsometatarsus, and a complete tibiotarsus from the Northumberland Formation of British Columbia (Morrison et al., 2005).

1.3.2 Other avian clades in North America

Basal ornithurines appear to have coexisted with other avian groups. However, while enantiornithine birds were apparently dominant in Early Cretaceous assemblages elsewhere, they are comparatively scarce in the Late Cretaceous of North America. The enantiornithine *Avisaurus archibaldi* has been recovered from the Hell Creek Formation in Montana, as well as a number of unnamed specimens from the Campanian Northumberland Formation in British

Columbia (Morrison et al., 2005), and the Maastrichtian Frenchman Formation in Saskatchewan (Longrich et al., 2011). To date, however, no enantiornithine material has been positively identified from Alberta.

A substantial number of fragmentary remains from various assemblages across North America have in the past been assigned to the Neornithes, suggesting that crown birds originated in the Mesozoic (Marsh, 1880; Marsh, 1892; Brodkorb, 1963; Hope, 2002; Currie, 2005). These diagnoses are generally tentative, however, as they are largely based on single elements. For example, *Torotix clemensi*, from the Maastrichtian Lance Formation of Wyoming, was described from a partial humerus as a relative of modern flamingos. It was assigned first to Phoenicopteriformes, then to Charadriiformes, and was compared most recently with Pelecaniformes (Brodkorb, 1963; Hope, 2002). *Apatornis celer*, Marsh 1873 was first considered to be closely related to *Ichthyornis*. Hope (2002) conclusively assigned *Apatornis* to crown anseriformes, although Clarke (2004) identified it instead as a derived ornithurine bird. *Piksi barbarulna* from the Two Medicine Formation of Montana was described from a partial humerus, ulna, and radius, and originally suggested to be a primitive member of Ornithothoraces–a clade including enantiornithes and ornithuromorpha–in spite of its similarity to crown galliforms (Varricchio, 2002). However, the specimen has been reinterpreted instead as a small pterosaur, although this too has been questioned (Agnolin and Varricchio, 2012; Martin-Silverstone et al., 2016).

A significant number of North American bird fossils consist of partial coracoids. Several of these have been referred to the genus *Cimolopteryx* and subsequently placed in the family Cimoloptergyidae, which was originally thought to nest within Charadriiformes (Marsh, 1892; Brodkorb, 1963; Tokaryk and Tim, 1989; Hope, 2002). This material has been reinterpreted as representing advanced ornithurines that have been provisionally designated as Ornithurine A, B, C, D, E, and F (Longrich, 2009; Longrich et al., 2011). Currently, the Antarctic fossil anseriform *Vegavis* is among the most complete and best evidence for the presence of Neornithes in the Late Cretaceous (Clarke et al., 2005, Agnolin et al., 2017).

1.3.3 Avian Teeth in Alberta

Edentulism and evolution of a keratinous beak, or rhamphotheca, evolved multiple times within the avian lineage. However; many Cretaceous birds retained teeth in the jaws (Louchart and Viriot, 2009). In both *Hesperornis* and *Ichthyornis,* rows of small teeth occurred in the posterior region of the maxilla and dentary, although skull material is not commonly found (Marsh, 1892; Clarke, 2004; Dumont et al., 2016). If toothed ornithurine birds were the most abundant bird group in the Late Cretaceous of Alberta (Fox, 1974; Fox, 1984; Longrich, 2006; Longrich, 2009; Longrich et al., 2011; Aotsuko and Sato, 2016), we would expect to find both teeth and skeletal elements belonging to these taxa. Therefore, a large number of isolated teeth have been referred to Aves. These were recovered from several Albertan formations spanning the Late Santonian to the Late Maastrichtian, and include the Milk River (Upper Santonian–Lower Campanian, 84.5–83.5 Ma), Oldman (Upper Campanian, 77.5–76.5 Ma), Dinosaur Park (Upper Campanian, 77–75.5 Ma), Horseshoe Canyon (Upper Campanian–Lower Maastrichtian, ~74.0–67.0 Ma), and Scollard (Upper Maastrichtian–Lower Paleocene) Formations (Payenberg et al., 2002; Eberth and Deino, 2005; Eberth, 2005; Langenberg et al., 2007; Arbour et al., 2009; Eberth and Braman, 2012). Isolated teeth, similar to those in the Alberta sample, have also been described from other Maastrichtian localities, including the Hell Creek Formation in Montana (Sankey, 2008; Gates et al., 2015), and the Lance Formation in Wyoming (Longrich, 2008;

Sankey, 2008). These teeth vary considerably in shape and size, ranging from 1 to 4.5 mm in height, and none are associated with any jaw or skeletal material. Although apical wear and minor damage to the crown is present in most examples, these teeth are in comparatively good condition and show few signs of deformation. Fine ornamentation on the enamel of the lingual and labial faces often remains well-preserved, as do some features on the anterior and posterior edges. Most do not preserve large portions of the root, indicating that these are likely shed teeth (Dumont et al., 2016).

1.4 Gaps in our knowledge

The level of avian diversity seen in Lower Cretaceous localities elsewhere is not reflected in Cretaceous assemblages of Alberta, with the possible exception of putative avian footprints (McCrea et al., 2014). Trends in avian evolution in the latter half of the Cretaceous are difficult to assess due to the relative scarcity of material, particularly in North American localities. This is exacerbated by the prevalence of and diagnoses based on single, fragmented bones, and isolated teeth. Identifying isolated material is clearly difficult and highly problematic. Distinguishing ornithurine and neornithine material is challenging, and frequent re-interpretations of partial elements often differ both anatomically and taxonomically (Brodkorb, 1963; Hope, 2002; Varricchio, 2002; Clarke, 2004; Longrich, 2009; Longrich et al., 2011; Agnolin and Varricchio, 2012; Martin-Silverstone et al., 2016). Similarity in tooth shape and ornamentation between birds and other archosaurs also hinders positive identification of isolated teeth (Sankey et al., 2002; Longrich, 2008; Larson et al., 2010). For example, avian teeth can be difficult to distinguish from some non-avian theropod teeth, i.e. *Paronychodon* and *Richardoestesia*, as a result of shared characteristics, such as crown shape (Sankey et al., 2002; Gates et al., 2015). In spite of extensive research, no comprehensive descriptions of the Alberta sample from across multiple units currently exist (Sankey et al., 2002; Currie and Coy, 2008; Larson and Currie, 2013). Also, whereas bird teeth have been compared to those of non-avian theropods, they have not been compared to the dentition of crocodilians.

The precise nature of these bird fossils is poorly understood as a result. A re-examination of the current understanding of fragmentary Cretaceous bird fossils of North America is justified, and an assessment of postcranial elements and dentition of Alberta fossil birds is presented here.

1.5 Research Design and Hypotheses

1.5.1 Institutional Abbreviations

AMNH, American Museum of Natural History, New York, BMNH, British Museum of Natural History, London, NUVF, Nunavut Vertebrate Fossil collection (Canadian Museum of Nature, Ottawa), SDSM, South Dakota School of Mines, Rapid City, South Dakota, SMNH, Saskatchewan Museum of Natural History, Regina, Saskatchewan, TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, UAM, Alabama Museum of Natural History, University of Alabama, Tuscaloosa, Alabama, UCMP, University of California Museum of Paleontology, Berkeley, California, YPM, Yale Peabody Museum, New Haven, Connecticut.

1.5.2 Skeletal Material

Similarities between the postcranial skeleton of ornithurine and neornithine birds are evident in the coracoid (Hope, 2002). The scarcity and poor preservation of fossil avian material in Alberta excludes a large number of specimens from proper study. However, due to the abundance of fossil coracoids in North America, UALVP 55089 was selected for qualitative description, CT scanning, and phylogenetic analysis. A review of this material has broader implications for the interpretation of partial avian elements from other localities.

UALVP 55089 represents a fairly well-preserved proximal end of a left coracoid from the Campanian Dinosaur Park Formation, Dinosaur Provincial Park. A comparison of UALVP 55089 with other coracoids showed that it was similar to members of the genus *Cimolopteryx*, for which the family Cimolopterygidae was erected by Brodkorb (1968) and referred to the neornithine order Charadriiformes (Marsh, 1880; Marsh, 1892; Tokaryk and Tim, 1989; Hope, 2002; Agnolin, 2010; Longrich, 2009; Longrich, 2011). UALVP 55089 likely represents a distinct species, although previous phylogenetic analysis including this material resulted in an unresolved polytomy comprising crown birds and fossil taxa (Longrich et al., 2011). The monophyly of Cimolopterygidae is hence called into question. The addition of UALVP 55089 and five new morphological characters to the matrices of Zhou et al. (2004) and Longrich et al. (2011) failed to resolve relationships between these fossil coracoids and crown birds.

Finally, a pneumatized coracoid is a synapomorphy for Neornithes (Clarke, 2004). Breakages on the acrocoracoid process of the head and ventrally on the shaft of UALVP 55089 reveal hollow chambers bounded by bony endosteal struts indicative of pneumaticity. The bone is pervaded by air-filled sacs, or pneumatic diverticula (O'Connor, 2006). However, it is unknown if UALVP 55089 possessed a pneumatic foramen–a feature critical for reliably identifying the presence of pneumaticity (O'Connor, 2006). Both CT and Micro-CT scans of UALVP 55089 and the coracoids of the modern great blue heron (*Ardea herodias,* Pelecaniformes) and sandhill crane (*Grus canadensis,* Gruiformes) attempt to distinguish internal features of the coracoid head to discern pneumaticity in the absence of a pneumatic foramen. As ornithurine birds were the dominant avian group in the Late Cretaceous of North America

(Tokaryk and Harington, 1992; Clarke, 2004; Morrison et al., 2005; Longrich, 2006; Longrich, 2009; Longrich et al., 2011; Bono et al., 2016), it is probable that UALVP 55089 represents an ornithurine bird.

1.5.3 Dentition

Studying isolated bird teeth is important because they are relatively abundant compared to skeletal material and therefore may be stronger indicators of avian diversity. Referring avian teeth from Alberta to a particular group is difficult due to the lack of associated jaw and postcranial material. Several examples have been analyzed alongside those of non-avian theropods to compare and evaluate variation in the shape of the crown in an attempt to identify taxa from isolated teeth (Sankey et al., 2002; Currie and Coy, 2008; Longrich, 2008; Sankey, 2008; Gates et al., 2015). The disparity in shape and size among these teeth may also have significant implications for evolutionary trends affecting birds in the Late Cretaceous (Larson et al., 2016). The variability observed in putative avian teeth allows them to be assigned to distinct morphotypes based on shape and surface features. The morphotypes can then be used for comparative purposes, as a number of these dental features are also often present in other taxa, such as theropods and crocodilians (Martin, 1980; Sankey et al., 2002; Longrich, 2008; Gates et al., 2015). The notion that some putative avian teeth may belong to crocodilians has not been widely considered; however, examination of fossil *Leidyosuchus* and extant specimens of juvenile *Alligator*, *Caiman*, and *Crocodilus* shows strong similarities with numerous “avian” teeth from Alberta. Additionally, these taxa have heterodont dentition within the maxilla, premaxilla, and dentary, potentially raising doubt that variability in isolated teeth represents species diversity.

This qualitative assessment allows for predictions regarding tooth shape to be tested quantitatively. Various attempts have been made to quantitatively analyze isolated teeth as a means of differentiating between non-avian theropods and/or birds, and identifying potential distinguishing characters (Sankey et al., 2002; Larson, 2010; Larson and Currie, 2013; Williamson and Brusatte, 2014; Gates et al., 2015; Dumont et al., 2016). A series of measurements of the tooth crown in lateral and basal aspects effectively can be applied to a Principal Component Analysis (PCA), which functions to explain the maximal amount of variation in shape between teeth in the sample. The amount of overlap between clusters of teeth represents the overall similarity of assigned putative avian tooth morphotypes. Moreover, the separation or clustering together of teeth represents the level of disparity in tooth shape between putative avian, crocodilian, and non-avian theropod teeth. In combination with morphological comparisons, multivariate analysis resulting in overlap of these tooth groups would underscore the similarities between these taxa and encourage re-examination of the evidence supporting the referral of isolated teeth to Aves.

Chapter 2. An Ornithurine Coracoid from the Late Cretaceous of Alberta, Canada

2.1 Introduction

Cretaceous bird material in Alberta is rare and consists of fragmentary and isolated postcranial elements, most of which are not specifically diagnosable (Currie, 1995). As a result, relatively little is understood about the Late Cretaceous avifauna of the province. Despite expectations to the contrary, definitive examples of neornithine and enantiornithine birds from this period remain unknown in Alberta (Longrich, 2006; Longrich, 2009). Current fossil evidence suggests that ornithurine birds were the predominant and most diverse group present, although much of this material has unclear taxonomic affinities due to its fragmentary nature (Brodkorb, 1963; Longrich, 2009; Longrich et al., 2011). Here, the term "ornithurine" refers to a basal monophyletic stem group excluding the crown group Neornithes (modern birds). Ornithurines identified in Alberta include members of Hesperornithes, Icthyornithiformes, and Palintropiformes (Fox, 1974; Fox, 1983; Hope, 2002; Currie, 2005; Longrich, 2006; Longrich, 2009; Aotsuko and Sato, 2016). Additionally, Hope (2002) briefly described a specimen from the Dinosaur Park Formation and assigned it to Cimolopterygidae, making this the first purported cimolopterygid from the Campanian. All other specimens assigned to this family are Maastrichtian in age. However, Longrich (2009) questioned the identification of this specimen due to a lack of shared derived diagnostic characters for Cimolopterygidae, in spite of overall similarity among Maastrichtian specimens. The family Cimopterygidae originally included *Cimolopteryx rara*, Marsh 1892, with *Ceramornis major* Brodkorb 1963, *Cimolopteryx maxima* Brodkorb 1963, and *Cimolopteryx minima* Brodkorb 1963 added later. Recent additions include *Cimolopteryx petra* Hope 2002, *Lamarqueavis australis* Agnolin 2010, and *Lamarqueavis sp.*

(Agnolin 2010). Agnolin (2010) also renamed *Cimolopteryx minima* and *Cimolopteryx petra* as *Lamarqueavis petra* and *Lamarqueavis minima*. Tokaryk and James (1989) described a partial coracoid from the Maastrichtian of Saskatchewan as *Cimolopteryx sp.* (SMNH P1927.936). This specimen, plus the partial coracoid described here (UALVP 55089), and numerous unassigned ornithurine bone fragments described by Longrich (2006, 2009), add to the list of avian specimens derived from non-marine sediments in western Canada.

Other fragmentary non-dental bird material in the collections at the Royal Tyrrell Museum of Palaeontology and the University of Alberta Laboratory for Vertebrate Paleontology is not diagnosable beyond "Aves *incertae sedis*", and is therefore left to future workers (Table 2.1). As fossil birds are poorly represented in Alberta, the partial coracoid (UALVP 55089) warrants consideration in order to add to the current understanding of avian diversity in the province and its relationships to other birds in North America.

Systematic Paleontology

Aves Linnaeus, 1758

Ornithurae Haeckel, 1866

Ornithurine G

2.2 Materials and Methods

UALVP 55089 is a partial left coracoid, in the collections of University of Alberta Laboratory of Vertebrate Paleontology, Department of Biological Sciences.

The specimen was examined using a Wild M3 stereomicroscope, and photographed with a Nikon D500 camera and Nikkor 60mm Micro AF-D f. 2.8 lens. Micro-CT scans of UALVP 55089 were acquired using a Skyscan1174 at 50 kV, 800 µA, 40 W, 35 µm image size, 2500 ms exposure, and 360° rotation at 0.2° per step. A coracoid of *Grus canadensis* was Micro-CT scanned with an aluminum filter at 50 kV, 800 μA, 40 W, 35 μm image size, 2500 ms exposure, 180° rotation at 1° per step. A scapulocoracoid of *Ardea herodias* was CT scanned for comparison, using a Siemens Sensation 64 at 80 KV, 90.00 mAs, a pixel size of 0.502 mm and slice increment of 1.00 mm. Images were processed with Mimics 14.0.

2.3 Locality

BB010 (BB = Bonebed), 12U 465507: 5621617 (50.74531°N 111.488896°W) Dinosaur Park Formation, Belly River Group (Campanian), Dinosaur Provincial Park, Alberta, Canada. BB010 is a vertebrate microfossil site in the middle to upper Dinosaur Park Formation, below the Lethbridge Coal Zone (Eberth, 1990; Tanke, 1999).

2.4 Description

UALVP 55089 (Fig. 2.1) consists of the proximal end of a left coracoid from a bird estimated to be roughly the size of a large gull, e.g. *Larus argentatus* (Charadriiformes: Lari) (Field et al., 2013). The fragment is 24.7 mm in length. The scapular cotyle is 4.4 mm in diameter, strongly concave and circular, and slightly flattened along the circumference near the triosseal canal. The coracoid shaft is slender, dorsoventrally compressed, and elliptical in cross-section. The foramen for the supracoracoid nerve is positioned close to the anterior edge of the coracoid shaft and posteroventral to the scapular cotyle. The dorsal opening of the supracoracoid foramen is situated within a long, shallow groove that is angled towards the procoracoid process. The maximum anteroposterior length of the glenoid is 9.9 mm. It is also triangular and positioned anterior to the scapular cotyle. The prominent procoracoid process projects anteriorly with a slight upward hook. The acrocoracoid process is long, straight, and robust, although the upper portion of the process is missing.

The internal structures of the coracoid of UALVP 55089 are visible along breaks and some worn areas, particularly on the acrocoracoid process (Fig. 2.1D). This break reveals extensive endosteal struts forming small chambers throughout the coracoid body. A micro-CT scan of UALVP 55089 shows a large hollow chamber extending from just below the scapular cotyle into the acrocoracoid process, in addition to further endosteal struts (Fig. 2.1). Many of the chambers are connected, suggesting the coracoid was pneumatic, although an external pneumatic foramen is not preserved (Clarke, 2004; O'Connor, 2006). A small foramen is present on the medial edge of the procoracoid process (Fig. 2.1D). However, this is likely a nutrient foramen because the canal is short and does not extend into any of the open spaces in the bone.

2.5 Remarks

UALVP 55089 is diagnosed as an ornithurine bird on the basis of the concave scapular cotyle, the anteriorly-projecting glenoid, the triosseal canal situated ventromedial to the scapular cotyle, lack of a dorsal fossa, and presence of a procoracoid process. Longrich (2002) suggested that an intermuscular ridge is an additional ornithurine trait, but this feature is not preserved on this specimen. The coracoid head is only slightly shorter than in Ornithurine C (SDSM 64281) from the late Maastrichtian of Montana. The latter was tentatively assigned to *Graculavus augustus,* due to its large size (Longrich et al., 2011).

UALVP 55089 is similar in overall appearance to members of the Cimolopterygidae, with the exception of *Lamarqueavis* (Agnolin, 2010). These include *Ceramornis major*, *Cimolopteryx maxima*, *Cimolopteryx minima*, *Cimolopteryx petra*, and *Cimolopteryx rara*, (Brodkorb, 1963; Hope, 2002; Longrich et al., 2011). It also resembles a number of partial ornithurine coracoids from other regions in North America, all of which date to the Maastrichtian. These include SMNH P1927.936, referred to *Cimolopteryx sp*. by Tokaryk and James (1989); TMP 1993.019.0001, referred to “Ornithurine E” by Longrich (2009); TMP 1993.116.0001, referred to *Cimolopteryx sp.* by Hope (2002) and to “Ornithurine F” by Longrich (2009)); UCMP 53963, referred to “Ornithurine A”; and SDSM 64281, referred to “Ornithurine C” by Longrich et al. (2011). Lastly, UALVP 55089 bears some resemblance to *Anatalavis oxford* Olson 1999, an Eocene anseriform from England, of which largely complete coracoids have been found, including BMNH A5922. It is larger than Ornithurine A, E, F, *Ceramornis*, and *Cimolopteryx*, and only slightly smaller than *Anatalavis* and Ornithurine C.

It should be noted that Campanian ornithurines A, C, E, and F described in Longrich (2009) are not the same specimens or species as those in Longrich et al. (2011), which are from the Maastrichtian. Including specimen numbers helps avoids confusion.

UALVP 55089 is distinguished from these other specimens by a particular set of features. The coracoid shaft is more robust than those of *Cimolopteryx petra* and *Cimolopteryx rara*, although less so than in *Anatalavis*, *Cimolopteryx minima* and Ornithurine A (UCMP 53963) (Hope, 2002; Longrich et al., 2011). The shafts of Ornithurine E (TMP 1993.019.0001) and Ornithurine F (TMP 1993.116.0001) from Longrich (2009) are not well-preserved and therefore not comparable. SMNH P1927.936 is incomplete, although the specimen was described by Tokaryk and James (1989) as being most similar to *C. rara*, which our comparisons support. *C. petra* was described by Hope (2002) and also closely resembles SMNH P1927.936. Specimens of *Cimolopteryx maxima* do not preserve the coracoid shaft and so cannot be compared.

The procoracoid process of UALVP 55089 is roughly similar to specimens that also preserve this feature, with minor variation in the degree to which the process hook inwards into the triosseal canals. In *Anatalavis* the procoracoid differs in that it extends anteriorly and hooks laterally at its tip (Olson, 1996). Unlike *Cimolopteryx rara*, UALVP 55089 lacks the distinct ridge or strut extending from the procoracoid into the triosseal canal as described by Longrich et al. (2011).

The dorsal opening of the supracoracoid foramen in UALVP 55089 is situated in the center of a conspicuous depression or groove that extends towards the procoracoid. This feature is absent in most other specimens that preserve supracoracoid foramina, although *Ceramornis major*, *Cimolopteryx rara*, *Ichthyornis dispar*, Ornithurine D (UCMP 187207) from Longrich et al. (2011), which is otherwise dissimilar from UALVP 55089), and Ornithurine E (TMP 1993.019.0001) may show weakly-developed, less extensive grooves (Brodkorb, 1963; Hope, 2002; Clarke, 2004; Longrich, 2009; Longrich et al., 2011).

The scapular cotyle of UALVP 55089 is circular, although as in many other specimens the edge adjacent to the triosseal canal is relatively straight. It is most similar in shape to Ornithurine A (UCMP 53963) (Longrich et al., 2011). The cotyla of *Ceramornis*, *Cimolpteryx minima*, *Cimolopteryx petra*, *Cimolopteryx rara*, and Ornithurine C (SDSM 64281) are more sub-circular in comparison. The cotyle of *Anatalavis oxfordi* is damaged but also appears to be sub-circular. The cotyla of Ornithurine E (TMP 1993.019.0001) and Ornithurine F (TMP 1993.116.0001) described in Longrich (2009) are transversely elongate, with the former extending onto the procoracoid, which is absent in UALVP 55089.

The glenoid of UALVP 55089 is proportionally large and notably broader distally than proximally, resulting in a triangular shape. It resembles those of Ornithurine E (TMP

1993.019.0001) and Ornithurine F (TMP 1993.116.0001) (Longrich, 2009), although the posterior margin of the glenoid in UALVP 55089 is less curved. However, the glenoid is semicircular in *Cimolopteryx rara*, and more rounded in *Anatalavis*, *Ceramornis, Cimolopteryx maxima*, *Cimolopteryx minima*, *Cimolopteryx petra*, and Ornithurines A (UCMP 53963) and C (SDSM 64281) (Hope, 2002; Longrich et al., 2011). The degree of deflection of the glenoid relative to the scapular cotyle is moderate in UALVP 55089; less so than *Anatalavis*, *Cimolopteryx minima*, *Cimolopteryx rara*, and Ornithurines A (UCMP 53963) and C (SDSM 64281). It is more deflected than *C. petra*, and most similar to *Ceramornis, Cimolopteryx maxima*, Ornithurine E (TMP 1993.019.0001), and Ornithurine F (TMP 1993.116.0001).

The acrocoracoid process is long and straight in UALVP 55089, giving it a robust, pillar-like appearance. Ornithurine A (UCMP 53963) and *Cimolopteryx rara* are similar, although the acrocoracoid is shorter in these taxa. In *Anatalavis*, *Ceramornis*, *Cimolopteryx maxima*, *Cimolopteryx petra*, Ornithurine E (TMP 1993.019.0001), and Ornithurine F (TMP 1993.116.0001) this feature is slightly more curved. In *Cimolopteryx minima* the acrocoracoid is tilted more posteriorly. The dorsal margin of the acrocoracoid in Ornithurine C (SDSM 64281) is strongly hooked inwards.

Micro-CT scans of UALVP 55089 show large, hollow cavities and extensive endosteal strutting (Fig. 2.2). Although taken at a lower resolution, CT scans of the coracoid of *Ardea herodias* show similar structures, including a large hollow chamber near the center of the coracoid head (Fig. 2.2, E).

2.6 Phylogenetic Analysis

To determine whether a phylogenetic analysis might shed additional light on the relationship of UALVP 55089 to other fossil ornithurines, a matrix of 27 taxa and 34 coracoid characters (Table 2.2) was compiled in Mesquite and run in TNT 1.1 using the heuristic search algorithm TBR (Tree Bisection Reconnection) at 1000 replications. A strict consensus tree of the 10 most parsimonious trees and a 75% majority rules tree were then constructed. The matrix was constructed using coracoid characters from Longrich et al. (2011), which were modified from Zhou et al. (2008). Although characters 1, 11, 28, 29 all scored similarly because the analysis did not include basal taxa, removal of these characters did not alter the results and they were therefore left in the matrix. Ornithurines B (UCMP 129143) and E (AMNH 13011) from Longrich et al. (2011) were also included in the matrix despite not having been mentioned in the preceding comparisons, as they are structurally dissimilar to UALVP 55089. The following additional characters were also included in the matrix (Appendix 1):

30) Procoracoid process extended medially by a thin sheet of bone: absent (0), present (1)
31) Supracoracoideus nerve foramen located proximally on coracoid head (0), or located distally on coracoid shaft (1)
32) Supracoracoideus nerve foramen flush with surface of coracoid shaft (0), depressed into shaft (1), situated in deep groove (2)
33) Prominent, shelf-like dorsal projection of the scapular cotyle: absent (0), present (1)
34) Procoracoid process restricted proximally to coracoid head (0), terminates distal to coracoid head and onto shaft (1), extends towards the sternal end on coracoid shaft (2)

The shapes of both the glenoid and scapular cotyle amongst ornithurine and neornithine coracoids are highly variable between the specimens and so were not scored as characters.

In Longrich et al. (2011), Ornithurine E (AMNH 13011) was scored as “?” for the following characters from Zhou et al. (2008):

1) Scapula and coracoid: (0) fused, (1) unfused

2) Scapula and coracoid articulation: (0) pit-shaped scapular cotyla developed on the coracoid, and coracoidal tubercle developed on the scapula ("ball and socket" articulation), (1) scapular articular surface of coracoid convex, (2) flat.

Like the other sampled ornithurines, Ornithurine E (AMNH 13011) lacks a fused scapula and coracoid, and possesses a pit-shaped scapular cotyle that forms a socket for articulation with the scapula. Ornithurine E (AMNH 13011) was therefore rescored for these characters as "1" and "0", respectively.

Likewise, *Cimolopteryx petra* was scored as "?" for the following characters by Longrich et al. (2011):

11) Glenoid facet is: (0) dorsal to, or at approximately same level as, acrocoracoid process/ "biceps tubercle", (1) ventral to acrocoracoid process

The acrocoracoid process of *C. petra* is well-preserved relative to other members of the genus *Cimolopteryx*, and the glenoid is positioned ventral to the acrocoracoid process. As a result this character was rescored as "1".

Longrich et al. (2011) also scored Ornithurine F (UCMP 53957) as "1" for this character:

14) Medial surface, area of the foramen n. supracoracoideus (when developed): (0) strongly depressed, (1) flat to convex.

However, like *Cimolopteryx maxima* and Ornithurine C (SDSM 64281), this region is missing and therefore rescored as "?".

Even with these minor changes the resulting tree topology (Fig. 2.3) is consistent with that of Longrich et al. (2011). Ornithurine G, *Ceramornis*, *Cimolopteryx*, most other unassigned ornithurine birds excluding Ornithurine D, and neornithine birds group together in a polytomy.

Additionally, the majority rules tree further recovers *Crax pauxi* (Galliformes: Cracini), *Crypturellus undulatus* (Tinamiformes: Tinaminae), and *Gallus gallus* (Galliformes: Phasiani), as a polytomy. *Lamarqueavis australis* and *Lamarqueavis sp.* are recovered as a clade just basal to this polytomy with a single synapomorphy: the presence of a lamina extending from the procoracoid process, despite this feature being unknown in *Lamarqueavis sp*.

2.7 Phylogenetic placement of UALVP 55089

The addition of new characters to the matrix of Longrich et al. (2011) did not better resolve relationships between neornithine and ornithurine birds, likely due to the fragmentary nature of the specimens and the significant contribution of similar coracoid characters in both analyses. The strong morphological similarities between ornithurine and neornithine coracoids results in the tendency for specimens to code similarly for character states (Longrich et al., 2011). As a result, UALVP 55089 falls into a polytomy with neornithine birds and most unassigned ornithurines, excluding Ornithurine D (Fig. 2.3). The unassigned ornithurines and *Cimolopteryx* may well be related to modern birds, but resolving this question requires additional material. The similarities between fossil elements and those of modern birds may instead be homoplasious, potentially because these taxa all inhabited wet, floodplain environments that characterized some Cretaceous localities, including the Dinosaur Park Formation (Eberth, 2005). The recovery of *Crax pauxi* (Galliformes: Cracini), *Crypturellus undulatus* (Tinamiformes: Tinaminae), and *Gallus gallus* (Galliformes: Phasiani) as a polytomy – a monophyletic group including a paleognath and two members of Galliformes to the exclusion of other clades, including Anseriformes – is not supported by morphological or molecular studies (Clarke, 2004; Yonezawa et al., 2016). While coracoids are useful diagnostic elements, a large number of coracoid characters are insufficient for resolving species relationships. Although unresolved, this nevertheless underscores the close relationship between ornithurine fossils and modern birds.

Due to size, stratigraphic level, and a variety of characteristics, UALVP 55089 likely represents a new taxon. Additionally, Longrich et al. (2011) suggest that within a species, coracoids are largely consistent in form and that any variation can be attributed to taxonomic differences. However, a single broken element does not warrant the establishment of a generic name. UALVP 55089 is referred to here as Ornithurine G following the naming system of Longrich (2009) and Longrich et al. (2011). As the fossil record of derived ornithurines is sparse and many remain unnamed, maintaining this consistency is practical and will simplify the process when referring to these fragmentary elements. It is also recommended that further use of this naming system to describe new fragmentary specimens should proceed alphabetically, as was done here.

2.8 Discussion

2.8.1 Pneumaticity of Ornithurine G

Birds are well-known for their characteristic pneumatic skeleton, where pneumatic diverticula pervade hollow spaces within the bone. The coracoids of the ornithurines *Iaceornis* and *Ichthyornis*, however, are apneumatic (Clarke, 2004). A pneumatic coracoid is a synapomorphy of neornithine birds, including some members of Anseriformes, as well as Paleognathae and Galliformes (Clarke, 2004). The fossil record of neornithine birds in the Cretaceous is sparse, often contested, and mostly based on fragmentary elements, with the best example so far being the Maastrichtian fossil anseriform *Vegavis* from Antarctica, clearly signifying a Mesozoic origin for Neornithes (Hope, 2002; Clarke, 2005; Brusatte et al., 2014).

Pneumaticity is unknown in Cimolopterygidae and Ornithurines A through F. Micro-CT scans of Ornithurine G show large, hollow cavities and extensive endosteal strutting consistent with pneumaticity. This suggests that Ornithurine G should be placed within Neornithes; however, CT scans of the apneumatic coracoid of *Ardea herodias* show similar structures, including a large hollow chamber near the center of the coracoid head (Fig. 2.2, H, I) (Zelenkov, 2011). Comparisons with Micro-CT scans of the pneumatic coracoid of *Grus canadensis* likewise show similarities to *Ardea herodias* and Ornithurine G, including proximally-located hollow chambers (Fig 2.2, E, F, G) (Olson, 1972). Examination of the vertebrae of extant taxa show that the most dependable parameter for identifying pneumaticity conclusively is the occurrence of cortical openings or foramina connecting internally to large hollow chambers in the bone (O'Connor, 2006). As UALVP 55089 is missing the sternal region and much of the coracoid shaft, it is unknown if a pneumatic foramen was present, preventing definitive placement within Neornithes.

2.8.2 *Cimolopteryx* and Cimolopterygidae

Brodkorb (1963) refers Cimolopterygidae to Charadriiformes, a conclusion cautiously supported by Hope (2002). Furthermore, Brodkorb (1963) remarks that the coracoid of *Cimolopteryx rara* appears most closely comparable to that of the Recurvirostridae (Charadriiformes: Charadrii), although the details of this similarity are not presented. Instead, a number of differences between *Cimolopteryx rara* and Recurvirostridae are listed, notably a long, curved procoracoid process, which is present in other charadriiformes, such as *Larus delawarensis* (Charadriiformes: Lari)*, Phalaropus tricolor* (Charadriifornes: Scolopaci), and *Uria algae* (Charadriiformes: Alcini). The acrocoracoid process of *Recurvirostra americana* (Recurvirostridae) is also proportionally larger, more robust, and hooks medially to a much greater degree than *Cimolopteryx*. Overall, *Cimolopteryx rara* resembles only members of its genus as well as the unnamed ornithurine coracoids, including UALVP 55089, more than members of Charadriiformes. Schufeld (1914) after comparing *Cimolopteryx rara* with a number of "water birds," including members of Charadriiformes, determined that there were no living representatives of the genus. However, he also suggested that *Cimolopteryx rara* was likely a toothed bird closely related to *Ichthyornis*. This is an assertion not supported by Longrich et al. (2011) or this paper (Fig. 2.3). Hope (2002) noted that Charadriiformes are particularly difficult to interpret, owing both to the presence of primitive features shared with many other neornithines, and to the possession of derived traits that are also present in other semi-aquatic birds, such as Pelecaniformes and Procellariiformes. Hope (2002) interpreted this mosaic-like pattern of characters as indicating that Charadriiformes and other semi-aquatic birds maintained a host of ancestral traits following an early, fast divergence. This may instead be interpreted as convergence, which could easily extend to other closely-related Cretaceous birds occupying similar aquatic and shoreline habitats. The pes of the ornithurine *Gansus* was reported to show convergence with neornithine diving birds, such as loons and diving ducks (Hope, 2002), indicating that the presence of homoplastic traits in neornithine and ornithurine birds was not unusual. Additionally, traits linking cimolopterygids with modern forms, such as a deeply concave scapular cotyle, are primitive for Ornithurae (Clarke, 2004; Longrich, 2009; Agnolin, 2010). The lack of articulated fossil material, the likelihood of convergence, and the predominance of ornithurine birds in the Late Cretaceous (Fox, 1974, 1983; Tokaryk et al., 1997; Clarke, 2004; Longrich, 2006, 2009; Longrich et al., 2011; Aotsuko and Sato, 2016; Bono et al., 2016), all suggests that there is little support for the placement of *Cimolopteryx* or similar unassigned coracoids within Neornithes. Thus, both the monophyly of Cimolopterygidae and its inclusion within Charadriiformes are unsubstantiated. Cimolopterygidae is most parsimoniously considered a provisional taxon of ornithurine birds that possess similar coracoids and may be closely related.

Agnolin (2010) placed *Lamarqueavis australis* (MML 207) and *Lamarqueavis sp.* (Ornithurine B (UALVP 47943, or the "Irvine Bird")) from Longrich (2009) in Cimolopterygidae based on the following traits that unite the family: humeral articular facet (glenoid) ventrally oriented, procoracoid process sternally-extended and developed as a thin lamina, and supracoracoid nerve foramen large and positioned ventrally. However, any difference in orientation of the glenoid between these taxa and non-cimolopterygid ornithurines is not evident in the figures (Agnolin, 2010). The thin lamina that comprises the procoracoid process in *Lamarqueavis* was also described as autapomorphic for the genus. It extends farther distally than in any other member of Cimolopterygidae. As such, this particular trait cannot be used to describe the family as a whole. The lamina also increases the width of the coracoid shaft in *Lamarqueavis*, extending the distance between the tip of the procoracoid process and the scapular cotyle relative to other cimolopterygid coracoids, and Ornithurine A, C, E, F, and G (Longrich, 2009; Longrich et al., 2011). The ventrally positioned supracoracoid nerve foramen presumably refers to the position of the foramen relative to the scapular cotyle. This trait is present in other ornithurines including *Iaceornis*, *Ichthyornis*, Ornithurine A, C, D, E, F, and G, and is therefore not a synapomorphy of *Lamarqueavis* and Cimolopterygidae. The size of the supracoracoid nerve foramen in *Lamarqueavis* is also proportionately large compared to any cimolopterygid. Likewise, the foramen is situated at a markedly greater distance distally from the scapular cotyle than other *Cimolopteryx* species, if not Cimolopterygidae as a whole (Fig. 2.3 and Agnolin, 2010).

The genus *Lamarqueavis* (Agnolin 2010) was proposed for a species within *Cimolopteryx* erected by Hope (2002). *Cimolopteryx minima* and *Cimolopteryx petra* were reassigned to *Lamarqueavis* based on a combination of unique traits that *Cimolopteryx minima*, *Cimolopteryx petra, Lamarqueavis australis, and Lamarqueavis sp.* share, including: procoracoid process large, posteriorly-extended, and straight or convex along its medial margin; humeral articular facet subrectangular in shape, and scapular cotyle transversely elongate. However, these are refuted here as not all members of *Lamarqueavis* share these. The large, convex procoracoid process is an autapomorphy of *Lamarqueavis australis* alone (Agnolin, 2010), and in *Cimolopteryx minima* and *Cimolopteryx petra* the procoracoid margins are concave, not convex (Brodkorb, 1963; Longrich et al., 2011). The procoracoid in *Lamarqueavis sp.* appears to resemble that of *Lamarqueavis australis*, although its edge is broken and its exact shape is difficult to discern (Longrich, 2009). The shapes of the humeral articular facets in Cimolopterygidae and the unassigned ornithurines show a range of subtle variation. The dorsal and ventral edges of the glenoids of *Cimolopteryx minima*, *Cimolopteryx petra*, and *Lamarqueavis sp.* are ovate, not subrectangular (Brodkorb, 1963; Longrich, 2009; Agnolin, 2010; Longrich et al., 2011). As well, the scapular cotyles of *Cimolopteryx minima* and *Cimolopteryx petra* are ovate to subtriangular, not transversely elongate and strongly tear-dropped shape as in *Lamarqueavis australis*. The cotyle of *Lamarqueavis sp*. is also circular, not elongate.

Additional characteristics of *Lamarqueavis* include a procoracoid process that hooks anteriorly towards the triosseal canal in *Lamarqueavis australis*, a condition also seen in *Ichthyornis* and Ornithurine D (Clarke, 2004; Agnolin, 2010; Longrich et al., 2011). The glenoid of *L. australis* is positioned anterior to the scapular cotyle as in *Ichthyornis* and Ornithurine D

(Clarke 2004; Longrich et al., 2011). In contrast, the glenoid is positioned anterolateral to the cotyle in Cimolopterygidae, as well as in Ornithurine G (Fig. 2.3). It is not clear whether the acrocoracoid, typically longer in other members of Cimolopterygidae, is complete or fragmentary. For these reasons, *Cimolopteryx minima* and *Cimolopteryx petra* are not considered in this paper to be species of *Lamarqueavis*. This conclusion is supported by the recovery of *Lamarqueavis australis* and *Lamarqueavis sp.* as a distinct clade separate from *Cimolopteryx* in both the strict consensus and majority rule trees (Fig. 2.3). Mayr (2016) also noted *Lamarqueavis* more closely resembles the neornithines Psophiidae and Messelornithidae (Gruiformes) than Cimolopterygidae. As a result, the precise relationships of *Lamarqueavis* remain unclear.

In conclusion, UALVP 55089 represents a new ornithurine bird from the upper Campanian Dinosaur Park formation of Alberta, larger than other similar ornithurines from the Cretaceous of North America. UALVP 55089 is referred to as Ornithurine G following the system of Longrich (2009) and Longrich et al. (2011). The presence of pneumaticity cannot be established as a pneumatic foramen is not preserved. Although fragmentary and difficult to assign with certainty, it most closely resembles several unnamed ornithurines from North America, many of which are similar to members of the enigmatic family Cimolopterygidae.

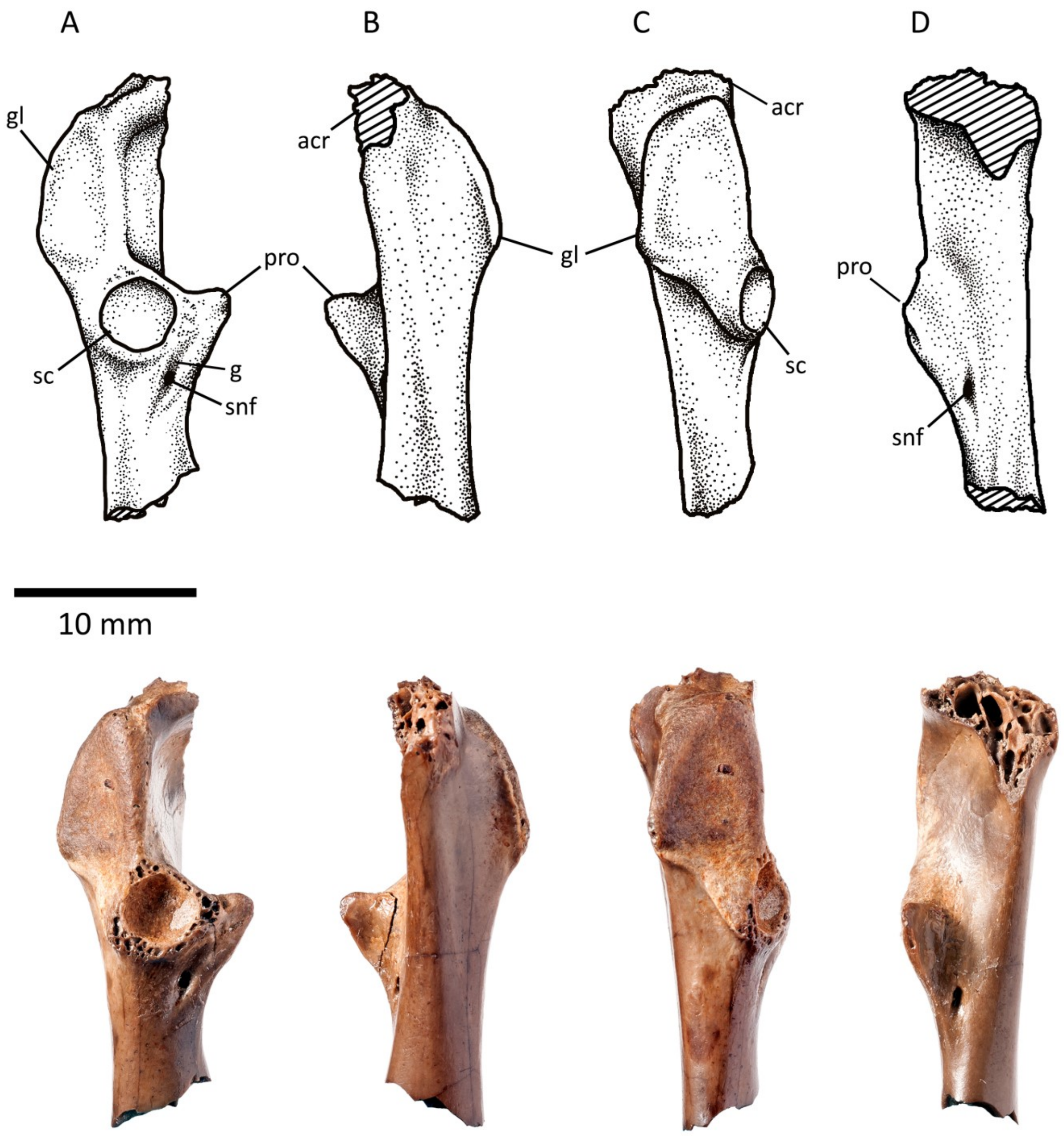

Figure 2.1. UALVP 55089, proximal end of left coracoid, Dinosaur Park Formation. A, dorsal, B, ventral, C, lateral, D, medial views. Abbreviations: acr, acrocoracoid process; g, groove; gl, glenoid; pro, procoracoid process; sc, scapular cotyle; snf, supracoracoid nerve foramen.

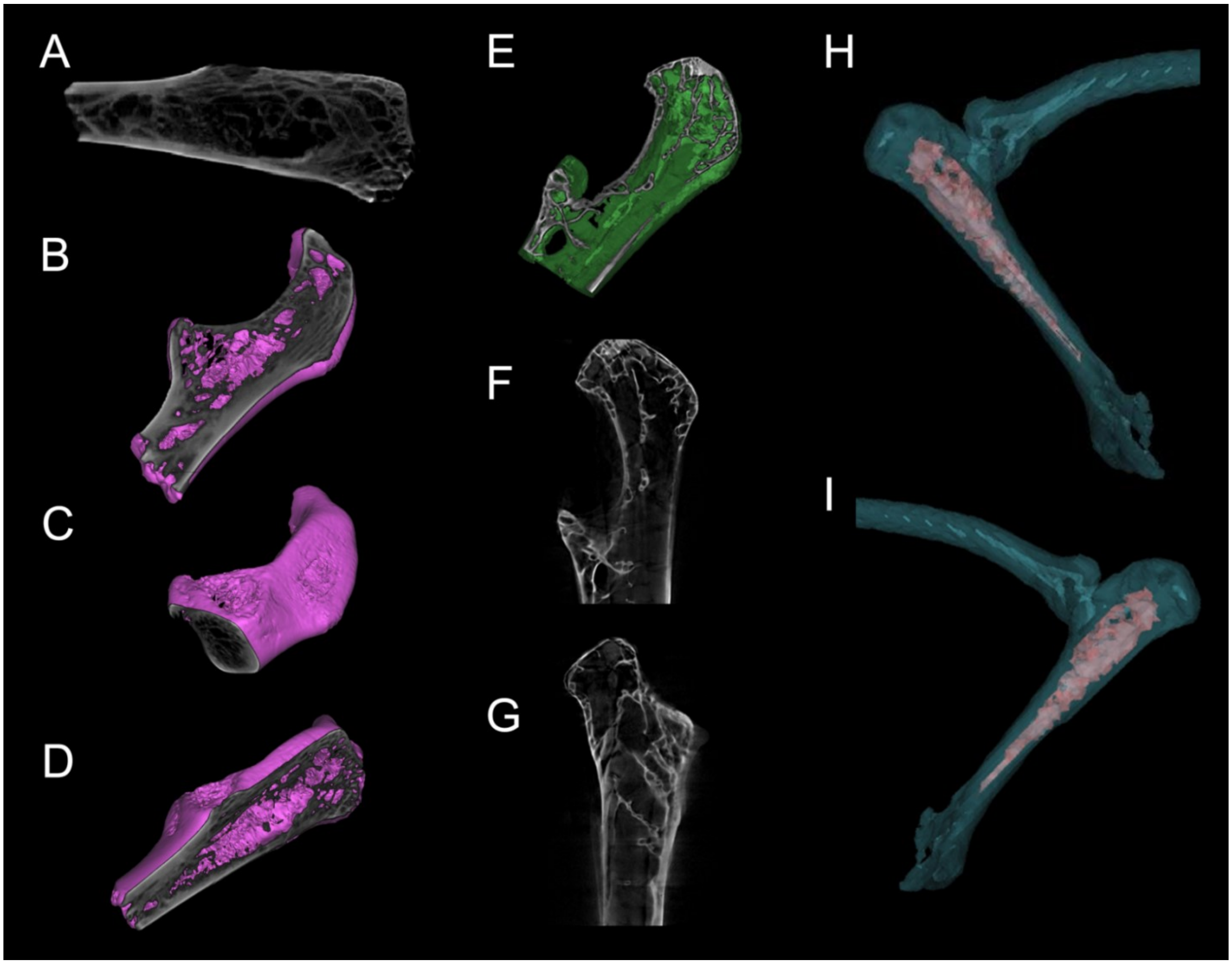

Figure 2.2. MicroCT scan of UALVP 55089, *Grus canadensis*, and *Ardea herodias*. A large central chamber is present near the center of the coracoid head**,** connecting to a series of smaller distally and proximally located that pervade the entirety of the bone**.** These vacuities are demarcated by a series of endosteal struts. This is compared with the non-pneumatic coracoid of *Ardea herodias*, where red indicates open space within the bone. Cross-sections of UALVP 55089 in A, sagittal, B, transverse, C, coronal, D, sagittal views. Cross-sections of *Grus canadensis* in A, transverse, F, coronal, G, sagittal views. Ghosting is a result of soft tissue remnants. 3D model of *Ardea herodias* scapulocoracoid in H, lateral and I, medial views. Images not to scale.

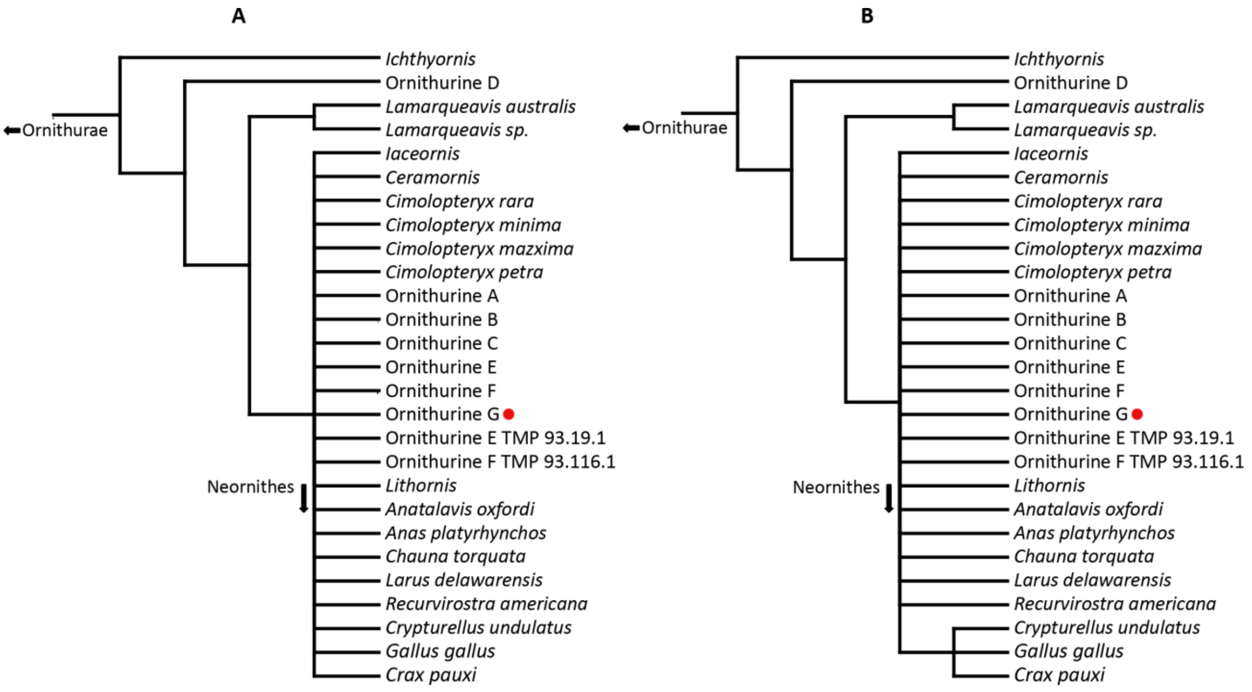

Figure 2.3. Strict consensus (A) and majority rule (B) trees showing unresolved relationships between most ornithurines and Neornithes. Arrow (Ornithurae) indicates base of clade (including Hesperornithes) is not included in this study. Arrow (Neornithes) indicates crown taxa. Ornithurine G (UALVP 55089) indicated by red circle.

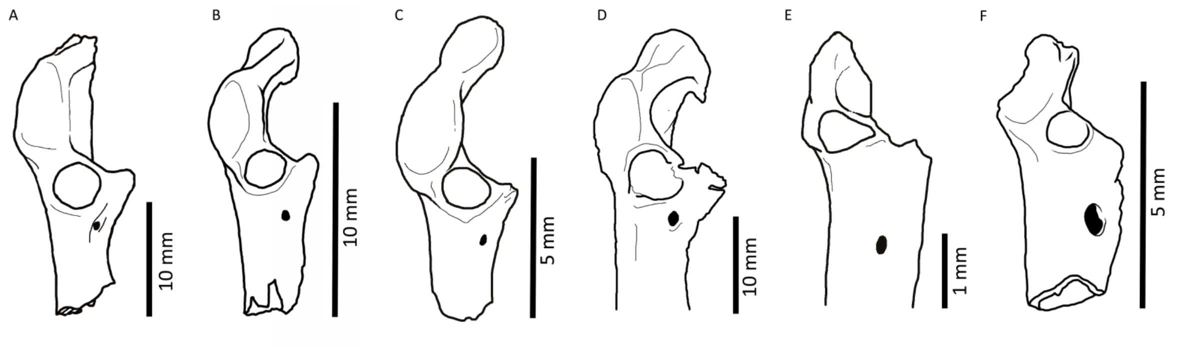

Figure 2.4. Comparison of UALVP 55089 (Ornithurine G), *Cimolopteryx rara*, *Cimolopteryx petra*, *Anatalavis oxfordi*, *Lamarqueavis australis*, and *Lamarqueavis sp*. A, Dorsal view of UALVP 55089 (Ornithurine G), B, *Cimolopteryx rara* (UCMP 53963); modified from Brodkorb (1963), C, *Cimolopteryx petra* (AMNH 21911); modified from Longrich et al. (2011), D, *Anatalavis oxfordi* (BMNH A5922); modified from Olson, (1999), E, *Lamarqueavis australis* (MML 207); modified from Agnolin, (2010), F, *Lamarqueavis sp.*(UALVP 47493); modified from Longrich (2009).

Skeletal Fragment	**Catalogue #**
Appendicular Skeleton	
Ungual	TMP 1982.020.0034 (complete), TMP 1983.070.0016 (partial), TMP 1989.069.0014 (partial), TMP 1990.081.0003 (complete), TMP 1991.036.0035 (partial), TMP 1993.079.0015 (complete), TMP 1993.079.0020 (partial), TMP 1993.117.0001 (partial), TMP 1994.012.0125 (complete), TMP 1995.178.0060 (partial), TMP 1995.178.0061 (partial), TMP 1997.607.0125 (partial), TMP 1997.666.0010 (complete), TMP 2015.012.0076 (complete)
Phalanx	TMP 1979.014.0585 (partial), TMP 1991.036.0012 (partial), TMP 1995.012.0081(complete)
Femur	TMP1979.014.0585 (distal), TMP 1987.014.0585, TMP 1989.089.0012 (shaft), TMP 1991.061.0001 (shaft), TMP 1996.142.0023
Tarsometatarsus	TMP 2011.012.0005 (shaft), TMP 2013.012.0005 (partial distal)
Ulna	TMP 1996.012.0433 (partial?)
Scapula	TMP 1985.063.0076 (partial?), TMP 1999.125.0001 (proximal)
Coracoid	TMP 1984.090.0011 (glenoid and cotyle)
Unidentified limb fragment (mid-shaft)	TMP 1979.088.0576, TMP 1981.016.0237, TMP 1983.063.0014(?), TMP 1983.067.0011, TMP 1984.089.003(?), TMP 1984.099.0003, TMP 1985.066.08
Sternum	TMP 1990.035.0032(partial?)
Axial Skeleton	
Skull	TMP 1979.008.1056 (partial skull bone?)
Vertebral Column	TMP 1989.001.0002

Table 2.1. A sample of undescribed Cretaceous fossil bird material from the Royal Tyrrell Museum of Paleontology. The majority of specimens are small broken fragments, rather than complete elements. "?" indicates an uncertain identification.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Ichthyornis	1	0	1	1	0	1	0	?	1	1	1	1	0	1	1	1	0
Iaceornis	1	0	1	1	0	1	0	?	1	1	1	1	0	1	1	2	1
Ceramornis	1	0	?	?	?	?	?	?	?	?	1	1	?	?	1	2	1
Cimolopteryx rara	1	0	1	1	1	1	0	?	1	1	1	1	0	1	1	2	1
Cimolopteryx minima	1	0	1	1	?	1	?	?	?	?	1	1	0	1	1	2	1
Cimolopteryx maxima	1	0	?	?	?	?	?	?	?	?	1	1	?	?	1	2	1
Cimolopteryx petra	1	0	1	1	?	?	?	?	?	?	1	1	?	?	?	2	1
Ornithurine A	1	0	1	1	?	?	?	?	?	?	1	1	0	?	?	2	1
Ornithurine B	1	0	?	1	?	?	?	?	?	?	1	1	0	?	1	2	1
Ornithurine C	1	0	1	1	?	?	?	?	?	?	1	1	0	?	1	2	1
Ornithurine D	1	0	1	1	?	1	?	?	?	?	1	1	0	1	1	1	0
Ornithurine E	1	0	1	1	0	1	0	?	?	?	1	?	0	?	1	2	?
Ornithurine F	1	0	1	?	?	?	?	?	?	?	1	1	0	?	1	2	1
Ornithurine G	1	0	1	1	?	?	?	?	?	?	1	1	0	1	1	2	1
Lamarqueavis australis	1	0	1	1	1	1	?	?	?	?	1	?	0	?	?	1	1
Lamarqueavis sp.	1	0	1	1	?	1	?	?	?	?	1	?	0	?	?	1	1
Ornithurine E TMP 93.19.1	1	0	1	1	?	?	?	?	?	?	1	1	?	?	1	2	?
Ornithurine F TMP 93.116.1	1	0	1	?	?	?	?	?	?	?	1	1	?	?	1	2	?
Lithornis	1	0	1	1	0	1	1	0	1	1	1	1	0	1	1	2	1
Crypturellus undulatus	1	2	1	1	0	1	1	0	1	0	1	1	1	1	1	2	1
Anatalavis oxfordi	1	0	1	1	0	1	1	1	?	1	1	1	0	1	1	2	0
Anas platyrhynchos	1	0	1	1	0	1	0	?	1	0/1	1	1	1	1	1	2	1
Chauna torquata	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	2	0
Gallus gallus	1	2	1	1	0	1	1	1	1	1	1	1	1	1	1	2	1
Crax pauxi	1	2	1	1	0	1	1	1	1	1	1	1	1	1	1	2	1
Larus delawarensis	1	0	1	1	0	1	1	?	1	1	1	1	0	1	1	2	1
Recurvirostra americana	1	0	1	1	0	1	0	?	1	1	1	1	0	1	1	2	1

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Ichthyornis	1	1	0	1	0	1	1	1	1	1	0	0	1	0	1	1	0
Iaceornis	?	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	?
Ceramornis	?	1	0	?	1	?	?	1	1	?	0	0	0	0	0	1	1
Cimolopteryx rara	0	1	0	0	0	1	?	1	1	1	0	0	0	0	0	1	1
Cimolopteryx minima	?	1	0	0	0	?	?	?	1	?	0	0	0	0	0	0	1
Cimolopteryx maxima	?	1	0	?	1	?	?	?	?	?	0	0	?	?	?	?	?
Cimolopteryx petra	0	1	0	?	0	?	?	?	1	?	0	0	0	0	0	0	1
Ornithurine A	0	1	0	?	0	?	1	1	1	?	0	0	0	0	0	0	1
Ornithurine B	?	1	0	?	1	?	?	1	1	?	0	0	0	0	0	0	1
Ornithurine C	0	1	0	?	1	?	1	1	1	?	0	0	?	?	?	?	?
Ornithurine D	1	1	0	1	0	?	1	1	1	?	0	0	0	0	1	1	0
Ornithurine E	?	1	0	0	0	?	?	?	1	?	0	0	?	0	?	?	?
Ornithurine F	0	1	0	?	1	?	?	1	1	?	0	0	?	?	?	?	?
Ornithurine G	0	1	0	?	0	?	?	1	1	?	0	0	0	0	0	1	1
Lamarqueavis australis	1	1	0	1	0	?	?	?	1	?	0	0	1	1	1	0	0
Lamarqueavis sp.	0	1	0	?	?	?	?	?	1	?	0	0	?	1	1	0	0
Ornithurine E TMP 93.19.1	?	1	0	?	1	?	?	?	1	?	0	0	?	0	1	?	?
Ornithurine F TMP 93.116.1	?	1	0	?	0	?	?	?	?	?	0	0	?	?	?	?	?
Lithornis	0	1	0	?	0	1	1	1	1	1	0	0	0	0	1	1	1
Crypturellus undulatus	1	1	0	0	0	1	1	1	1	0	0	0	0	?	0	1	1
Anatalavis oxfordi	0	1	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1
Anas platyrhynchos	0	1	1	0	1	1	1	1	1	1	0	0	0	?	1	?	1
Chauna torquata	0	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0
Gallus gallus	?	1	1	0	0	1	1	1	1	0	0	0	0	?	0	?	1
Crax pauxi	?	1	1	0	0	1	1	1	1	0	0	0	0	?	0	?	1
Larus delawarensis	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0
Recurvirostra americana	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	?

Table 2.2 Matrix of character scores for phylogenetic tree. Entries include characters from Zhou et al. (2008), Longrich et al. (2011), and this paper.

Chapter 3. A reassessment of putative avian teeth from the Late Cretaceous of Alberta, Canada: comparison with the dentition of juvenile crocodilians.

3.1 Introduction

The Late Cretaceous avifauna of Alberta consists of only isolated, postcranial elements, such as taxonomically semi-informative coracoids (Fox, 1974, 1984; Longrich, 2009; Longrich et al., 2011; Aotsuko and Sato, 2016), and numerous isolated teeth. Although modern crown birds, or Neornithes, are characterized by having edentulous horny beaks, or rhamphotheca, most Mesozoic fossil birds possessed teeth in their jaws (Louchart and Viriot, 2011). The most extensive analysis of the dentition of *Hesperornis* and *Ichthyornis* also included isolated teeth from Alberta, and described morphology, microstructure of the enamel and dentine, implantation, and replacement mechanisms (Dumont et al., 2016). Currie and Coy (2008) describe a single tooth with crown and root as avian, perhaps belonging to a hesperornithid, although this identification has since been questioned (Larson and Currie, 2013; Dumont et al., 2016). As well, a small sample of presumably avian teeth from Alberta were described and analyzed alongside non-avian theropod teeth, the main goal of the analysis being to more precisely define variation in isolated teeth from the late Campanian (Sankey et al., 2002). Similar teeth from the early Maastrichtian were included in a vertebrate microfossil assemblage dominated by terrestrial taxa (Larson et al., 2010).

Larson (2009) and Larson and Currie (2013) summarized the challenges associated with identifying isolated teeth, including the presence of similar characters in distantly-related taxa, and large spatial and temporal gaps between specimens assigned to the same taxon. Variation in tooth morphology within a species due to heterodonty or ontogeny may also complicate tooth identification. Describing genera and/or species based on isolated teeth alone is not recommended (Larson and Currie, 2013; Williamson and Brusatte, 2014; Gates et al., 2015).

Longrich (2008) described possible bird teeth, in addition to non-avian theropod teeth, from the Maastrichtian Lance Formation of Wyoming that are similar to several examples from Alberta. However, these teeth seemed too large for any known contemporaneous bird taxon, and certain characteristics of these teeth are also found in other taxa–most notably crocodilians. In spite of these similarities, qualitative and quantitative comparisons of crocodilian dentition with those of non-avian theropods and birds have not been performed. Multivariate ordinations have been successful in separating teeth at the level of genera and species (Smith et al., 2005; Larson and Currie, 2013), and higher taxa (Longrich, 2008; Sankey, 2008), although one study failed to differentiate between similarly-shaped teeth belonging to different taxa (Smith et al., 2005). Non-avian theropod teeth in Alberta and elsewhere have been the subject of extensive study (Sankey et al., 2002; Larson, 2009; Larson and Currie, 2013). Numerous species of dromaeosaurid and troodontid theropods have been characterized extensively (Sankey and Currie, 2002; Longrich, 2008; Sankey, 2008; Larson, 2009; Larson and Currie, 2013). A large sample of theropod teeth from Alberta was used to test the possibility of quantitatively identifying isolated teeth and assessing patterns of diversity over long periods of time (Larson and Currie, 2013). Both avian and non-avian theropod teeth from the Late Cretaceous were analyzed to assess patterns of extinction during the Late Cretaceous, suggesting that a seed-rich diet was a major factor in the survival of neornithine birds following the mass-extinction (Larson et al., 2016). The fact remains, however, that the only taxa in this assemblage known from teeth in jaws are *Hesperornis* and *Ichthyornis*, and the identity of other putative avian teeth is largely a matter of consensus among workers. Confirming or refuting the avian nature of putative bird teeth from Alberta has important ramifications for current research on avian evolution and extinction in the Late Cretaceous. For this reason, this study uses both qualitative and quantitative analyses to test whether these “cf. Aves” teeth are morphologically distinct from those of the toothed birds *Hesperornis* and *Ichthyornis*, non-avian theropods, and crocodilians, both fossil and extant.

3.2 Materials and Methods

Sixty-four isolated teeth, identified by others as avian, were examined in the Royal Tyrrell Museum of Palaeontology (TMP) and University of Alberta Laboratory of Vertebrate Paleontology (UALVP) collections. Additional teeth were available but were excluded from this study due to poor preservation. Teeth were originally recovered through screen-washing or surface collection from numerous sites and formations across Alberta (Sankey et al., 2002). These include the Milk River (Santonian-Campanian), Oldman (Campanian), Dinosaur Park (Campanian), St. Mary River (Campanian-Maastrichtian), Horseshoe Canyon (Campanian-Maastrichtian), and Scollard (Maastrichtian) formations. Localities included Devil’s Coulee, Dinosaur Provincial Park, Dry Island, Iddelsleigh, Milk River, Onefour, and Tolman, Alberta, Canada. In most cases, data for exactly where in stratigraphic section teeth were collected were not available.

For qualitative description purposes, specimens were examined and arranged into more-or-less distinct morphotypes based on discrete characteristics of the crown, including overall shape in lateral and basal views, curvature, features on the enamel surface, and presence or absence of denticles (Table 3.2). Putative avian teeth are diverse in shape, and although specimens were grouped based on shared features, some variation may be present within morphotypes. Anatomical tooth terminology for shape and ornamentation follows Smith et al. (2005) and

Hendrickx et al. (2015), although here the terms anterior and posterior are preferred over distal and mesial. In many cases, basal shape (based on cross-sectional profile at the cervix, or near the junction of the crown and root) among the teeth examined here was comparable to more than one type described by Hendrickx et al. (2015). When present, the carina typically protrudes beyond both anterior and posterior edges of the crown, and was included when observing the overall shape in basal view.

For linear morphometrics, partial or highly fragmented specimens missing key features were excluded from this study. The remaining sixty-four teeth were measured from the sample, as well as a tooth of *Richardoestesia gilmorei* (TMP 1988.091.0028), a tooth of *Troodon sp.* (TMP 1986.177.008), *Hesperornis regalis* (YPM 1206B), and *Ichthyornis dispar* (UAM_PV93.2.133_2). Fossil crocodilian teeth included UALVP 54359A, and four samples from TMP 1986.008.0074. Modern material was also examined. Five juvenile *Alligator mississippiensis* teeth (UAM2 R949, 6.3 cm skull length) and four teeth of *Caiman crocodilus* (uncatalogued specimen from the University of Alberta Zoology Museum, 16.25 cm skull length) were also measured. Teeth were examined using a Nikon SMZ1500 stereomicroscope, and photographed in lateral and basal views using a Q-imaging Retiga 4000r Fast 1394 digital camera at 50x magnification. Images were processed and measurements were performed in NIS-Elements BR 3.0. Three teeth of a juvenile *Crocodylus niloticus* were measured from images in Dumont et al. (2016) using ImageJ (Rasband, 1997-2016). Additional photographs, used for illustrations only, were made using a Nikon D500 camera, a Nikkor 105mm micro lens, a Nikkor 1.7X teleconverter, and a Nikon 5T two-element closeup lens.

Discrete characters, which could not be measured as continuous variables, such as enamel ornamentation and shape and number of denticles were not included within the multivariate analysis. Most tooth measurements (Fig. 3.1) were based on previous studies, (Sankey et al., 2002; Smith et al., 2005; Larson and Currie, 2013; Hendrickx et al., 2015). Fore-aft basal length (FABL) was measured at the anteroposteriorly longest part of the base of the crown from the anterior and posterior edges. Crown height (CH) was measured perpendicular to FABL, from the posterior edge of the FABL measurement to the apex of the crown. As the tips of most teeth were worn, CH was measured to the remaining apex. Apical length (AL) was measured diagonally from the anterior end of FABL to the centre of the remaining apex. Novel measurements, in lateral view, were also assessed. Apical distance (AD) was measured from a point level with the crown apex and directly above the anterior end of FABL, to the centre of the remaining apex. AD was measured to assess the displacement of the apex relative to the crown base, such that values of AD roughly equal to one half of FABL represent straighter crowns, whereas greater values of AD represent strongly rearward-directed crowns. Anterior-apical length (MAL) was measured at the maximum distance from the AL line to the anterior edge of the crown in order to provide a measure of convex anterior curvature. Basal constriction (BC) of the tooth below the crown was measured as a minimum horizontal distance below and parallel to FABL. In basal view, two measurements were modified from Smith et al. (2005) and Hendrickx et al. (2015). Crown basal length (CBL) is the maximum distance between the anterior and posterior edges of the tooth, including the carinae, if present. In many instances this value is identical to FABL, however, in some teeth the root of the crown is longer and expands beyond this point (Fig. 3.1A). Crown basal width (CBW) was measured in the center of the crown, perpendicular to CBL. To better capture variations of shape in basal view, anterior crown basal width (ACBW) and posterior crown basal width (PCBW) measurements were made at points half way between CBW and the ends of CBL. In most cases, one of these measurements was the maximum width value. In the few instances where it was not, the maximum width value differed by only 0.01-0.04 mm from either ACBW or PCBW. Measurements of CH, CBL, and CBW for *Hesperornis* and *Ichthyornis* performed by Dumont et al. (2016) were taken and the new measurements described here were added.

Ratios are often used in tooth analyses (Smith et al., 2005; Larson, 2009; Hendrickx et al., 2015), but because ratios include the raw measurements from which they are derived, and because these raw measurements were included in the analysis, ratios were excluded from the analysis to ensure statistical independence and avoid potential mixing of data types and values.

Collectively, these measurements characterize the basic geometry of the teeth, and were used to quantify the variation for linear morphometrics. Values were log-transformed to approximate a normal distribution of data, and a total of the ten variables described here were included. A principal components analysis (PCA) using these variables was performed in PAST version 3.15 statistical software to assess the variance present in the sample.

A number of measurements were initially made but not included in the analysis. Studies of non-avian theropod teeth typically measure the density of denticles per unit of measurement (Smith et al., 2005; Larson, 2009; Larson and Currie, 2013), and/or the height and length of individual denticles (Sankey et al., 2002). However, in most cases, the denticles on putative bird teeth were irregular both in shape and extent on the carina, varying widely in size, length, and height. As a result, the number of denticles per given length was not readily discernable, and therefore it was not possible to consistently measure individual denticles with certainty for the purposes of analysis. Thus, the crowns of teeth with denticles were measured for shape in the same way as the other specimens. Likewise, the presence or absence and extent of the carinae on the anterior and posterior margins were difficult to interpret and measure, due to wear and damage.

As well, an attempt was made to quantify the distance from the posterior concave curvature of each tooth, as the minimum distance from the posterior margin of the tooth to the midpoint of a line, extending from the posterior end of FABL to the apex the tooth. However, these measurements were found to vary only slightly across the sample, unlike anterior curvature, which was more informative. As a result, posterior curvature was excluded from the final analysis. The distance from FABL to the basal constriction, or basal height (BH), was also excluded. In the PCA, this variable had remarkably high loading values for the first two axes, but a review of the measurements suggested the high variance for this measurement resulted from lack of discrete landmarks for the exact placement of FABL and BC.

Basally, many teeth were somewhat curved along their long axis. For these teeth, an angle was estimated from the center point of the CBW and CBL lines through the anterior and posterior edges. This angle was omitted from the PCA as initial ordinations showed this variable contributed little to each component axis, and because excluding the angle did not affect the form of the ordination.

3.3 Tooth Morphotypes

Morphotype 1

Morphotype 1 is characterized by its comparatively large size (maximum height 4.56 mm), wide base, and two types of ridges on the enamel surface (Fig. 3.4A, B). The anterior and posterior margins are more or less straight in lateral view. The lingual surface has a wide, shallow concavity that narrows towards the tip. On a number of specimens, the surface enamel on both faces shows either one of two types of longitudinal ridges. The first, referred to here as primary ridges, are a series of straight, broad, rounded ridges roughly equal in size and extending from the base of the crown to the apex. The secondary ridges are fine, short, and often undulating, running roughly parallel to each other and concentrated on the middle part and apex of the crown. The carinae are also subtly textured with very fine and closely-spaced wavy striae that extend apically from the edges of the crown and onto the carinae. The carinae are prominent and continuous along both anterior and posterior margins. The carinae terminate abruptly at the base of the crown, below which the root may be very slightly constricted. In better-preserved specimens, the root expands outwards, often becoming wider than the widest part of the crown. Some crowns are straight, while are others slightly inclined posteriorly. A clear margin on the enamel surface on the both lingual and labial faces is present on most examples of Morphotype 1, as well as in Morphotypes 2 and 3 (Fig 3.4). The anterior and posterior edges of the crown extend basally past the highest point of this margin, giving it an arched appearance. The enamel surface and ornamentation terminates abruptly at this line, below which the surface is largely featureless. This margin is not clearly present in other Morphotypes aside from 2 and 3. Basally, the tooth is curved and ovate (reniform) in cross-section and strongly compressed laterally. This type was featured in Sankey et al. (2002, Fig. 5. 35-38), and similar teeth were described from the Maastrichtian Lance Formation by Longrich (2008, Figs. 3.9A, B, D). This Morphotype is found in the Dinosaur Park Formation, the Horseshoe Canyon Formation, and the Scollard Formation (Table 3.2).

Morphotype 2

These teeth closely resemble teeth from Morphotype 1, with prominent, textured anterior and posterior carinae, and a series of either primary longitudinal ridges, secondary longitudinal ridges on the crown surface, or both (Figs. 3.4C, D). The crown is also slightly curved, and is narrower and often more tapered than Morphotype 1, although as in Morphotype 1 the anterior and posterior margins are relatively straight. The carinae are continuous from the base to the apex of the crown. The central concavity on the lingual surface is more restricted to the base of the crown, rather than tapering towards the apex. A slight indentation is present ventral to the termination point of the carinae, and the roots are often expanded. On some teeth, the extent of the fine ridges may be restricted to the apical half of the crown, or extend more basally. In cross-sectional view, the teeth are strongly compressed and reniform in shape. This type also seems to have been included in Longrich (2008) (Fig. 3.9C, E) and is similar to one in Sankey et al. (2002) (Fig 5. 39-42). These teeth are found in the Milk River Formation and Dinosaur Park Formation (Table 3.2).

Morphotype 3

Morphotype 3 consists of only three teeth, including TMP 2014.006.0244A, TMP 1995.168.0013B, and UALVP 57560C. Morphotype 3 is strongly similar in shape to teeth in Morphotype 2, although these particular examples are smaller and have a slight lingual curvature (Fig. 3.4E). Densely spaced and often irregular secondary ridges are abundant on both TMP 1995.168.0013B and the UALVP 57560C, and only slightly visible and sparse on TMP 2014.006.0244A (this tooth is also somewhat smooth in appearance, and some features may have been worn away). The ridges on the labial surface are larger, more irregular, and splay slightly outwards in a fan onto the carina, whereas those on the lingual face are straighter, longer, and extend upwards towards the apex. The large, rounded primary ridges seen on most examples of

Morphotype 1, and some teeth in Morphotype 2, are absent. A slight constriction is present beneath the termination point of the carinae, and the expansion of the root is visible in most examples. Basally, TMP 1995.168.0013B is only slightly compressed and oval in section, although TMP 2014.006.0244A and UALVP 57560C are more similar to these characters in Morphotype 2 and are reniform in profile, as well as wider at the anterior edge. These teeth were recovered from the Dinosaur Park and St. Mary River formations (Table 3.2).

Morphotype 4

Morphotype 4 is represented by a single tooth (TMP 1996.062.0050A) that is also the smallest in the sample (1.2 mm in height) (Fig. 3.4G). The crown is low and broad, with convex anterior and posterior margins in lateral view and a strong basal constriction. As in Morphotypes 1, 2, and 3, it has fine, apically-directed ridges are present on the carinae, which produces a slightly folded or crenulated appearance. Longitudinal ridges appear to be absent on the lingual and labial faces, and the surfaces are otherwise featureless. The base of the crown is relatively rounded and lacks a central groove. In basal view the tooth is asymmetrical and wider anteriorly, but overall elliptical to lenticular in cross-section. This tooth was recovered from the Oldman Formation (Table 3.2).

Morphotype 5

Morphotype 5 is represented by two teeth, including TMP 1994.144.0114, which is among the smallest teeth included here at only 2mm in length (Fig. 3.4H). The crown is straight, fairly narrow, and arrowhead-like in shape, with large carinae and subtle longitudinal ridges near the middle of the crown and extending towards the apex. The middle of the crown from the base to the apex is somewhat bulbous. The basal constriction is prominent and the base of the tooth overall is relatively uniform in length. The basal cross-section is laterally compressed and subrectangular to oval in shape, although the anterior portion is greater in width than the posterior edge. The outline of TMP 1996.062.0054A in basal view is relatively long compared to TMP 1994.144.0114, and labiolingually the tooth is wider anteriorly than posteriorly. These teeth are from the Oldman Formation (Table 3.2).

Morphotype 6

Teeth from Morphotype 6 are triangular in lateral view with an anteroposterior wide base and narrow apex (Fig. 3.5A, B). This type of tooth is somewhat uncommon but distinctive in having restricted sections of denticles on the edges of the crown. Shallow grooves on the labial and lingual faces are occasionally located at the base of the crown in some specimens. The anterior margin near the crown base in lateral view is typically strongly curved and emphasizes the degree of basal constriction between the crown and root. In some specimens, the base of the posterior edge slopes outwards and forms a small, angled heel. The crown is curved and has either a thin carina that lacks denticles, or lacks a carina altogether. On all specimens, denticles are present on the lower posterior edge of the crown, although the number and size of each vary considerably and can be difficult to discern. In some instances (TMP 1995.181.0066G), the "denticles" appear to be simple waves or crenulations. For those teeth on which denticles were more easily observable, measurements were taken of the number of denticles, and average width and height were recorded to demonstrate the variation present (Table 3.3). Whereas some specimens, such as TMP 1987.158.76, have a slight figure-8 cross-section, most teeth in this sample are laterally compressed, lenticular to parlinon (linguoanteriorly and linguoposteriorly-angled margins) in cross-section, and typically labiolingually wider anteriorly than posteriorly.

This type is comparable to TMP 1989.103.0025 (Currie and Coy, 2008), although this particular tooth also preserved a small series of denticles on both the anterior and posterior edges. Due to the general faintness of the serrations in the sample or poor preservation, no denticles were readily discernable on the anterior face in other teeth. Sankey et al. (2002) described a tooth similar to TMP 1995.181.0066G that also had denticles on the posterior margin only (Fig 5. 43-36). These teeth were found in the Oldman, Dinosaur Park, and Horseshoe Canyon Formations (Table 3.2).

Morphotype 7

Morphotype 7 is the most disparate in terms of shape. Crown shape is overall similar to that of Morphotype 6, but lacks serrations and varies in the width of the crown base (Fig. 3.5C). The teeth are curved with a strongly bowed anterior margin. Like Morphotype 6 teeth, a small, angled shoulder is often present at the base of the posterior edge, beneath which the crown and root are noticeably constricted. The base of the anterior edge is either sharply angled or forms a smooth curve. The crowns of some specimens have a pinched appearance in lateral view due to the slight concave margin of the anterior and posterior faces near the apex (TMP 1996.181.0060H). Low carinae are typically present from the base to the apex on both anterior and posterior margins and are situated on the midline. The enamel surfaces are smooth and lack ornamentation on the labial and lingual faces. Preservation is variable, but some specimens may have had expanded roots in lateral view, whereas in others it appears the root was straight. The outline of the basal cross-section also varies slightly, although all are laterally compressed and elliptical to lenticular, despite the presence of slight indentations in some specimens that give the base a trapezoidal or weak figure-8 shape. This morphotype originates from the Oldman, Dinosaur Park, and Scollard Formations (Table 3.2).

Morphotype 8

Morphotype 8 is an uncommon tooth type that is distinct in having large longitudinal ridges on the labial and lingual faces of the crowns (Fig. 3.5D, E, F). The ridges are broad, separated by deep flutes, and extend longitudinally from the base towards the apex, although these are more poorly developed and are restricted to the base of the crown in TMP 1995.181.0066D. Carinal striae are absent. In lateral view, the crown is tall, narrow, and recurved with a rounded anterior edge and a relatively straight posterior edge. Small carinae are present on both margins, and are offset from the midline and angled lingually in basal view. The base of the crown is moderately rounded and gently slopes towards the weak basal constriction, rather than being more sharply angled as in Morphotypes 6 and 7. TMP 1996.181.0066J has a more pronounced basal shoulder on the anterior margin that projects past the root of the tooth. Cross-sections are laterally compressed and either rectangular to figure-8 in shape, or elliptical to slightly lenticular. Morphotype 8 is found in the Oldman and Dinosaur Park Formations (Table 3.2).

Morphotype 9

In lateral view Morphotype 9 is similar in shape to Morphotype 8, although the enamel surfaces are generally featureless (Fig. 3.6A, B). There are possible carinal striations or ridges similar to those of Morphotypes 1 and 2 on TMP 2000.045.0052. Crowns are long, narrow, and curved. Most specimens are anteroposteriorly broad at the base and taper near the apex. In some cases, most curvature occurs towards the apex. The anterior and posterior edges are straight to slightly curved, and rounded at the base. The lengths of the carinae vary (Table 2), and serrations are absent. Carinae are typically offset and angled lingually, giving some cross-sections a parlinon shape. The carinae in other specimens are situated on the midline of the tooth. Basal cross-sections are oval or rectangular to figure-8 in outline. Teeth are moderately laterally compressed and basal constrictions are weak to absent in lateral view. Morphotype 9 is fairly common and found in the Milk River, Dinosaur Park, and Horseshoe Canyon Formations (Table 3.2).

Morphotype 10

Morphotype 10 is somewhat similar to Morphotype 9 in being narrow and tall in lateral view. They appear to curve strongly forward due to the crown being shifted anteriorly with respect to the root (Fig. 3.6C, D). Both the anterior and posterior edges have a prominent posterior curvature distally. Minute carinae are present on the entirety of both the anterior and posterior margins. The labial and lingual surfaces are smooth and lack ornamentation, although a shallow and narrow indentation may be present at the base of the crown. There is no basal constriction, but the roots appear slightly expanded. In cross-section the teeth are compressed and weakly reniform to figure-8 in outline. TMP 2003.089.0033 was first mentioned in Brinkman et al. (2005). These teeth have been recovered from the Oldman and Scollard Formations (Table 3.2).

Morphotype 11

Morphotype 11 is represented by two specimens, each of which have a wide base and a straight, narrow crown that make them among the most conical of the teeth in the sample (Fig 3.6E). The base of the labial and lingual faces appears somewhat bulbous in anterior and poster views, and the anterior and posterior edges are rounded and curve inwards at the cervix. A slight constriction may be present as a result. The surface is smooth, although both examples appear worn. Minute carinae are present on the anterior and posterior margins of TMP 1995.181.0066B, and absent on TMP 1996.001.0014; however, the latter specimen may be more weathered. The teeth are weakly compressed and elliptical in cross-sections. Morphotype 11 is from the Dinosaur Park Formation (Table 3.2).

3.4 Principal Component Analysis

Principal component analysis clustered most putative avian teeth and crocodilian teeth separately (Fig. 3.2A, B). However, axes 1 and 2 failed to separate most putative avian morphotypes, with the exception of Morphotypes 4 and 11. Morphotype 4 plotted between *Ichthyornis* and *Richardoestesia*, and Morphotype 11 plotted between the putative avian and crocodilian clusters. Juvenile Nile crocodile teeth grouped with putative avian teeth on the first three component axes, but separated from juvenile *Alligator*, *Caiman*, and fossil crocodilian teeth. Although slight overlap with the avian cluster occurred, examples of Morphotype 1 tended to separate slightly from other morphotypes. Morphotype 3 was included within the Morphotype 2 hull. The tall and narrow shapes of Morphotypes 2 and 3 also overlap slightly with the similarly shaped crowns of Morphotype 9. Morphotype 5 overlapped with Morphotypes 6, 7, 8 and 9. The denticulate teeth of Morphotype 6 are mostly contained within the similarly shaped but non-denticulate teeth of Morphotype 7. *Hesperornis* and *Troodon* consistently plotted outside the main clusters. *Ichthyornis* clustered with putative avian teeth on axes 1 and 2, but outside of this group on axis 3. *Richardoestesia* fell outside the putative avian clusters on axes 1 and 2, but grouped with putative avian teeth on axis 3. TMP 1996.062.0050A (Morphotype 4) also separated from the putative avian clusters and plotted with *Hesperornis*, *Ichthyornis,* and *Troodon* in the third quadrant. Ninety-five percent of the variance was accounted for by axes 1 through 6; 72 percent variance was accounted for by axis 1, 13 percent by axis 2, and five percent by axis 3. Loadings for all variables were largely equal for axis 1, but dominated by AAL, and CBW, MCBW, and DCBW for axis 2. AL dominates axis 3 as well, with a moderate contribution from CH, and slight contribution from FABL, BC, and AD.

As CBW separated crocodilian and putative avian teeth (Figs. 2A, B), the analysis was repeated without CBW variables included. This resulted in the clustering of crocodilian and putative avian teeth (Fig. 3.3). *Alligator* in particular overlaps with Morphotypes 1, 2, 7, and 10, and Morphotypes 5, 6, 7, 8, and 9 to a lesser extent. *Caiman* overlaps primarily with Morphotype 1, but also slightly 6 and 10. Fossil crocodilian teeth and Nile crocodile teeth overlap primarily with other crocodilians, but also with Morphotype 1. *Richardoestesia* overlaps with Morphotypes 9 as in the PCA including CBW, but now clusters with 7 and 8 as well. *Ichthyornis* and Morphotype 4 clusters near to but outside the main putative avian teeth, although *Hesperornis* and *Troodon* are separated mainly by apical distance as a result of their strong posterior curvature. 80 percent variance was accounted for by axis 1, 10 percent by axis 2, and slightly less than five percent by axis 3. As with the previous PCA, variable loadings are equal in axis 1, but AAL and AD contributed most to axes 2 and 3, with some input from FABL, BC, and CBL.

3.5 Discussion

3.5.1 Principal Component Analysis

Unquestionable avian and non-avian theropod teeth mostly separated from putative avian teeth, particularly in the case of *Hesperornis*. The *Hesperornis* tooth used here is very strongly curved (Dumont et al., 2016), and consistently plotted separately from the main clusters in PCA. Also, it is reported that curvature in *Hesperornis* teeth varies depending on position in both the upper and lower jaws (Dumont et al., 2016); measurements representing curvature played a role in separating teeth in PCA, and the addition of more examples would possibly result in *Hesperornis* teeth clustering in varying positions throughout the graph. *Hesperornis* and *Ichthyornis* teeth also differ substantially in terms of shape, and as a result they tended to plot separately both from each other and putative avian teeth.

In an analysis by Dumont et al. (2016), workers found considerable overlap of teeth with respect to height and length, while measures similar to those used here (CH, FABL, etc.) had minimal influence on clustering of morphotypes. Dumont et al. (2016) found that the ratio of basal crown width to crown height was the only parameter able to separate avian, assumed avian, and similar non-avian theropod teeth; otherwise bird and non-avian coelurosaurian teeth could not be distinguished. CBW was also found to play a major role here, although this was secondary to AAL and AD. AAL, AD, and basal width measurements contribute substantially to axis 2. These represent curvature of the crown and degree of lateral compression, respectively. Axis 3 is dominated by AAL, but also by CH and CBW, indicating there is some influence of size in both lateral and basal aspects, but also of crown curvature.

Due to the approximately equal loading values of variables for axis 1, this axis is interpreted as a composite index of size. Small teeth plot on the left and increase in size towards the right (Fig. 3.2A). In addition to a low percent variance, the loadings of axes 4 and following components are highly variable and therefore more difficult to interpret, and as such are not considered here. Thus, axes 2 and 3 may be more informative as they are more indicative of relative shapes. The differentiation of Morphotype 1 in axes 2 and 3 was largely due to variables including AD, CH, FABL, and BC (Fig 3.3). The tall, broad, straight, and strongly compressed crowns likely account for most of the separation of Morphotype 1 from other types, as others

(Morphotypes 3, 6, 7, 8, 9, 10) typically have more curved crowns and are narrower with less lateral compression. Most notably, PCA was also able to distinguish between most crocodilian teeth and putative avian teeth. In general, the wider, elliptical teeth of juvenile *Alligator*, *Caiman*, and fossil crocodilian teeth were not as strongly compressed as putative avian teeth from Alberta. Basal width measurements are therefore the main variables separating teeth in axes 2 and 3. However, strongly-compressed juvenile *Crocodylus* teeth clustered with putative avian teeth rather than other crocodilians, and overlapped with several morphotypes. The repeated PCA with CBW removed resulted in Morphotype 1, 2, 4, and 10 overlapping almost entirely with other extant and fossil crocodilian teeth, primarily *Alligator* (Fig. 3.3). The slight overlap of Morphotypes 6, 7, 8, and 9 with crocodilian hulls underscores the similarities observed between crown shape in putative avian and crocodilian teeth. The addition of laterally compressed fossil crocodilian teeth would likely result in a similar outcome.

TMP 1995.181.0066B and TMP 1996.001.0014 (Morphotype 11) have intermediate crown basal widths, hence their placement between the avian and crocodilian clusters. As AAL dominated PC 2, Morphotype 4 (TMP 1996.062.0050A) clustered outside the main groups and near *Ichthyornis*, both of which have relatively straight crowns. The high AAL value of this example is likely due to its proportionally wide base and strongly convex anterior and posterior margins. Interestingly, *Richardoestesia* was not distinguishable from putative avian teeth in axes 2 and 3, and overlapped with Morphotype 9. If Morphotype 9 teeth are indeed avian, at least in terms of AAL, CBW, and AD, some non-avian theropod teeth may be more bird-like than either *Hesperornis* or *Ichthyornis*.

Despite the overlap in both PCA's, the presence or absence of surface ornamentation maintains the separation of various morphotypes. Although crown shape is similar, the slight lingual curvature and extent and types of surface ornamentation separate Morphotype 3 from Morphotype 2. Morphotype 9 is distinct from Morphotypes 2, 3, and 8 due to absence of surface ornamentation. Denticles separate Morphotype 6 from similarly-shaped teeth of Morphotype 7, and other overlapping Morphotypes, such as 2 and 9.

The overlap of most putative avian morphotypes could suggest that these represent a single taxon. However, PCA doesn't necessarily distinguish between similarly shaped teeth belonging to different taxa (Smith et al., 2005), as was the case here with overlapping *Alligator*, *Caiman*, and fossil crocodilian teeth (Fig. 3.2, 3.3). Several morphotypes also derive from different stratigraphic sections and different stages within the Upper Cretaceous (Table 3.2); thus, it is less likely that this tooth sample represents only a single taxon.

The single clustering of morphotypes, variable overlap with known avian and non-avian theropod teeth, overlap with laterally compressed crocodilian teeth, and overlap of avian and crocodilian teeth in the absence of CBW variables suggest that there is no particular shape variable that is distinctly avian, or can distinguish between various types of archosaurian teeth. While fossil crocodilian teeth clustered separately and with extant taxa, PCA was used as an assessment of variance in shape and excludes features such as surface ornamentation. Morphotypes 1, 2, 3, 4, and possibly 5 share a number of surface features with modern and fossil crocodilians, including primary and secondary ridges, and carinal striae.

3.5.2 Qualitative Comparison of Putative Avian Teeth with Other Taxa

A number of features have been proposed as diagnostic of bird teeth, although most if not all have also been found in other archosaurs (Dumont et al., 2016). Currie (1987) suggested that a basal constriction between the root and crown was a synapomorphy for both birds and troodontids. However, Dumont et al. (2016) noted that various studies have reported both a basal constriction and a lack of denticles on teeth of other theropods, including certain therizinosaurs, alvarezsaurids, and ornithomimosaurs. Sankey et al. (2002) described bird teeth that lack denticles, with straight, triangular, and laterally compressed crowns with indented bases, and frequently carinae on the anterior and posterior edges. These were identified as avian because of their similarity to *Hesperornis* teeth, although they also resembled the dentition of closely related non-avian theropods, namely *Microraptor zhaoianus*, *Richardoestesia gilmorei* and *Richardoestesia isosceles*. The posterior teeth of *Microraptor* are constricted between the root and crown as in troodontids and birds (Currie, 1987; Xu et al., 2000). In rare instances, avian teeth possess denticles and crenulations on restricted areas of the crown on avian teeth (Currie and Coy, 2008; Wang et al., 2015). Currie and Koppelhus (2015) also identified bird teeth by a bulbous crown, although *Hesperornis*, *Ichthyornis*, although most putative avian specimens from the TMP and UALVP collections lack this feature (Dumont et al., 2016). Dumont et al. (2016) also noted that an expanded root was originally described as an avian feature, but this too is present in some theropods, and in this study was also observed in crocodilians. In fact, all features typically described as avian, including a basal constriction, can be found in at least some crocodilians as well.

3.5.3 Comparisons with the Dentition of Crocodilians

Crocodilian fossils are relatively common in Alberta and typically consist of isolated teeth and scutes (Brinkman, 2005). Described taxa include the neosuchian *Gilchristosuchus palatinus* from the Milk River Formation, the alligatoroids *Leidyosuchus canadensis* and *Albertochampsa langstoni* from the Dinosaur Park Formation, the alligatorine *Strangerochampsa mccabei* from the Horseshoe Canyon Formation, and a probable crocodyloid *Albertosuchus knudsenii* from the Scollard Formation (Wu et al., 1993; Wu et al., 2001*b*; Wu, 2005; Wu et al., 2015).

Leidyosuchus is the most common and is also well-represented by skull and jaw material (Wu et al., 2001*b*), although very young crocodilian skeletal (and especially jaw material) is unknown in Alberta. As a result, the only juvenile crocodilian teeth I had access to were from *Alligator mississippiensis* (6.3 skull length), and possibly *Caiman crocodilus* (unknown age, 16.25 skull length).

In *Leidyosuchus* and modern crocodilians, tooth morphology varies widely within the adult jaw, although shapes are generally similar between opposing positions within the maxillary and dentary teeth (Fig. 3.8). Teeth in the premaxilla, anterior maxilla and dentary are caniniform and often curved lingually and posteriorly. In juvenile *Alligator* these teeth are also procumbent. In cross-section, these teeth are circular to subcircular (Fig 3.8). In larger specimens of *Leidyosuchus*, a basal constriction is not present and the root instead expands abruptly at the cervix of the tooth (Fig 3.8B, C, E). In *Caiman* and juvenile *Alligator*, a basal constriction between the root and crown is more pronounced and present throughout the jaw (Fig. 3.7). Midway along the maxilla and dentary, tooth crowns are straighter and shorter with little or no lingual curvature. The anterior and posterior edges are straighter, although these gradually become more bulbous progressing posteriorly in the jaw. The most posterior teeth are distinctive in being smaller, low, and bulbous with no lingual or posterior curvature. In adult *Leidyosuchus*, the apices of the more posterior teeth are typically blunt due to wear, although in juvenile *Alligator* and *Caiman* the apex is a rounded point. *Leidyosuchus* teeth are also slightly compressed ellipses in cross-section, although less compressed than in *Alligator* and *Caiman*. The posterior teeth in the lower jaw of juvenile *Alligator*, *Caiman*, and *Leidyosuchus* appear to be more compressed than those in the upper jaw. Posterior teeth are also more compressed than anterior teeth, which are subcircular in cross-section (Fig. 3.7, Fig. 3.8). These teeth are often closely spaced in the jaw and lack lingual or posterior curvature. Most if not all teeth have carinae on the anterior and posterior edges which may be along the midline of the tooth, or slightly offset and angled lingually.

Many teeth in all three taxa also have fine features on the enamel surface and isolated crocodilian teeth from Alberta show similar features to modern examples. Primary longitudinal ridges are most easily visible on teeth in the mid-portion of the jaw of *Caiman* (Fig. 3.7D), and are also evident in synchrotron images of a juvenile *Crocodilus* in Dumont et al. (2016) (Additional file 10, Fig. S3). TMP 1986.008.0074 from the Dinosaur Park Formation is comprised of a large sample of isolated teeth roughly similar in size to those from the avian sample (Fig 3.4A). Four examples show prominent longitudinal ridges that either extend the full height of the crown or are restricted to the upper portion (Fig 3.9A). The ridges run parallel along both lingual and posterior faces and can be straight or wavy. Small ridges or striae are visible on the carina in some examples. One tooth is fairly worn, but may have a margin midway on the crown similar to some examples of Morphotypes 1, 2, and 3 (Fig. 3.4). In basal view, teeth vary in the amount of lateral compression and range from elliptical to subcircular.

UALVP 54359 comprises two small isolated teeth from the Dinosaur Park Formation (Fig. 3.9B, C). UALVP 54359A is slightly larger than teeth from Morphotype 1, and is similar in shape in lateral aspect. The crown is mostly straight with a slight lingual curvature and has prominent primary and secondary longitudinal ridges, as well as striations along the carinae (Fig. 3.9B, Fig. 3.10D). In cross-section the tooth is elliptical in shape with lingually-offset carinae. The crown of UALVP 54359B is tall, narrow, conical and slightly curved lingually (Fig. 3.9C). Although this tooth is very different in shape from UALVP 54359A, slight primary and secondary longitudinal ridges extend midway on the crown to the apex. Carinae are present on the anterior and posterior edges, although they appear to lack the ridges or striae visible on UALVP 54359A.

UALVP 48607 comprises two medium-sized isolated crocodilian teeth from the Dinosaur Park Formation, Dinosaur Provincial Park (Fig 3.8E). UALVP 48607A is similar in shape to UALVP 54359A and straight-crowned examples of Morphotype 1. The surface of the crown is only slightly ornamented, with faint irregular texturing midway on the crown to the apex. It is difficult to discern whether or not these are longitudinal ridges. Possible primary ridges may also be present in the middle portion of the tooth, but these are difficult to discern. UALVP 48607B is long, conical, curved, and similar in shape to UALVP 54359B. The carinae are prominent and feature slight angled striae visible in UALVP 543559A and various examples of putative avian teeth from Morphotypes 1, 2, and 3. Very faint primary longitudinal ridges are visible in the middle section of the crown.

In spite of PCA separating most crocodilian teeth from putative avian teeth, parallels in shape and surface ornamentation can also be observed. Previous comparisons between crocodilian and avian teeth found some similarity in enamel ornamentation in the form of fine ridges on the anterior and posterior faces, but putative bird teeth were far more laterally compressed than would be typical for a crocodilian (Longrich, 2008). While both modern and fossil crocodilians are best known for their tall, conical teeth with rounded bases, examination of the dentition in juvenile *Alligator mississippiensis* and *Caiman crocodilus* found laterally compressed teeth that vary widely in shape (Fig. 3.7E, F). Martin (1980) also reported various similarities in crocodile and avian tooth morphology and implantation, noting that juvenile crocodilian teeth were laterally compressed. Initially this resemblance was presented as evidence of the non-theropod ancestry of birds, although this has since been refuted (Dumont et al., 2016).

Hesperornis teeth, for example, are situated in a continuous and constricted groove somewhat similar to that seen in juvenile crocodilians (Martin, 1980), although the septa are comprised of jaw bone in the former and alveolar bone in the latter (Dumont et al., 2016).

Morphotypes 1, 2, 3, and 4 in particular closely resemble crocodilian teeth. Shape among these teeth varies widely, and several morphotypes are comparable to teeth in the maxilla and dentary of juvenile *Alligator mississippiensis*, *Caiman crocodilus*, and to some extent isolated crocodilian teeth and the teeth of older specimens of *Leidyosuchus.* Prasad and Lapparent de Broin (2002) documented several cross-sectional shapes in isolated crocodilian teeth including subcircular, elliptical, lenticular, figure-8, and salinon, all of which are also present throughout the Alberta sample. Small, laterally compressed teeth with enamel ornamentation have been referred to as crocodilian by some authors (Rana and Sati, 2000; Prasad and Lapparent de Broin, 2002), whereas similar teeth are categorized as possibly avian by others (Sankey et al., 2002; Sankey, 2008; Longrich, 2008). In regards to cross-sectional shape, there is considerable overlap between avian, theropod, and crocodilian teeth. The variation in lateral and basal tooth shapes both in a single crocodilian jaw and across taxa is a continuum, such that tooth shapes grade into each other. As a result, some crocodilian teeth may closely resemble avian ones. This is demonstrated by the clustering of laterally compressed extant crocodilian teeth with putative avian teeth, and wider crocodilian teeth clustering outside this main group (Fig. 3.2B). Many morphotypes vary in the amount of lateral compression of the crown, such as Morphotype 3, where basally the cross-sectional shape is either a broad reniform or ovate profile. The crowns of Morphotype 3, however, are similar to those of Morphotype 2, which have more strongly-compressed reniform cross-sections. Degree of compression also varies widely within one side of a single jaw in crocodilians (Fig. 3.7E, F, Fig. 8D). Dumont et al. (2016) showed that salinon, reniform, and elliptical teeth are present in juvenile crocodiles. Martin (1977) and Dumont et al. (2016) also reported that the teeth of *Hesperornis* and *Ichthyornis* vary, but are often conical and appear to range from lenticular in cross-section, to almost subcircular. The lenticular or ovate *Ichthyornis* teeth are less compressed than many putative avian teeth from Alberta, particularly Morphotypes 1, 2, and 3. As a result, the degree of lateral compression alone is not necessarily reliable for distinguishing among avian, non-avian theropod, and crocodilian teeth.

In lateral view, Morphotype 1 is similar to those teeth present midway on the maxillae and dentaries of crocodilian jaws (Fig 3.7B, D). These teeth are broad with relatively straight anterior and posterior edges, and are typically ornamented with longitudinal ridges on both labial and lingual faces. Large, primary longitudinal ridges are particularly visible in *Caiman* (Fig. 3.7D), and on SEM and synchrotron images of juvenile crocodile teeth (Dumont et al., 2016). The isolated crocodilian teeth TMP 1986.008.0072 and UALVP 54359A are also similar in shape and bear the same combination of ridges on the carinae and lingual and labial faces of the crown. The most notable difference is the amount of lateral compression of teeth in Morphotype 1, which is more pronounced than in TMP 1986.008.0072, UALVP 54359A, and *Leidyosuchus*. TMP 2009.137.0018, TMP 2009.137.0019, and TMP 2009.139.0005 described as *Archosauria indet.* by Larson et al. (2010) also feature secondary longitudinal ridges resembling those in teeth of Morphotype 1. TMP 2009.139.005 is similar, and also appears intermediate in width to Morphotypes 1 and 2. Although crocodilian teeth are often more rounded in cross-section, this nonetheless varies both in the jaw and across taxa (Fig 3.7). Teeth from TMP 1986.008.0072, UALVP 48607, UALVP 54369A and medium to large specimens of *Leidyosuchus* are elliptical to sub-circular. The teeth of juvenile *Alligator* and *Caiman* are ovate to sub-circular. Synchrotron images of juvenile crocodile teeth included in Dumont et al. (2016) show a similar degree of compression to teeth in Morphotype 1 (Additional file 10, Fig. S3). Both are also reniform in cross-section, with a small groove on the lingual face and lingually-angled anterior and posterior edges. Even in more rounded crocodilian teeth, the carinae are frequently offset and the anterior and posterior edges are likewise angled lingually.

Apart from the fan-like pattern of ridges on the labial surface and lingual curvature of the crown in Morphotype 3, these teeth are broadly similar in shape to and therefore comparable with Morphotype 2. These teeth are caniniform in shape and relatively tall and narrow. Lingual curvature seen in Morphotype 3 is a common feature in crocodilian teeth, and most easily visible in the long, narrow teeth in the anterior portions of the jaw (Fig. 3.7C). Although Morphotype 2 is similar in shape to some *Hesperornis* teeth (eg., YPM 1206A, Dumont et al. (2016)), the narrow, tall and slightly curved teeth are also similar to the premaxillary and anterior maxillary and dentary teeth of juvenile *Alligator*. A slight constriction present in Morphotype 2 and 3 is also visible in similarly shaped teeth in juvenile *Alligator* and *Caiman*, although this feature is often absent in larger *Leidyosuchus* teeth (Fig. 3.7, Fig. 3.8). In *Leidyosuchus*, UALVP 48607B, and UALVP 54369B, the cross-sectional shape is more circular unlike the strongly compressed and weakly reniform profile of teeth in Morphotype 2. Certain examples of Morphotype 3 have a slightly wider reniform profile, although they can also be elliptical in shape and similar to some small crocodilian teeth. Carinae are observed on both Morphotypes 2 and 3, and all crocodilians studied, although like juvenile *Alligator* teeth, the carinae may be more centered on the midline of the crown (Fig 3.4C, D, E, Fig. 3.10B, C, E, F). Primary and/or secondary ridges visible in Morphotypes 2 and 3 are present in juvenile *Alligator*, *Caiman* and fossil crocodilian teeth (Fig 3.4, Fig. 3.7, Fig. 3.10). Angled striae present on the carina in Morphotype 2 are also often visible on larger crocodilian teeth. Isolated fossil caniniform teeth nearly identical to

Morphotypes 2 and 3, although larger, were described and identified as crocodilian by Prasad and Lapparent de Broin (2002). Heavily worn, longitudinal ridges were present midway on the crowns, which also had slight lingual curvature. Unlike teeth from Alberta, the crocodilian teeth were elliptical in cross-section.

The distinct enamel margin visible in most specimens of Morphotypes 1, 2, and 3 has also not been described in avian teeth. This feature is not visible in modern crocodilian teeth, but may be present in fossil crocodilian teeth (Fig 3.4, Fig. 3.9A). The margin is consistent in shape and extent across all specimens included in these morphotypes, and is present in similar teeth from various localities and different formations. Likewise, teeth assigned to different Morphotypes yet found in the same locality lack this feature, so that it is unlikely to be a result of taphonomy or erosion. Potentially representing the gum line, both this feature and enamel ornamentation links these Morphotypes 1, 2, and 3 together.

Although fine ridges have been reported on the teeth of *Hesperornis* (Dumont et al., 2016; Wilson et al., 2016), the morphology and distribution of surface ornamentation on the crowns of Morphotype 1, 2, and 3 most closely resembles that seen on crocodilian teeth (Fig. 3.7, Fig. 3.9, Fig. 3.10). The enamel surface of Morphotype 9 is featureless, although some examples (eg.,TMP 2000.045.0052) have a prominent carina with slight, angled ridges that may link some curved, caniniform examples with the highly ornamented and crocodilian-like Morphotypes 1, 2, and 3. The isolated crocodilian tooth UALVP 54359B also shares this feature, and is also more conical in cross-section like a typical crocodilian tooth (Fig 3.9C). Unserrated carinae and surface ornamentation in the form of longitudinal ridges is shared by some non-avian theropods (*Paronychodon*), birds (*Hesperornis*) and crocodilians, although the presence of both striated carinae and either large, rounded, or small, fine longitudinal ridges currently seems to be unique to crocodilians. Apically-angled striae located on the carinae in these teeth has also been described on the laterally compressed, unserrated teeth of "false-ziphodont" crocodilians (eg., *Asiatosuchus*, *Trematochampsa* (Prasad and Lapparent de Broin, 2002)). The low, broad crown and crenulated carinae of Morphotype 4 bear strong resemblance to crocodilian teeth situated in the upper and lower posterior regions of the jaws in *Alligator*, *Caiman*, and *Leidyosuchus*. Similarly shaped teeth from the Nile Crocodile (*Crocodilus niloticus*) have also been illustrated in Poole (1961), in Late Cretaceous fossil *Crocodylia indet.* (Prasad and Lapparent de Broin, 2002), and Paleocene *Asiatosuchus sp*. (Rana and Sati, 2000), all of which have crenulations or serrations along the anterior and posterior carinae.

The small, arrowhead-like shape of Morphotype 5 is similar to *Ichthyornis* teeth (Dumont et al., 2016), although the angled root appears to be absent, and small teeth with straight to slightly-curved edges are also present in the middle portion of the jaws of juvenile *Alligator* (Fig 3.7B). In both cases, the anterior and posterior edges are rounded at the base of their crowns. TMP 1994.144.0114 is narrower than TMP 1996.062.0054A, and width also varies in crocodilian teeth. Although much broader, the overall shape is similar to juvenile crocodile tooth images from Dumont et al. (2016). In basal view, the broadly lenticular to elliptical shape of Morphotype 5 closely resembles teeth seen in juvenile *Alligator* and *Caiman*. As in many crocodilian teeth, possible ridges are present mid-crown or near the apex, although these are faint and possibly eroded. As the combination of primary and secondary longitudinal ridges and striated carinae is present in fossil and modern crocodilian teeth, but has not been described in a Mesozoic bird, this particular combination could potentially represent a distinguishing feature of crocodilian teeth. Additionally, enamel ornamentation tends to be most prominent in small crocodilian teeth (Fig. 3.9A), and can be reduced or more difficult to discern in larger examples, such as teeth within the jaws of larger *Leidyosuchus* (Fig 3.8). This gradation may be a result of ontogeny, with clear features on the crown diminishing with age, or be due to individual or interspecific variation in surface structure within the jaw.

Other Morphotypes, particularly 6, 7, 8, and 9, are more difficult to compare because they share features both with crocodilians, non-avian theropods, and some birds. Morphotype 8 is loosely similar to the long, narrow, and often curved teeth in the premaxilla and the middle and anterior portions of the maxilla and dentary in crocodilians (Fig. 3.7C). The crowns also bear large longitudinal ridges, roughly equivalent to primary longitudinal ridges in crocodilian teeth (Fig. 3.5D, E, F). In Morphotype 8, however, these ridges may be irregular or restricted to the base of the tooth rather than the entire crown, or concentrated near the apex, as seen in TMP 1986.008.0074, UALVP 54359B, *Caiman*, and *Leidyosuchus* (Fig. 3.7, Fig. 3.8). The rounded anterior and posterior edges of TMP 1995.191.0066F resemble those of some *Hesperornis* teeth described by Cumbaa et al. (2002), although a similar shape is also present in juvenile *Alligator* (Fig. 3.5F, Fig. 3.7C). Some examples of Morphotype 8, and TMP 1995.181.0066J in particular, also bear strong resemblance to teeth of the possible non-avian theropod *Paronychodon lacustris* (Fig. 3.5D), which also has a strong posterior curvature, strong longitudinal ridges, and a prominent projection at the base of the anterior edge of the crown (Sankey et al., 2002). The lenticular to elliptical and figure-8 shaped cross-section typical of Morphotype 8 is also present in *Caiman* (Fig. 3.7F), some crocodilian teeth described by Prasad and Lapparent de Broin (2002), and *Paronychodon* (Sankey et al., 2002; Gates et al., 2015), or *Paronychodon*-type teeth (suggested to be synonymous with *Richardoestesia sp*., although see Larson (2009)) (Longrich, 2008).

Non-avian theropods seem to account for the larger ziphodont teeth from Alberta, and none have been attributed to crocodilians (Sankey et al., 2002; Larson and Currie, 2013). However, a crocodilian identification cannot necessarily be ruled out for the denticulate teeth in Morphotype 6. The teeth of the ziphosuchian crocodyliform *Doratodon ibericus* from the Campanian of Spain are laterally compressed with relatively straight denticles on the anterior and posterior edges (Company et al., 2005). A basal constriction was reported as absent, although in Fig. 3A, a slight indentation between the crown and root is drawn in tooth 9. As in *Leidyosuchus* and modern alligatorids, the anterior teeth of *Doratodon* were described as conical and sub-circular in cross-section and curve lingually, and mid and posterior teeth are straighter and more laterally compressed than those in the anterior portion of the jaw, which are typically conical and sub-circular. Unlike in *Caiman* and *Leidyosuchus*, surface ornamentation is absent on the labial and lingual faces, a feature that is shared with *Richardoestesia* (Sankey et al., 2002). Company et al. (2005) described the teeth of *Doratodon* as highly similar to those of *Richardoestesia isosceles*, which they regarded as more crocodilian-like, and as such may instead be a crocodyliform rather than a non-avian theropod. *Richardoestesia isosceles* teeth are however described as tall and narrow in Sankey et al. (2002), while *Doratodon* teeth are illustrated in Figure 3 of Company et al. (2005) as low and broad like the teeth of *Richardoestesia gilmorei*, which may also vary in the degree of constriction between the root and crown (Sankey et al., 2002; Longrich, 2008). Additionally, the cross-sectional trapezoidal shape in *Richardoestesia* teeth as described by Sankey et al. (2002) is also seen most clearly in the upper and lower mid-portion jaw of modern *Caiman crocodilus* (Fig 7F), and Late Cretaceous *Crocodylia indet.* (Prasad and Lapparent de Broin, 2002). This shape, however, is not evident in in situ crocodilian teeth from the Late Cretaceous of Alberta. Likewise, no ziphodont crocodilians have been described from the province. As a result, precise affinities of denticulated Morphotype 6 teeth are difficult to determine without further material. Morphotype 7 is also problematic as serrations are absent, but many examples closely resemble Morphotype 6 in shape. In PCA these two types overlap considerably, such that most specimens in Morphotype 7 fall within the same morphospace as Morphotype 6 (Fig. 3.2). The amount of curvature in Morphotype 7 varies such that some specimens are nearly straight and similar to teeth in the middle to posterior areas of the jaw, as well as isolated crocodilian teeth (Fig. 3.7B). The lenticular cross-sections are also more typical of crocodilians, although this particular shape can grade into more trapezoidal or figure-8 shapes also seen in non-avian theropods.

In some examples, crown shape of Morphotype 9 is tall and narrow and may be reminiscent of some examples of Morphotypes 2, 3, and 8 (Fig. 3.4, Fig. 3.5). Larson et al. (2010) referred TMP 2003.057.0002 to Avialae indet. However, it and other examples of Morphotype 9 resemble non-avian theropod teeth (Sankey et al., 2002; Longrich, 2008; Sankey, 2008), including dromaeosaurids and *Richardoestesia*. Examples with straighter crowns are similar to long, narrow crocodilian teeth positioned anteriorly in the jaw (Fig. 3.7C). A basal constriction is typically present, as in juvenile *Alligator* and *Caiman,* and some examples of *Richardoestesia* (Longrich, 2008). Denticles are absent in Morphotype 9, although a prominent carina in some examples is similar to those in Morphotypes 1, 2, 3, and 4, and is present in some crocodilian teeth, including *Leidyosuchu*s (Fig. 3.4, Fig. 3.8, Fig. 3.9). Norell et al. (1994) also described a neonate dromaeosaurid with unserrated teeth, which were more conical in shape, rather than laterally compressed. *Paronychodon* teeth are also unserrated, and the presence of denticles on *Richardoestesia* can vary (Sankey et al., 2002; Longrich, 2008). In cross-section teeth included in Morphotype 9 are less compressed than those in Morphotypes 1 and 2, and are similar to broad lenticular, elliptical, and figure 8-shaped teeth seen in *Alligator*, *Caiman*, and *Leidyosuchus* (Fig. 3.7E, F, Fig. 3.8). Rectangular figure-8 shaped cross-sections also occur in these and crocodilian teeth, which is a feature shared with most small non-avian theropods including *Richardoestesia* (Currie et al., 1990; Prasad and Lapparent de Broin, 2002; Sankey et al., 2002; Longrich, 2008).

Although Morphotype 11 lacks the curvature and surface ornamentation seen in Morphotypes 2 and 3, it may be comparable to some teeth in the middle portions of upper and lower crocodilian jaws (Fig. 3.7B). The straight anterior and posterior edges and rounded base are most similar to those in juvenile *Alligator*. Basally, Morphotype 11 is similar to crocodilian teeth in being broadly lenticular or elliptical in shape (Fig. 3.7B, E, F). This particular type may be among the most difficult to interpret as they are rare and relatively nondescript, in addition to being fairly worn. These teeth also grouped outside both crocodilian and putative avian teeth following PCA (Fig. 3.2).

Most Morphotypes (1, 2, 3, 4, 5, 11) are directly comparable to crocodilian teeth in terms of both shape and enamel features. In many cases this diagnosis cannot be ruled out for those teeth that also bear similarity to other taxa (6, 7, 8, 9), including non-avian theropods and birds.

3.5.4 Toothed Birds in Alberta

While other more basal lineages, including the Enantiornithes and Ornithuromorpha, are abundant in assemblages from the Early Cretaceous of Asia, non-neornithine ornithurine birds appear to have been the predominant avian group in Late Cretaceous of North America (Longrich, 2009; Longrich et al., 2011). Most fossil avian material from Alberta has been referred to Ornithurae, including *Hesperornis*, *Ichthyornis,* and *Palintropus* (Fox, 1968, 1974; Longrich, 2009), whereas a large number of isolated fragments of the postcranial skeleton were designated as provisional ornithurine taxa (Longrich, 2006, 2009; Longrich et al., 2011). If any of these teeth are referable to Aves, it is likely that they belong to a toothed ornithurine bird. Some of this material was tentatively attributed to Neornithes (Hope, 2002), although this has been refuted (Longrich, 2009; Longrich et al., 2011). The more basal and toothed Enantiornithes were also likely present, although material has only been positively identified from the Late Cretaceous of nearby British Columbia, Saskatchewan, and Montana (Martin, 1982; Morrison et al., 2005; Longrich et al., 2011). In contrast to the rows of teeth in the maxilla and dentary of known ornithurine birds, enantiornithine teeth also occur in the premaxilla, and teeth in the dentary and maxilla can be restricted anteriorly, or absent altogether (O'Connor and Chiappe, 2011). The dental morphology of enantiornithine birds is also highly diverse, although most teeth are similar to those of *Archaeopteryx* and are curved, conical, have constricted bases, and bear no surface ornamentation or denticles (Louchart and Viriot, 2011; O'Connor and Chiappe, 2011). Low, conical, and largely straight teeth are present in the premaxillae, dentary, and maxillae of *Pengornis* (Zhou et al., 2011). Also, those placed more posteriorly in the jaw are blunter and show wear facets, suggesting that tooth morphology can differ with age. *Longipteryx* has large, highly curved teeth with slight lateral compression, although the robust dentition of *Shenqiornis* is circular in cross-section (O'Connor and Chiappe, 2011). Multiple longitudinal grooves run parallel along the bulbous crowns in *Sulcavis*, which were seemingly specialized for crushing (O'Connor et al., 2013). While *Sulcavis* teeth possessed small grooves only on the lingual surface, raised ridges are present on both faces in the teeth from the Alberta sample (Fig. 3.4, Fig. 3.10). Precise comparisons of cf. Aves teeth with enantiornithine teeth can be problematic as many enantiornithine specimens often preserve teeth in the jaw and tend to be highly compressed, making it difficult to measure teeth in basal view. Incorporating enantiornithine teeth into multivariate analyses would therefore be problematic where CBW's are major variables that separate tooth shapes.

3.5.5 Comparisons with the Dentition of *Hesperornis* and *Ichthyornis*

The teeth of the extinct North American ornithurine birds *Hesperornis* and *Ichthyornis* were first described by Marsh (1880), and then in greater detail by Martin (1977). Small, triangular teeth were present in the maxillae and dentaries of both *Hesperornis* and *Ichthyornis*, although absent in the premaxilla. The crown of *Ichthyornis* is straight, although it is angled relative to the root and therefore appears to have a strong posterior orientation in the jaw (Dumont et al., 2016). The carinae in *Ichthyornis* teeth were described as larger than those of *Hesperornis* and extend from the base to the apex. The enamel surfaces lack ornamentation, and the teeth are conical in shape and more constricted at the base than in *Hesperornis*. Basally, isolated teeth of *Hesperornis* and *Ichthyornis* are elliptical in cross-section, although when situated in a jaw, they may be more compressed as a result of deformation (Dumont et al., 2016). While some these features are shared with the Alberta sample, only a few teeth bear close resemblance to those of *Ichthyornis* as identified by Dumont et al. (2016). TMP 1994.144.0114 (Morphotype 4) is somewhat similar to UAM_PV93.2.133_1 and UAM_PV93.2.133_2 in having a straight, arrowhead-shaped crown with a large posterior carina extending from base to apex, although the medial and posterior edges are not as convex. The edges are also more rounded at the base in lateral view, and the basal constriction is more prominent, and lacks an angle between the crown and root visible in UAM_PV93.2.133_2 (Dumont et al., 2016). Two small jaw fragments containing teeth from the Cenomanian Greenhorn Formation of Kansas and comparable to those of Morphotype 10 were diagnosed as an unidentified avian by Bell and

Everhart (2011). Although largely lacking diagnostic features, the fragments were identified as avian based on the curved, unserrated teeth and prevalence of foramina on the jaw. As in TMP 1996.062.0052B, TMP 2003.089.0033, TMP 2009.163.0081B (Morphotype 10), enamel ornamentation is absent and the anterior and posterior edges are strongly curved. The bases of the posterior margins of the crowns in particular are strongly angled, giving the teeth a swept-forward appearance. Although Morphotype 10 is considerably younger in age, it is among the most similar to avian teeth with associated jaw material.

Dumont et al. (2015) described the teeth of *Hesperornis* as curved or hook-like, with fine longitudinal ridges extending from the base of the crown to the apex. Carinae are small and do not reach the apex or base of the crown. UALVP 57560C has a tall, narrow, curved crown that is laterally compressed in basal view resembles teeth in YPM.1206B (Fig. 3.4F), a *Hesperornis* jaw described by Dumont et al. (2016). YPM.1206B was reported as compressed post-mortem, whereas the UALVP 5760C has no indication of taphonomic distortion. Long, longitudinal ridges extending from base to apex of crowns in *Hesperornis* teeth are absent in UALVP 57560C, although slight secondary ridges are restricted to the upper portion of the crown, similar to those seen in Morphotypes 1, 2, and 3 (Fig. 3.4). The overall shape of the UALVP tooth also closely resembles teeth in Morphotype 2.

Four isolated teeth from the Cenomanian Ashville Formation of Manitoba were identified as hesperornithiform by Cumbaa et al. (2002) (Fig 7.4). One tooth resembles the strongly curved and more conical YPM 1206A described by Dumont et al. (2016), and appears to lack a basal constriction, while the other three have slightly anteroposteriorly wider teeth with indentations between the crowns and roots. The roots are also expanded and anteroposteriorly longer than the broadest parts of the tooth crowns. Above the constriction, the base of the crown appears slightly bulbous, as the anterior and posterior edges at the base of these crowns are rounded. The crowns are curved, with the posterior margin being straighter than the anterior edge. Similar to what Dumont et al. (2016) described, carinae are small and do not extend to the bases or apices. A shallow groove is visible on the lingual face in the largest two specimens. Morphotype 8 is somewhat similar in having a small basal constriction and gently rounded anterior and posterior margins at the base of the crown, although the wide grooves and raised ridges extending from the base to the apex are not visible in the hesperornithiform teeth (Fig. 3.5D, E, F). Although similar in curvature, teeth from Morphotype 7 are distinct in having an often wider base, straighter anterior and posterior edges, and a more angled base above a pronounced basal constriction (Fig. 5C).

Four other isolated teeth were also described from the Campanian Kanguk Formation in Nunavut, Canada by Wilson et al. (2016) (NUVF 286, Fig. 4). SEM images show a textured appearance on the enamel surface formed by densely packed, fine, short, and irregular ridges that extend from the base to the apex. This differs from the ridges described on YPM 1206B by Dumont et al. (2016), in which a single ridge extends from the apex to the base. This suggests that enamel ornamentation may be more variable in at least some fossil bird taxa than previously thought. The ridges described in Dumont et al. (2016) are, however, different from examples from Alberta, although the small, fine ridges in NUVF 286 resemble the secondary longitudinal ridges described in Morphotypes 1, 2, and 3 (Wilson et al., 2016). Conversely, these are typically fewer in number, larger, and restricted to the middle or upper portion of the crown (Fig. 2.10, Fig. 4). Large primary ridges are also absent, and the carinae of NUVF 286 are either absent or smaller than those of Morphotypes 1, 2, and 3 and lack the distinct angled striae. This feature in some teeth of Morphotype 3 also differs in the fan-like distribution of the ridges from the center and base of the crown. Although ridges are present on the teeth of *Hesperornis* (Dumont et al., 2016; Wilson et al., 2016), the combination of primary and secondary longitudinal ridges and striae on the carinae of Alberta teeth has not been reported in *Hesperornis* or other fossil bird taxa. As a result, it is unlikely that these particular morphotypes represent bird taxa. Additionally, fine, irregular longitudinal ridges extending from the base of the crown to the apex similar to the teeth in NUVF 286 were described in the Cretaceous mesoeucrocodilian *Trematochampsa taqueti* (Prasad and Lapparent de Broin, 2002). The range of variation in crown shape and surface ornamentation underscore the difficulties in identifying small, isolated teeth, and this is made more problematic by the fact that many features recognized in bird teeth are also present in crocodilian dentition.

3.5.6 Comparisons with the Dentition of *Archaeopteryx*

Teeth in *Archaeopteryx* are described as being small and unserrated, with some variation in shape of the crown and root in the premaxilla and maxilla, as well as between specimens (Howgate, 1984; Mayr et al., 2007). Howgate (1984) described the teeth of the Berlin and London specimens as similar in shape; they are peg-like and lack ornamentation of the crown, although in some instances small carinae may be present (Louchart and Pouech, 2017). The teeth of the Eichstätt specimen were also similar overall, although they are more consistently curved along the jaw (Howgate, 1984). Additionally, Howgate (1984) stated that the Berlin specimen lacked a basal constriction between the crown and root, although this feature was later shown to be present to varying degrees in some teeth of the Berlin, Eichstätt, London, Münich, Solnhofen, and Thermopolis specimens (Louchart and Pouech, 2017). Howgate (1984) also noted a constriction roughly midway on the crown itself, and this was likewise reported in the Solnholfen and London specimens (Mayr et al., 2007). In spite of the variability in

Archaeopteryx teeth, crown shape tends to be fairly low and broad at the base, with pronounced curvature of the crown occurring along the anterior edge and near the apex. This particular combination of shape in lateral view is not reflected in the Alberta sample.

3.5.7 Comparisons with the Dentition of Non-Avian Theropods

Denticles were previously reported on an alleged avian tooth, although most are less complex in shape compared to theropod dentition (Currie and Coy, 2008). Structures referred to as crenulations were described along the posterior edge of the premaxillary teeth on a new specimen of *Longipteryx*, and were likewise less complex and irregular in shape (Wang et al., 2015). TMP 1989.103.0025 was originally diagnosed as a possible hesperornithiform, with denticles showing an enamel-covered dentine core (Currie and Coy, 2008). Examples of hesperornithiform teeth in Cumbaa et al. (2006), however, differ in having smoothly curved anterior and posterior edges on the base of the crown that slope more gently towards the basal constriction, rather than the sharply angled edges on TMP 1989.103.0025. This specimen is now thought to instead belong to *Richardoestesia isosceles* following quantitative analysis and comparison with other theropod teeth (Larson and Currie, 2013; Dumont et al., 2016). Sankey et al. (2002) stated that *Richardoestesia* teeth can be difficult to tell apart from avian teeth, but can be distinguished based on a lack of a basal constriction in *Richardoestesia isosceles*, and a stronger curve and larger denticles in *Richardoestesia gilmorei*. Also, neither have the distinct hourglass cross-section of the base of the crown in avian teeth as described by Sankey et al. (2002). Longrich (2008), however, described a slight constriction at the base of teeth of *Richardoestesia cf. gilmorei* from the Lance Formation. Also, denticles in *Richardoestesia gilmorei* and *Richardoestesia cf. gilmorei* are present on the posterior edge, although anteriorly denticles are either significantly smaller or absent altogether (Sankey et al., 2002; Longrich, 2008). This is similar to teeth in Morphotype 6, in which denticles are not visible on the anterior margin (Table 3.1, Fig. 3.5A, B). The serrations seen on the Alberta teeth are also simple in structure and irregular in shape, although it is difficult to discern whether or not a dentine core was present. Dumont et al. (2016) suggested that putative avian-like teeth with denticles were likely non-avian theropods. Although some teeth are lower and broader than TMP 1989.103.0025, the overall shapes of the crowns are similar, and these too may belong to non-avian theropods rather than birds. Dumont et al. (2016) also suggested teeth shaped similarly to TMP 1989.103.0025 and *Richardoestesia* also likely belong to non-avian theropods. The teeth and jaws of very small or juvenile non-avian theropods from Alberta are unknown, and may represent at least some putative avian teeth.

3.5.8 Comparisons with the Dentition of Ornithopods and Choristoderes

Although a basal constriction and triangular crowns lacking in serrations are features that are shared between putative avian teeth and the premaxillary teeth of some ornithopods (Longrich, 2008), avian teeth from Alberta are dissimilar in lacking a combination of a broad, rounded crown with a strong posterior curvature of the apex, and roots that are typically elliptical or circular in shape (Boyd, 2014). Ridges that encompass the whole of the tooth from the base to the rounded apex in *Thescelosaurus* are also absent in the Alberta sample.

Members of crocodilian-like Choristodera were represented by two genera for which tooth and jaw material has been described. *Champsosaurus* teeth from the Dinosaur Park and Horseshoe Canyon formations are typically tall and conical in shape with some lateral compression and either posterior or medial curvature. The enamel of the crown is striated and exhibits infolding near an expanded base (Gao and Brinkman, 2005; Matsumoto and Evans, 2016), neither of which is evident in the sample of putative avian teeth. Although the basal-most portion of some putative avian teeth is not preserved, the lack of enamel infolding, presence of a basal constriction, frequent presence of a basal groove, and strong lateral compression eliminates *Champsosaurus* from this sample. *Cteniogenys* teeth from the Oldman and Dinosaur Park formations may be superficially more similar to the cf. Aves teeth than *Champsosaurus*, although crowns are low, relatively straight and triangular with blunt, rounded tips, and a circular base with weak to no constriction. There are no grooves on the lingual and labial faces, which also tend to be finely striated but lack enamel infolding (Gao and Fox, 1998; Gao and Brinkman, 2005). As juvenile dental material of Choristodera from Alberta has not been identified or described, it is unknown if the teeth of subadults were laterally compressed like those of crocodilians.

3.6 Summary and Conclusions

Many of the putative avian teeth from the Cretaceous of Alberta appear to be crocodilian. TMP 1986.008.0074 and UALVP 54359 are derived from the Dinosaur Park Formation and represent early ontogenetic stages of known crocodilian taxa *Albertochampsa* or *Leidyosuchu*s (Brinkman, 2005; Wu, 2005). Juvenile jaw material with in situ teeth is not known for any Cretaceous crocodilians from Alberta, and very small crocodilian teeth similar in size or smaller than those from the juvenile *Alligator* used in this study are also absent. It is therefore possible that at least some of these avian teeth could represent an early ontogenetic stage of known crocodilian taxa.

Alternatively, while small, isolated crocodilian teeth resemble some purported bird teeth in terms of surface ornamentation and shape, they are elliptical rather than strongly compressed and reniform in cross-section. These slight differences between unequivocal fossil crocodilian and putative avian teeth suggest that some morphotypes represent the dentition of a species of small crocodilian, rather than juveniles of known taxa. Prasad and Lapparent de Broin (2002) stated that a greater diversity in tooth morphology is present in fossil crocodilians than in extant taxa, including in the Late Cretaceous, and small to medium-sized crocodilian taxa have been described from the Milk River (*Gilchristosuchus* (Wu and Brinkman, 1993), Dinosaur Park (*Albertochampsa*), and Horseshoe Canyon (*Strangerochampsa*) formations (Wu et al., 1996). As juvenile crocodilian material is rare, fossils of small taxa would predictably be just as uncommon, or possibility mistaken for a younger individual of a larger species.

In addition to bone beds, a large portion of the teeth used in the study were collected from microfossil sites. Within the Dinosaur Park Formation, most vertebrate microfossil sites fall into one of two categories; in-channel deposits where fossils are sourced from nearby interchannel deposits and transported following rip-ups or the collapse of banks, and splay deposits where fossils derived from a floodplain accumulate further during subsequent flooding (Eberth, 1990). In both instances, these sites involved localized transport of sediment and microfossils, and best represent diversity in the immediate area (Eberth, 1990; Brinkman et al., 2005). Non-avian theropods, hadrosaurs, and ceratopsian elements are present in some microsites (Brinkman, 2005), and birds may have been worked into these assemblages as well. However, a wide diversity of aquatic organisms including amphibians (albanerpetontids, frogs, salamanders), champsosaurs (*Champosaurus*, *Cteniogenys*), crocodilians, chondrichthyans (*Hybodus*, *Myledaphus*, etc.), chondrosteans (paddlefish and sturgeon), holosteans (*Belenostomus*, *Lepisosteus*, etc.), teleosts (*Coriops*, *Paratarpon*, etc.), and as many as twelve species of turtles tend to dominate these sites. Bird material is notably very rare, and currently no jaw material has been identified. Only three teeth (Morphotype 9) from the sample bear a particularly strong resemblance to teeth from two jaw fragments that were suggested to represent an unknown ornithurine bird taxon (Bell and Everhart, 2011). As a result, it is conceivable that many of these avian teeth instead belong to crocodilians or other aquatic taxa, which are often abundant in these vertebrate assemblages. Conversely, not all sites are dominated by aquatic taxa. Larson et al. (2010) described possible avian teeth from a terrestrially-dominated microvertebrate assemblage from the Horseshoe Canyon Formation. However, crocodilian teeth were reportedly absent. Avialae indet. (TMP 2003.057.0002) was compared to crocodilians and non-avian theropods, and Archosauria indet. teeth (TMP 2009.137.0018, TMP 2009.139.005, TMP 2009.137.0019 (included in analysis as Morphotype 1)) bear notably large carinae and longitudinal ridges on the crown like those in Morphotypes 1, 2, and 3, and crocodilian teeth (Fig. 3.9, Fig. 3.10). Overall shape of these unidentified archosaurian teeth is reminiscent of Morphotypes 1, 2, 3, and 5. Incidentally, Brochu (2013) noted that ziphodont crocodilians are typically considered to be terrestrial organisms, although this need not be the case as the small, extant *Osteolaemus* and *Paleosuchus* are both described as semiaquatic and possess compressed teeth. Consequently, the possibility that putative avian teeth instead belong to crocodilians is not necessarily discounted by their occurrence in terrestrial deposits.

The potential affinity of many purported avian teeth from Alberta with those of the Crocodylia also has strong implications for the interpretation of avian diversity in the late Cretaceous, and raises the question of why bird teeth would be rare or absent. Recently, isolated teeth primarily from the Hell Creek Formation and similar to those from Alberta were included in an analysis tracking disparity in tooth shape of non-avian theropods and birds over time (Larson et al., 2016). Using tooth shape as a proxy for ecological niche, the authors concluded that both non-avian theropods and birds were diverse and largely stable leading up to the mass-extinction event. However, in some instances this analysis may have instead recorded interspecific variation in crocodilian teeth and/or variation within the jaw. Additionally, putative avian teeth, with the exception of Morphotype 10, are not strongly comparable to toothed ornithurines such as *Hesperornis* or *Ichthyornis* (Fig. 3.2). Bird material is rare and mostly fragmentary, likely resulting from taphonomic bias and the fragility of the bird skeleton, and the same may be true of bird teeth (Brown et al., 2013). Alternatively, edentulous birds may have been more common than toothed birds, which could account for the potential lack of avian teeth, although this is questionable as most avian skeletal material from Alberta and nearby has been assigned to the toothed Ornithurae (Fox, 1974, 1984; Morrison et al., 2005; Longrich, 2006, 2009; Longrich et al., 2011; Aotsuko and Sato, 2016). Similar isolated putative avian teeth occur in various localities outside Alberta (Longrich, 2005; Sankey, 2005; Larson et al., 2016), and establishing a method by which to identify distinguishing characters may expand on the current understanding of vertebrate diversity in the Late Cretaceous. Aside from finding additional skeletal material, Dumont et al. (2016) described the microstructure of the enamel of *Hesperornis* and *Ichthyornis* as being very thin and comprising only of a single basal-unit layer. Similar techniques could be used on putative avian teeth as a potential means to differentiate isolated teeth, as crocodilian teeth tend to have thicker enamel than bird teeth (Dumont et al., 2016). Further comparisons and characterizing the disparity of these teeth may be achieved through analyses incorporating wider range of variables including surface ornamentation, geography, and time.

Formerly, teeth were thought to constitute a large proportion of known bird fossils in Alberta. However, without associated jaw material, it is difficult to definitively assign these teeth to any particular group or taxon. Both qualitative and quantitative analyses show strong potential for overlap of crown shape between putative avian, crocodilian and some non-avian theropod teeth. Several morphotypes are comparable in shape to teeth in the jaws of both extant and fossil crocodilians, and best represent tooth variation within the jaw. Enamel ornamentation in the form of longitudinal ridges and carinal striae are shared between crocodilian dentition and a number of putative avian teeth from Alberta, and may play a role in differentiating isolated teeth. This suggests that in most cases, evidence to support a referral of isolated teeth to Aves is currently lacking, and caution should be used for future diagnoses based on similar isolated teeth.

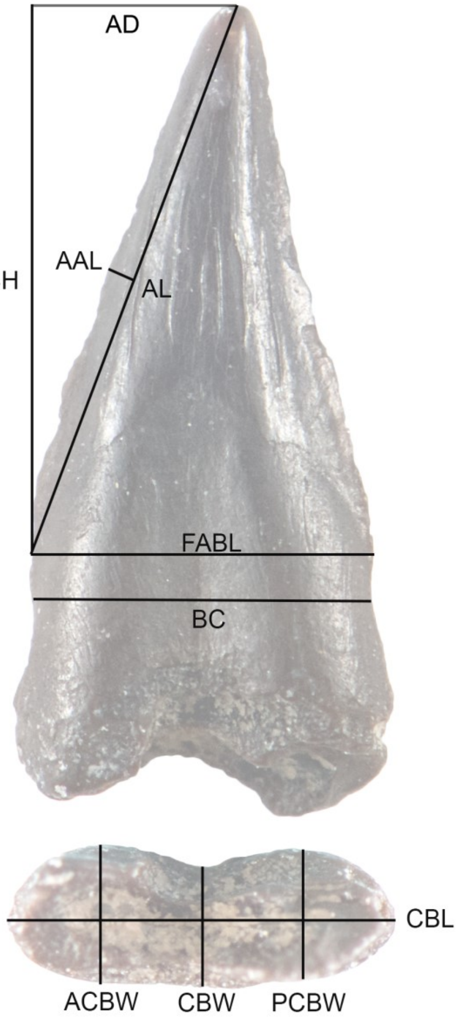

Figure 3.1. Isolated "bird" tooth TMP 95.184.20C with tooth measurements superimposed. Lateral view: **AD** (apical distance), **CH** (crown height), **AAL** (anterior-apical distance), **AL** (apical length), **FABL** (fore-aft basal length), **BC** (basal constriction). Basal view: **CBL** (crown basal length), **CBW** (crown basal width), **MCBW** (anterior crown basal width), **DCBW** (posterior crown basal width).

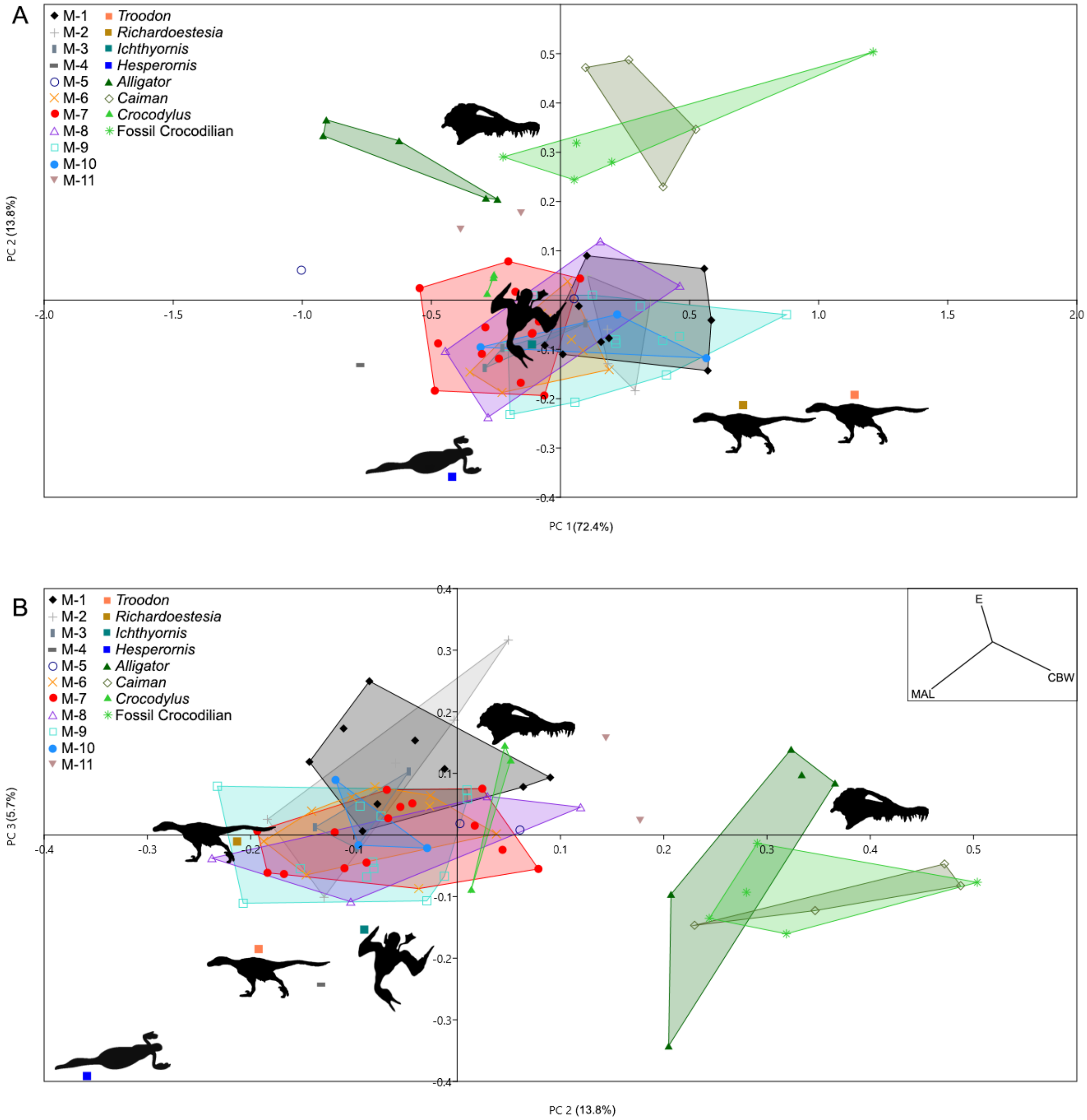

Figure 3.2. Principal Component Analysis of putative avian teeth morphotypes, selected non-avian theropod and bird teeth, and fossil and modern crocodilian teeth. A, Principal Component 1, x axis, Principal Component 2, y axis; **B**, Principal Component 2, x axis, Principal Component 3.y axis; Convex hulls are included around Morphotypes and taxa. Biplot of variables including in top right corner; CBW, crown basal widths; E, variables including AD, CH, BC, FABL; MAL, anterior apical distance.

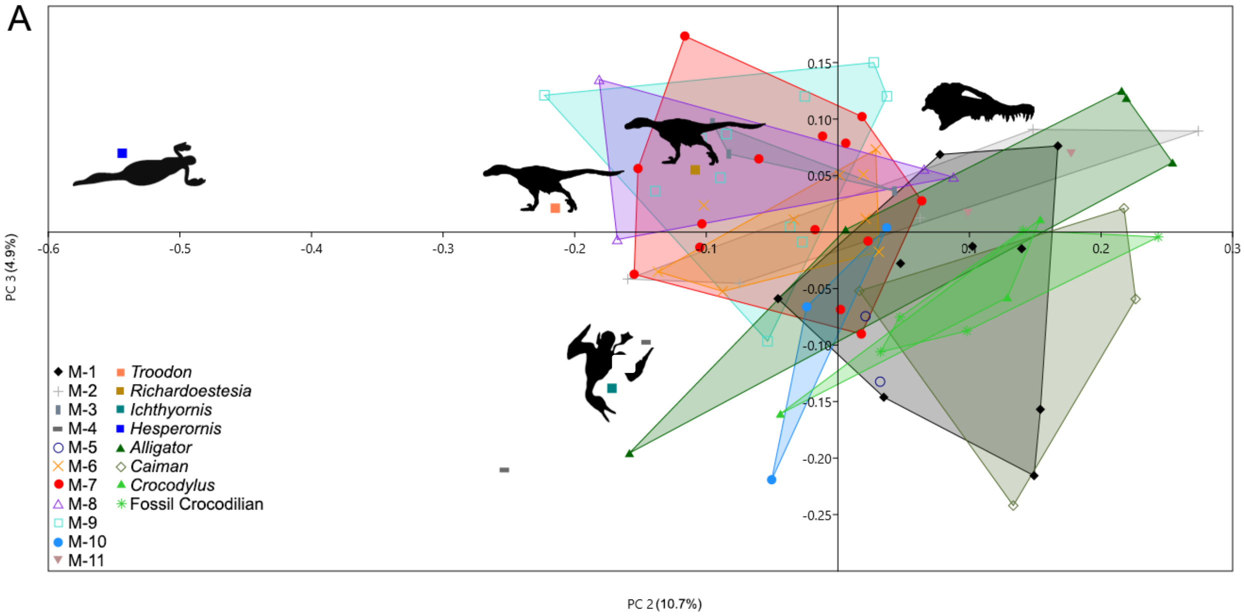

Figure 3.3. Principal Component Analysis of putative avian teeth morphotypes, selected non-avian theropod and bird teeth, and fossil and modern crocodilian teeth, with CBW variables removed. Principal Component 2, x axis, Principal Component 3, y axis. Convex hulls are included around Morphotypes and taxa.

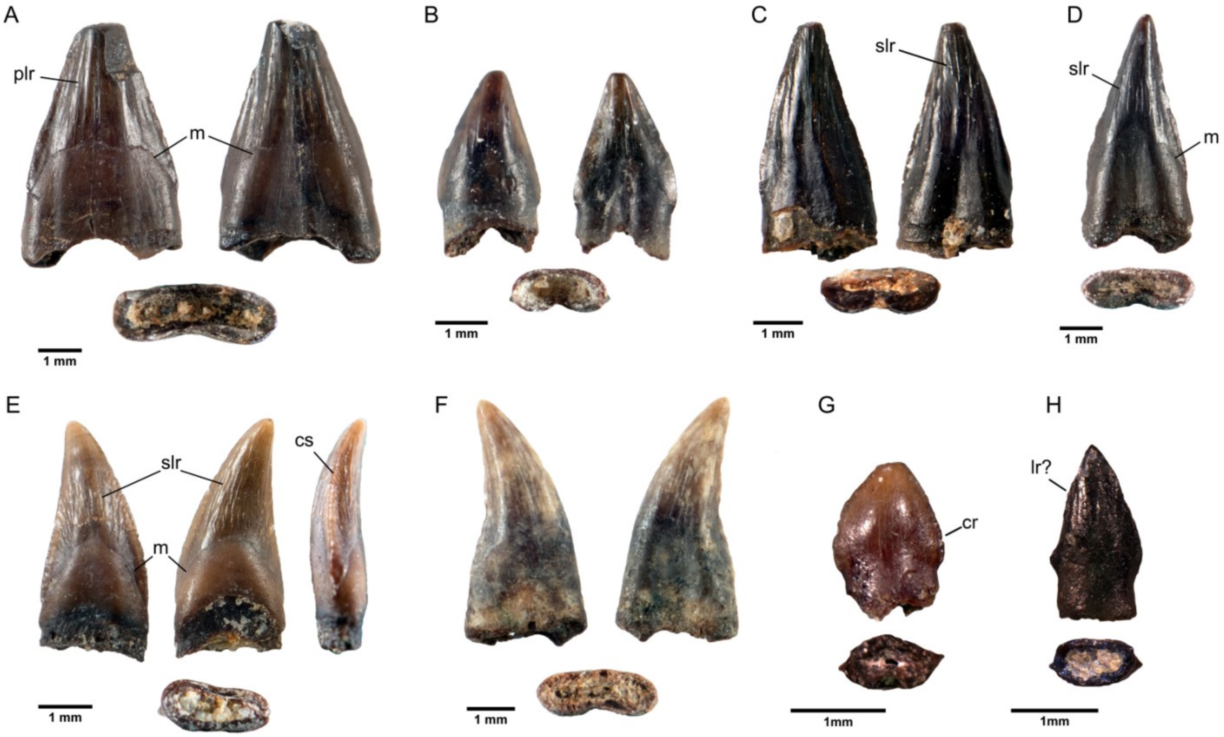

Figure 3.4. Putative isolated avian teeth in lateral and basal views. A, **B**, Morphotype 1; **C**, **D**, **F**, Morphotype 2; **E**, Morphotype 3; **G**, Morphotype 4; **H**, Morphotype 5. Abbreviations: cr, crenulations, cs, carinal striae, m, margin, plr, primary longitudinal ridges, slr, secondary longitudinal ridges. For A, B, C, E, and F, left is labial, right is lingual. E includes anterior aspect. D is in lingual view, G is in lingual(?) view, and H in lateral view.

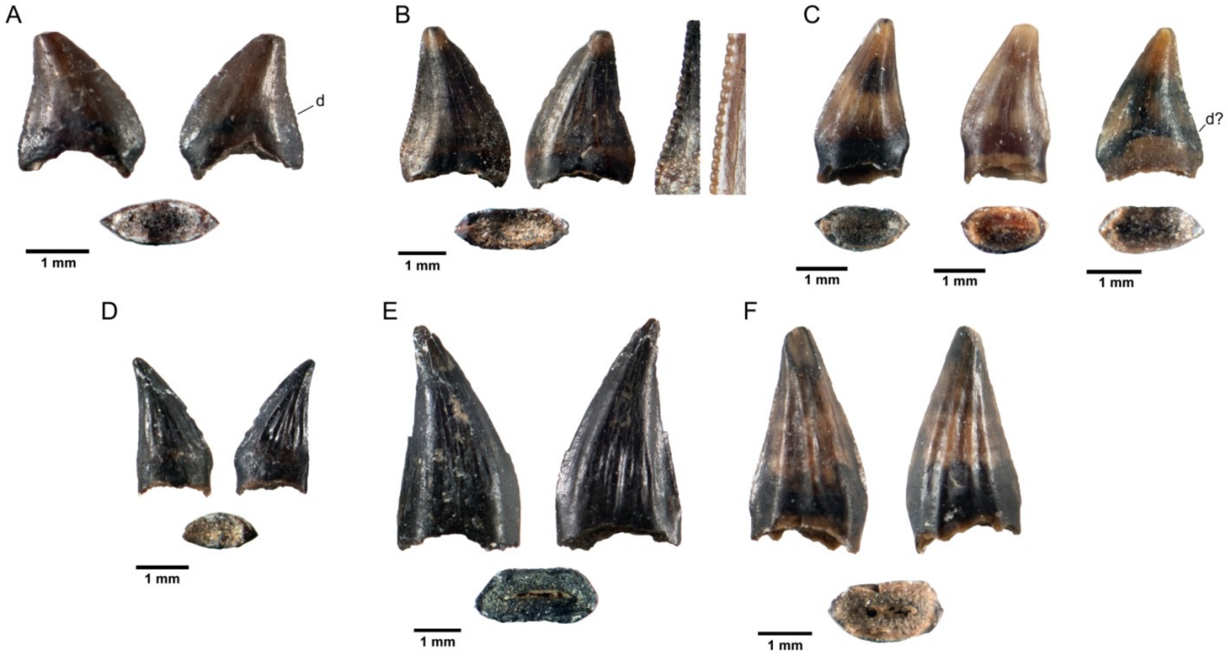

Figure 3.5. Putative isolated avian teeth in lateral and basal views. **A**, **B**, Morphotype 6; **C**, Morphotype 7, comparing shape of Morphotype 7 with Morphotype 6, TMP); **D**, **E**, **F**, Morphotype 8.

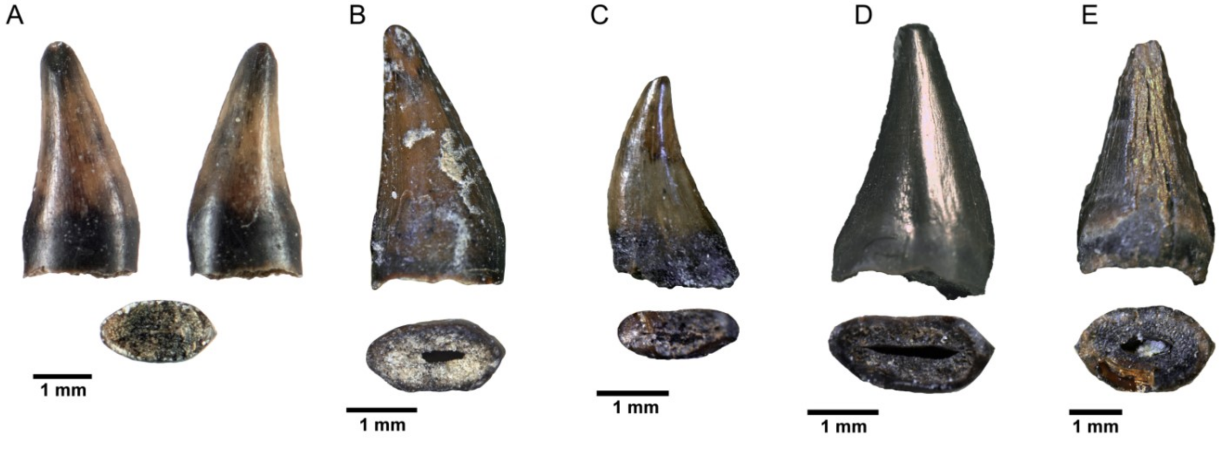

Figure 3.6. Putative isolated avian teeth in lateral and basal views. **A**, **B**, Morphotype 9; **C**, **D**, Morphotype 10; **E**, Morphotype 11.

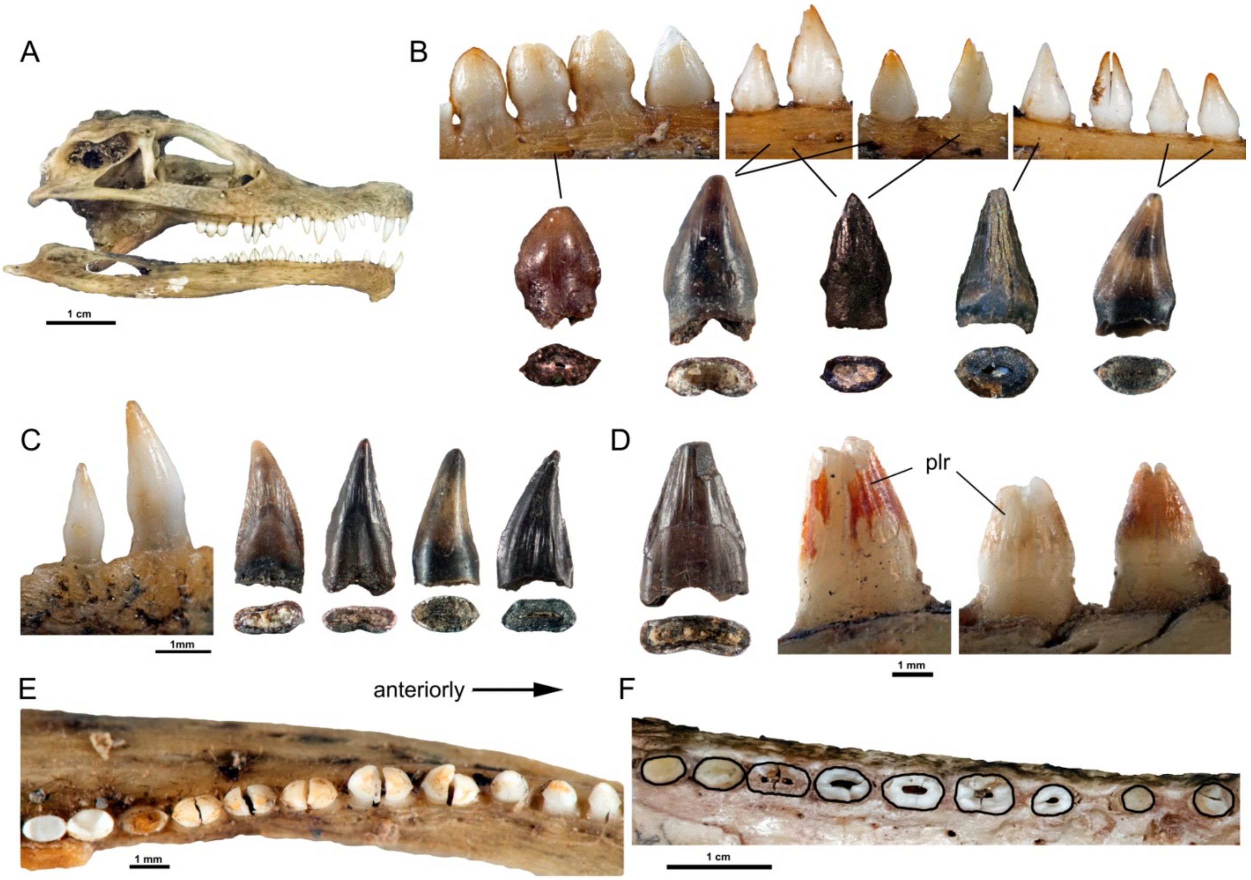

Figure 3.7. Comparison of putative fossil avian teeth with dentition of extant *Alligator* and *Caiman*. A, juvenile *Alligator* skull; **B**, left to right, posterior and mid-region maxillary teeth of juvenile *Alligator*, Morphotypes 4, 1, 5, 11, 7; **C**, right, juvenile Alligator caniniform teeth from the premaxilla, right ; **D**, left, Morphotype 1; **E**, dorsal aspect of juvenile Alligator dentary showing variation in tooth shape; **F**, dorsal aspect of *Caiman* maxilla with tooth shape in apical view outlined in black. Arrow indicates direction in E and F. Abbreviations: plr, primary longitudinal ridges. Crocodilian tooth rows in **B**, **C**, and all putative avian teeth images not to scale.

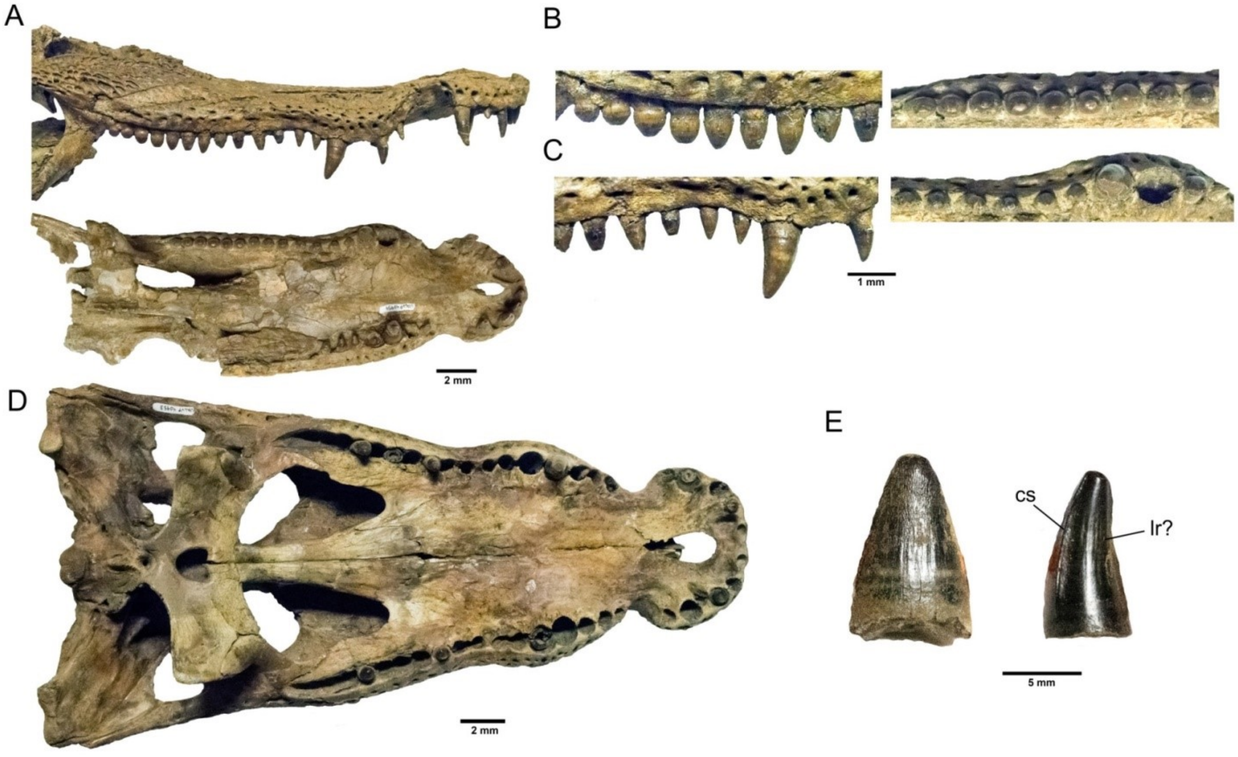

Figure 3.8. ***Leidyosuchus* skulls, jaws, and teeth**. **A**, skull of UALVP 40954 in lateral (upper) and ventral (lower) views; **B**, posterior region of UALVP 40954 maxilla in lateral (left) and ventral (right) views; **C**, anterior region of UALVP 40954 maxilla in lateral (left) and ventral (right) views; **D**, skull of UALVP 48607 ventral view; **E**, UALVP 48607A, right, and UALVP 48607B, left. Abbreviations: cs, carinal striae, lr, longitudinal ridges.

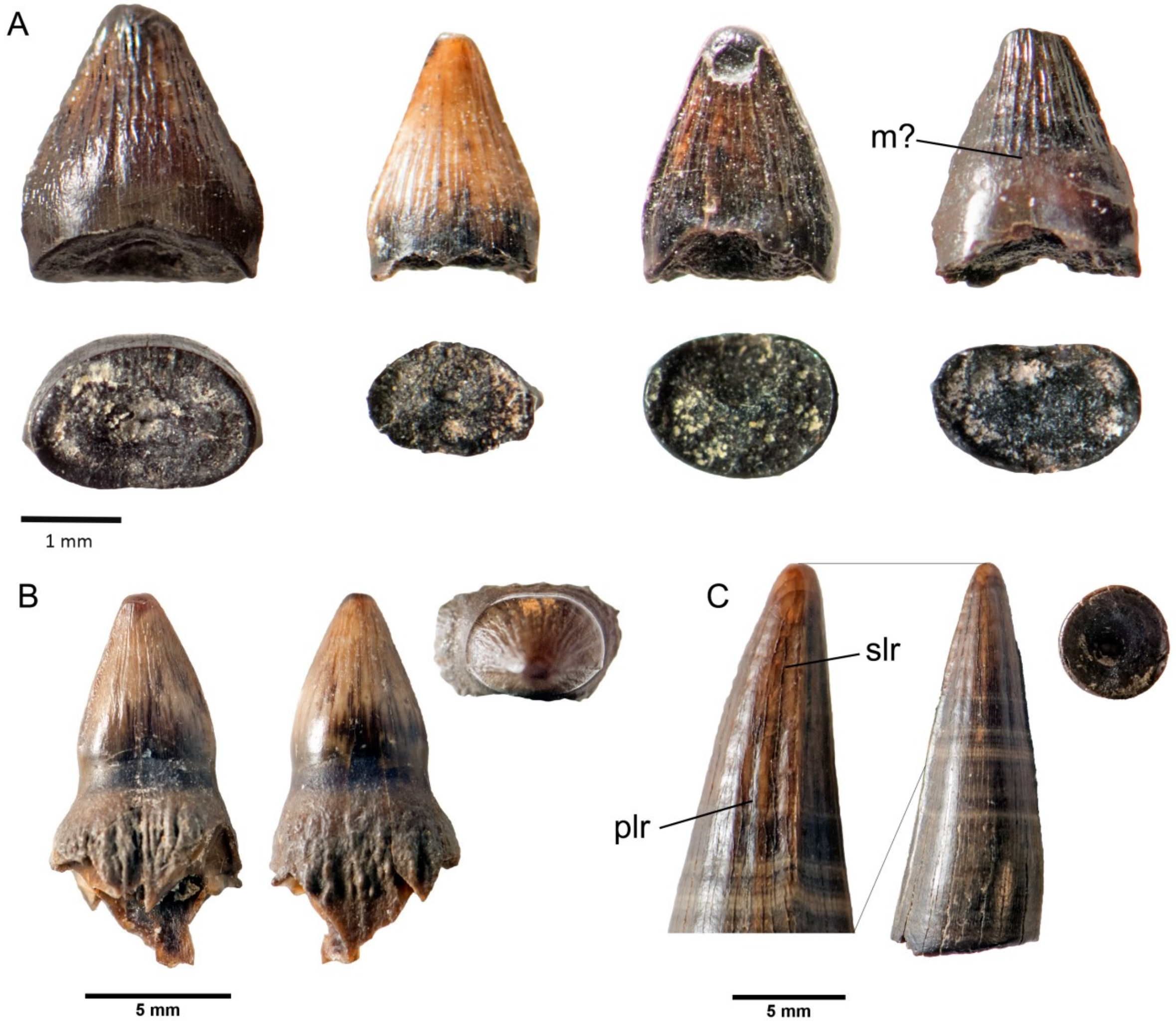

Figure 3.9. Small fossil crocodilian teeth from the Dinosaur Park Formation, Alberta. A, selection of teeth from TMP 86.8.74 in lateral and basal views. Note the ridges present on all four crowns, and possible enamel margin, **B**, UALVP 54359A in lingual, labial, and apical views, **C**, UALVP 54359B in lateral and basal views, including details of ridges near the apex of the crown. Abbreviations: m, margin, plr, primary longitudinal ridges, slr, secondary longitudinal ridges.

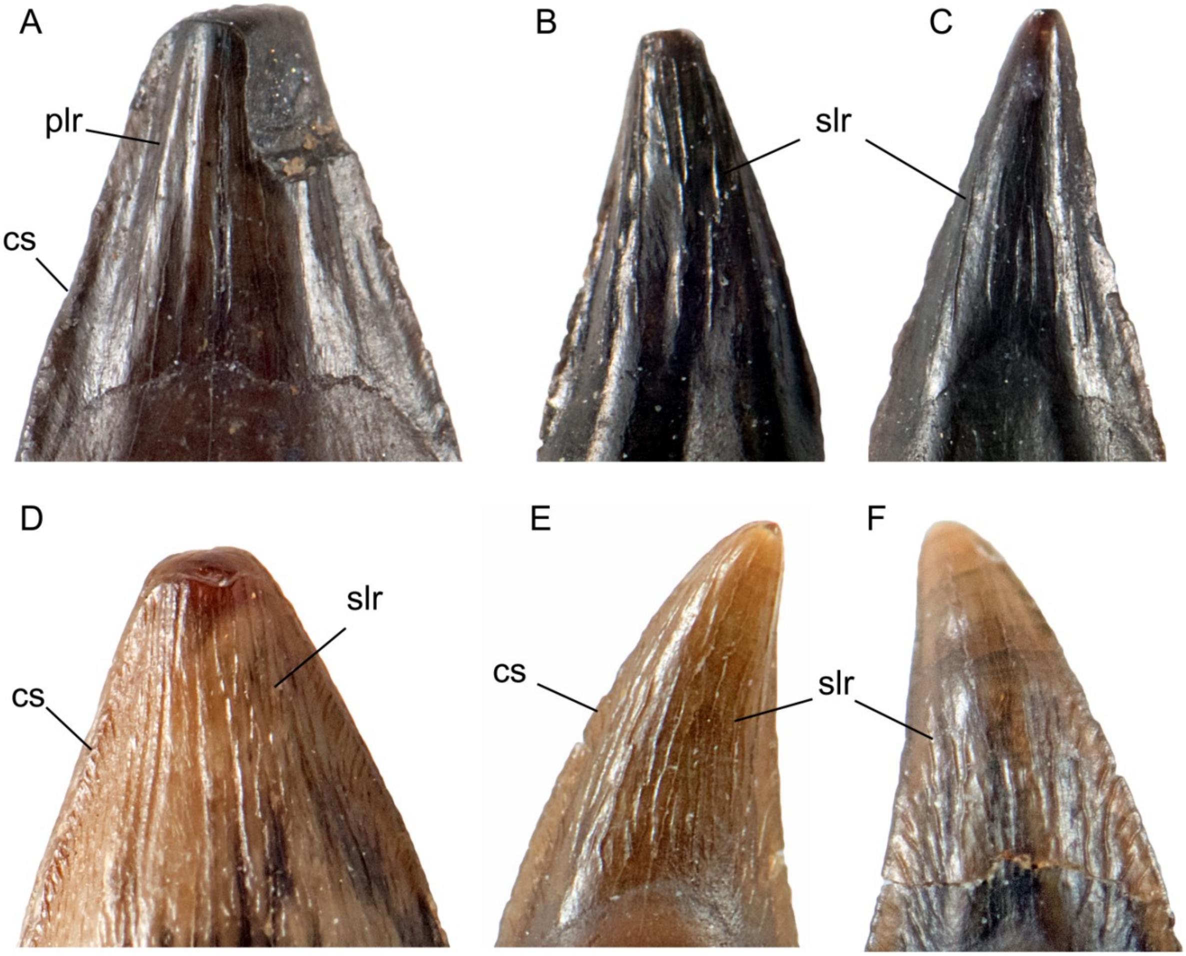

Figure 3.10. Details of surface features on the crowns of putative avian and crocodilian teeth. **A**, TMP 99.24.152 (morphotype 1); **B**, UALVP 852-4 (Morphotype 2); **C**, TMP 95.184.20C (Morphotype 2); **D**, UALVP 54359A (fossil crocodilian); **E**, **F**, lingual and labial views of UALVP 57560C (Morphotype 3). Abbreviations: cs, carinal striae; plr, primary longitudinal ridges; slr, secondary longitudinal ridges. Images not to scale.

Morphotype	Catalogue #
1	TMP 1981.031.0096, TMP 1995.184.0020A, TMP 1997.096.0026, TMP 1999.024.0152, TMP 2009.022.0092, TMP 2009.137.0019, TMP 2009.163.0081A, TMP 2014.006.0244B, UALVP 57560D
2	TMP 1994.184.0020B, TMP 1995.184.0020C, TMP 2009.025.0012, UALVP 852-4, UALVP 57560A, UALVP 57560B
3	TMP 1995.168.0013B, TMP 2014.006.0244A, UALVP 57560C
4	TMP 1996.062.0050A
5	TMP 1994.144.0114, TMP 1996.062.0054A
6	TMP 1986.009.0096, TMP 1987.158.0076, TMP 1995.174.0052, TMP 1995.181.0066A, TMP 1995.181.0066E, TMP 1995.181.0066G, TMP 2000.006.0002, TMP 2009.022.0029B
7	TMP 1986.006.0002, TMP 1995.143.0057, TMP 1995.151.0021, TMP 1995.168.0013A, TMP 1996.177.0079B, TMP 1995.181.0060A, TMP 1995.181.0060H, TMP 1996.066.0052A, TMP 1996.062.0053A, TMP 1996.062.0053B, TMP 1996.062.0054B, TMP 1996.062.0056A, TMP 1996.062.0063, TMP 2000.053.0060, TMP 2001.036.0006, TMP 2009.022.0091
8	TMP 1995.177.0079, TMP 1995.181.0066D, TMP 1995.181.0066F, TMP 1995.181.0066J
9	TMP 1986.021.0068, TMP 1986.033.0056, TMP 1986.045.0027, TMP 1987.004.0046, TMP 1995.181.0066C, TMP 1995.181.0066I, TMP 1996.062.0051, TMP 1996.062.0055B, TMP 1996.062.0055C, TMP 1996.062.0062, TMP 2000.045.0052, TMP 2003.057.0002, UALVP 483
10	TMP 1996.062.0052B, TMP 2003.089.0033, TMP 2009.163.0081B
11	TMP 1995.181.0066B, TMP 1996.001.0014

Table 3.1. List of measured isolated teeth. Specimens are from the Royal Tyrrell Museum of Palaeontology (TMP) and University of Alberta Laboratory of Vertebrate Paleontology (UALVP) collections and placed in their respective morphotypes, based on crown shape, enamel ornamentation, and presence or absence of denticles.

Morphotype	Crown Shape and Features	Formation
1	**Lateral** – Large, broad crown; central concavity on lingual surface; prominent carinae; expanded root; primary and secondary longitudinal ridges often present; carinal striae; straight or slight posterior curvature; may have enamel margin on both faces; slight basal constriction **Basal** – Curved, reniform cross-section; strong lateral compression	Dinosaur Park, Horseshoe Canyon, Scollard
2	**Lateral** – May resemble M-1, but smaller and with a narrower crown; central concavity on lingual surface; expanded root; carinae present; carinal striae may also be present; secondary longitudinal ridges on apical half of crown, possible primary longitudinal ridges; slight posterior curvature; weak basal constriction **Basal** – Reniform cross-section; strong lateral compression	Milk River, Dinosaur Park
3	**Lateral** – Small, narrow and similar in shape to M-2; lingual curvature; small carinae; wavy secondary longitudinal ridges splay outwards onto carinae; enamel margin on both faces; weak basal constriction **Basal** – Oval to reniform cross-section; laterally compressed	Dinosaur Park, St. Mary River
4	**Lateral** – Small, broad, rounded crown; crenulated carinae; smooth enamel surface; no concavity in center of crown; slightly bulbous crown base; prominent basal constriction **Basal** – Elliptical to lenticular cross-section; little lateral compression	Oldman
5	**Lateral** – Small, straight, “arrowhead-heaped” crown; carinae	Oldman

	present; possible longitudinal ridges near apex; slightly bulbous crown base; prominent basal constriction **Basal** – Subrectangular to oval cross-section, slight lateral compression	
6	**Lateral** – Triangular crown with a wide base and narrow apex; posterior curvature; strongly angled “heel” on posterior edge of crown base; denticles on posterior edge, size and number variable; smooth enamel; thin anterior carinae situated on midline, or no carinae; shallow grooves may be present on both faces; prominent basal constriction **Basal** – Lenticular to parlinon cross-section; laterally compressd	Milk River, Dinosaur Park, Horseshoe Canyon
7	**Lateral** – Similar shape to M-6; posterior curvature; lacks denticles; strongly curved anterior edge of crown; smooth enamel; small carinae situated on midline; may have strongly angled “heel” on posterior edge of crown; prominent basal constriction **Basal** – Elliptical to lenticular, or figure-8 cross-section; laterally compressed	Oldman, Dinosaur Park, Scollard
8	**Lateral** – Tall, narrow crown; posterior curvature; large ridges on both faces separated by flutes; small and lingually-angled carinae; concave anterior edge with relatively straight posterior edge; rounded base with weak basal constriction **Basal** – Rectangular to figure-8, or elliptical to slightly lenticular cross-section; laterally compressed	Oldman, Dinosaur Park
9	**Lateral** – Similar in shape to M-8; long, narrow, and curved crowns; smooth enamel on both faces; straight to slightly curved anterior and posterior edges; carinae varying in size and often lingually-angled; possible carinal striae; weak to no basal constriction **Basal** – Oval or rectangular cross-section; moderate lateral	Milk River, Dinosaur Park, Horseshoe Canyon

	compression	
10	**Lateral** – Tall, strongly curved crown; crown offset from root; small carinae; smooth enamel on both faces; possible shallow, narrow indentation at base of crown; no basal constriction **Basal** – Weak reniform or figure-8 cross-section; laterally compressed	Oldman, Scollard
11	**Lateral** – Straight crown; broad, bulbous base with narrow apex; smooth enamel on both faces; small or no carinae; slight basal constriction **Basal** – Elliptical cross-section; weak lateral compression	Dinosaur Park

Table 3.2. Distinguishing features and Stratigraphic distribution of morphotypes. List of distinguishing characters for Morphotypes 1-11 in both lateral and basal aspects. Teeth span the Late Santonian/Early Campanian to latest Maastrichtian of the Late Cretaceous in Alberta.

Catalogue #	Est. total # of denticles	Est. $\overline{x}$ height	Est. $\overline{x}$ width
TMP 1986.009.0096	14	0.07	0.04
TMP 1986.021.0068	11	0.08	0.02
TMP 1987.158.0076	18	0.09	0.04
TMP 1995.174.0052	6	0.09	0.03
TMP 1995.181.0060A	3	0.02	0.08
TMP 1995.181.0060E	8	0.13	0.03
TMP 1995.181.0060G	5	0.09	0.09
TMP 2000.006.0021	4	0.12	0.03

Table 3.3. Tentative denticle counts and measurements of teeth from Morphotype 6. In all cases, denticles were located on the posterior edge of the crown. Note the large variation in number of discernable denticles.

Chapter 4. Summary

The rarity and fragmentary nature of Cretaceous bird material in Alberta is highly problematic. A review of fossil collections at the University of Alberta and the Royal Tyrrell Museum produced a large number of isolated and broken elements, such as unguals, that cannot easily be referred to any particular taxon. Although most avian skeletal material from Alberta is not diagnosable, some elements, such as coracoids, are distinct and complex bones that provide adequate for identifying features specific to particular groups of taxa. One such hitherto undescribed coracoid is UALVP 55089, which, although fragmentary, is diagnosed as an ornithurine bird. A comparison with coracoids from various localities in North America demonstrated that UALVP 55089 represents a separate taxon, referred to here as Ornithurine G. It is possible Ornithurine G may represent a neornithine bird, as a pneumatized coracoid is a defining character of Neornithes. However, despite Micro-CT scanning of the fossil and comparisons with extant birds, pneumaticity cannot be determined if a pneumatic foramen is not preserved, as it the case with UALVP 55089. Phylogenetic analysis supported previous research and resulted in an unresolved polytomy including Ornithurine G, other provisionally-named coracoids, *Cimolopteryx*, and extant birds. The exclusion of *Lamarqueavis* from this polytomy suggests that this genus is not a member of Cimolopterygidae. Likewise, the monophyly of the Cimolopterygidae is not substantiated by my phylogenetic or morphological analysis. Evidence for the inclusion of *Cimolopteryx*, Ornithurine G, and other unnamed coracoids within Neornithes is lacking, and the predominance of basal ornithurine fossils in the Cretaceous of North America suggest that similar material from Alberta should most parsimoniously be referred to Ornithurae.

A substantial amount of Cretaceous bird material from Alberta is represented by isolated teeth that are typically well-preserved. These teeth and similar specimens from other localities have been referred to Aves in various studies (Sankey et al., 2002; Longrich, 2008; Sankey, 2008; Larson et al., 2016). Chapter 2 set out to determine if these teeth could be identified and interpreted within the context of fossil bird diversity and evolution, despite the fact that features often referred to as avian, such as a basal constriction, can be seen in other taxa, such as non-avian theropods and thescelosaurs (Sankey et al., 2002; Dumont et al., 2016). Expansion of the root and shared enamel structures between putative avian teeth and crocodilians have been reported by other (Martin, 1980; Longrich, 2008), and this study both confirmed and expanded upon these findings. I began by describing eleven discrete morphotypes based on shape of the crown in lateral and basal view, the presence of denticles, and surface ornamentation. All morphotypes were assignable to other groups at a variety of taxonomic levels, including unequivocal birds, non-avian theropods, and crocodilians. Morphological comparisons revealed that Morphotypes 1, 2, 3, 4, 5, and 11 were markedly similar to both extant and fossil crocodilian teeth in terms of both shape and surface ornamentation. Morphotypes 6, 8, and 9 closely resemble non-avian theropods, although referral to Crocodylia cannot be not ruled out, as similar shapes are found in the jaws of juvenile modern *Alligator* and *Caiman*. Large longitudinal ridges are present in both *Paronychodon* and some crocodilian teeth, including modern *Caiman*, both of which may share a similar shape in cross-section (Sankey et al., 2002). Non-avian theropod teeth typically possess denticles (Sankey et al., 2008), as does Morphotype 7. However, denticles are also present in ziphodont crocodilian teeth, which can resemble the teeth of the theropods *Richardoestesia* in shape. Morphotype 10 resembles avian teeth described by Bell and Everhart (2009). Qualitative analysis then found that a significant portion of this sample of isolated teeth are best represented most similar to teeth in the jaws of modern and fossil crocodilians, and are therefore not indicative of avian diversity in the Late Cretaceous. As well, those morphotypes that are also similar to non-avian theropod and known bird teeth can also not be differentiated from crocodilian teeth with any certainty. All teeth in the sample teeth underwent a set of ten measurements, alongside examples of non-avian theropod, bird, and crocodilian teeth. Principal component analysis (PCA) found considerable overlap of the eleven new morphotypes, but limited overlap with birds, theropods, and crocodilians.

This re-evaluation of tooth fossils, previously considered Late Cretaceous birds, demonstrates the issues associated with diagnosing and interpreting isolated and/or broken specimens. This thesis emphasizes the difficulty in interpreting bird fossils, and challenges the referral of fragmentary skeletal elements, such as coracoids, to particular groups in the absence of diagnostic material. The referral of these isolated skeletal elements to Neornithes is problematic due to the similarities they share with basal ornithurine birds. The assignment of a large sample of isolated teeth to Aves is likewise refuted here due to their similarities with crocodilian teeth.

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Appendix 1

Following is a list of characters from Zhou et al. (2008), Longrich et al. (2011), and this paper used in the phylogenetic analysis.

1. Scapula and coracoid: (0) fused, (1) unfused
2. Scapula and coracoid articulation: (0) pit-shaped scapular cotyla developed on the coracoid, and coracoidal tubercle developed on the scapula (?ball and socket? articulation), (1) scapular articular surface of coracoid convex, (2) flat.
3. Coracoid, procoracoid process: (0) absent, (1) present.
4. Coracoid: (0) height approximately equal mediolateral dimension, (1) height more than twice width, coracoid 'strut-like.' 90. Coracoid, lateral margin: (0) straight to slightly concave, (1) convex.
5. Coracoid, lateral margin: (0) straight to slightly concave, (1) convex.
6. Coracoid, dorsal surface (= posterior surface of basal maniraptoran theropods): (0) strongly concave, (1) flat to convex. 92. Coracoid, pneumatized: (0) absent, (1) present.
7. Coracoid, pneumatized: (0) absent, (1) present.
8. Coracoid, pneumatic foramen: (0) proximal, (1) distal.
9. Coracoid, lateral process: (0) absent, (1) present.
10. Coracoid, ventral surface, lateral intermuscular line or ridge: (0) absent, (1) present. 96. Coracoid, glenoid facet: (0) dorsal to, or at approximately same level as, acrocoracoid process/'biceps tubercle', (1) ventral to acrocoracoid process.
11. Coracoid, glenoid facet: (0) dorsal to, or at approximately same level as, acrocoracoid process/?biceps tubercle?, (1) ventral to acrocoracoid process.

12. Coracoid, acrocoracoid: (0) straight, (1) hooked medially.
13. Coracoid, n. supracoracoideus passes through coracoid: (0) present, (1) absent.
14. Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed): (0) strongly depressed, (1) flat to convex
15. Angle between coracoid and scapula at glenoid: (0) more than 90°, (1) 90° or less.
16. Coracoid, glenoid lateral to scapular articulation (0) anterolateral (1) or anterior (2) Ordered
17. Coracoid, acrocoracoid projecting anteriorly or weakly hooked medially (0) strongly hooked medially (1)
18. Coracoid, procoracoid process: medially projecting (0) or strongly hooked forward and wrapping around the triosseal canal in dorsal view (1)
19. Coracoid, triosseal canal passing ventromedial to scapular articulation: absent (0) or present (1) Coracoid, glenoid projects laterally from body of coracoid as a broad flange: absent (0) present (1)
20. Coracoid, glenoid projects laterally from body of coracoid as a broad flange: absent (0) present (1)
21. Coracoid, shaft straight in lateral view (0) or bowed dorsally (1)
22. Coracoid, acrocoracoid medial fossa absent (0) or present (1)
23. Coracoid, margin of sternal articulation convex (0) straight or concave (1)
24. Coracoid, acrocoracoid with a facet for articulation with the furcula: absent (0) or present (1)

25. Coracoid, acrocoracohumeral ligament scar on top of acrocoracoid: absent (0) or present (1)
26. Coracoid, medial margin with a continuous sheet of bone extending from the sternum to the scapula 0), reduced to a procoracoid process or lost (1)
27. Coracoid, simple tab-and-slot articulation with sternum (0), or articulation with a tongue-like dorsal process of the sternum (1)
28. Coracoid, medial surface of triosseal canal with a prominent crescentic scar ventrally bounding a fossa: absent (0) or present (1)
29. Coracoid, glenoid laterally or dorsolaterally oriented (0) or dorsally oriented, lying directly atop the head of the coracoid (1)
30. Coracoid, procoracoid process extended medially by a thin sheet of bone: absent (0), present (1)
31. Coracoid,pProcoracoid process restricted proximally to coracoid head (0), terminates distal to coracoid head and onto shaft (1), extends sternally on coracoid shaft (2)
32. Coracoid, n.supracoracoideus foremen located proximally on coracoid head (0), distally on coracoid shaft (1)
33. Coracoid, Supracoracoideus nerve foramen flush with surface of coracoid shaft (0), depressed into shaft (1), situated in deep groove (2)
34. Coracoid, prominent, shelf-like dorsal projection of the scapular cotyle, absent (0), present (1)