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An enantiornithine bird from the Campanian Kaiparowits Formation of Utah, USA

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ABSTRACT

An isolated coracoid represents the first described occurrence of an enantiornithine bird from the Kaiparowits Formation (Upper Cretaceous) of southern Utah, USA. The specimen is identified as enantiornithine by the convex scapular facet, approximate alignment of this facet with the humeral articular facet and acrocoracoid process, and the presence of an acrocoracoidal tubercle. This coracoid came from a comparatively large individual, consistent with previous reports of other large enantiornithines from Campanian-aged strata of North America, South America, and Europe. The occurrence of enantiornithines in the Kaiparowits Formation and their apparent absence in the similarly-aged and well-sampled Dinosaur Park Formation of Alberta represents yet another faunal difference between the two areas, although this may be due to environmental differences rather than the endemism proposed for non-avian dinosaurs.

Keywords: Aves, Enantiornithes, Grand Staircase-Escalante National Monument, Kaiparowits Formation

1. Introduction

Birds represent a widespread yet poorly known component of the terrestrial faunal assemblage from the Upper Cretaceous of western North America. Isolated bones from a number of formations indicate the presence of both ornithuromorph and enantiornithine taxa representing a variety of body sizes and phylogenetic affinities (e.g., Hope, 2002; Longrich, 2009; Longrich et al., 2011; Varrichio and Chiappe, 1995), but few are diagnostic at the generic or species levels. Nonetheless, the comparative rarity of avian fossils means that even the most incomplete material is important for better understanding the distribution, paleoecology, and evolution of this clade.

The Kaiparowits Formation, deposited in southern Utah during the late Campanian between 76 and 74.1 Ma (Roberts et al., 2005), preserves a sequence of terrestrial strata with abundant floral, invertebrate, and vertebrate fossil assemblages. Vertebrate fossils have been particularly well-sampled through surface collection, quarrying, and screenwashing, producing an increasingly detailed reconstruction of the Kaiparowits fauna. Non-avian dinosaurs (including various theropods, hadrosaurs, and ceratopsians), mammals, reptiles, amphibians, and fish have all been reported to varying degrees of taxonomic precision (see Titus et al., 2005, for a recent summary). To date no birds have been described or figured, aside from a brief abstract (Hutchison, 1993). Here we describe the isolated partial coracoid of an enantiornithine bird from the Kaiparowits Formation, the first full description of any avian fossil from this unit.

1.2. Institutional abbreviations

CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

2. Systematic Paleontology

Aves Linnaeus, 1758

Ornithothoraces Chiappe and Calvo, 1994

Enantiornithes Walker, 1981

Enantiornithes gen. et sp. indet.

Fig. 1

Referred material. RAM 14306, the proximal end of a right coracoid.

Locality and horizon. RAM 14306 was collected as isolated surface float at locality RAM V99018, a site located in the upper portion of the middle unit of the Kaiparowits Formation (*sensu* Roberts 2007), Grand Staircase-Escalante National Monument, Garfield County, Utah, USA. Detailed locality data are available to qualified investigators upon request.

3. Description

RAM 14306 includes the proximal end of a right coracoid (Fig. 1), with a preserved length of 25.9 mm. The preserved portion of the shaft of RAM 14306 is narrow, indicating that the overall shaft was strut-like as seen in most other birds (excluding *Archaeopteryx lithographica* and a handful of other basal taxa; O'Connor et al., 2009). In cross-section, the shaft is subtrapezoidal, approaching triangular (Fig. 1C), similar to the condition seen in *Enantiornis leali* and YPM 57235, a large enantiornithine from the Hell Creek Formation of Montana referred to cf. *Avisaurus archibaldi* (Longrich et al., 2011). The shaft measures 5.5 mm at its widest point. The region where the supracoracoid nerve foramen should occur is not preserved, so its presence or absence cannot be confirmed.

The humeral articular facet, acrocoracoidal process, and scapular facet are all approximately aligned proximodistally (Fig. 1E), characteristic of Enantiornithes (O'Connor, 2009). The acrocoracoidal process is unhooked and ovoid in dorsal view (Fig. 1E), with minor abrasion to the medial surface. This process measures 7.3 mm wide and is elongated compared to the condition in *Elsornis keni* (Chiappe et al., 2007), but comparable to the condition seen in *E. leali* (Chiappe and Walker, 2002; Walker and Dyke, 2010), Lancian enantiornithine A (CMN 9528, Longrich et al., 2011), and cf. *A. archibaldi* (Longrich et al., 2011).

The acrocoracoidal tubercle in RAM 14306 is small and rounded (Fig. 1A,B), measuring approximately 2.4 mm long and 1.6 mm wide. The scapular facet is convex (as is typical of enantiornithines; Chiappe and Walker, 2002), elongate and ovoid, measuring 8.4 mm long and 5.0 mm wide (Fig. 1A,B,D,E), but is more rounded than in *Eocathayornis walkeri* (Zhou, 2002), and protrudes less than seen in *E. leali* (Chiappe and Walker, 2002) or Lancian enantiornithine A (Longrich et al., 2011). Also, the scapular facet extends sternally relative to the humeral facet for a greater distance than seen in the coracoids of other previously described enantiornithines (Chiappe and Walker, 2002; Longrich et al., 2011; Walker and Dyke, 2010), resulting in comparatively little overlap between the two features. The humeral articular facet is 19 mm long and 6.6 mm wide, with a shallow depression near the acrocoracoidal tubercle. The distance from

the distal end of the scapular facet to the proximal end of the acrocoracoidal process is 12.0 mm.

The medial fossa is generally ovoid, measuring 2.3 mm wide and 7.2 mm long, although it is hooked at its dorsal end (Fig. 1A) and less deep than seen in Lancian enantiornithine A (Longrich et al., 2011). The prominent medial flange is narrow proximally (<1.3 mm wide), widening to 1.6 mm at its distal-most preserved point. This contrasts with the conditions in *Gobipteryx minuta* and YPM 57235, the coracoid of a large enantiornithine referred to cf. *A. archibaldi*, both of which lack a medial flange (Longrich et al., 2011). Some other enantiornithines do preserve a flange, however (e.g., *Enantiornis leali*; Chiappe and Walker, 2002).

4. Identification of RAM 14306

In order to assess the phylogenetic affinities of RAM 14306, the specimen was entered into the matrix of Ji et al. (2011), with the re-addition of *Rapaxavis pani* and *Longicrusavis houi* from O'Connor et al. (2010). RAM 14306 could only be scored for characters 82–90 (with scores for these characters of 1111?0100). The matrix was analyzed in TNT 1.1, reserving space for 10,000 trees in memory, with Dromaeosauridae set as the outgroup, using a traditional search with Wagner trees (random seed=1; 1,000 replicates; tree bisection reconnection swapping algorithm, saving 10 trees per replication) and all other settings as in previous analyses. This resulted in 7,041 equally parsimonious trees of length=646, with very poor resolution and no recovery of Enantiornithes in the strict consensus tree (see Supplementary Data). Following Ji et al. (2011), *R. pani* and *L. houi* were removed as “wildcard” taxa, and the analysis rerun. This improved tree resolution considerably, resulting in 19 equally most parsimonious trees of length=619. In the strict consensus tree (Supplementary Data), RAM 14306 was recovered at a basal polytomy within Enantiornithes, and the remaining topology matched that of Ji et al. (2011). One unambiguous synapomorphy for Enantiornithes (as recognized by O'Connor et al., 2009, 2010; Ji et al., 2011; not scored for *Q. graffini* and *L. houi*) is preserved in RAM 14306, representing the alignment of the scapular facet, humeral articular surface, and acrocoracoid process in dorsal view (character 88:1; O'Connor et al., 2009).

RAM 14306 also has a bulbous, convex scapular facet, a feature proposed as unique to enantiornithine birds (e.g., Chiappe and Walker, 2002; O'Connor, 2009; Sereno, 2000), as well as a distinct acrocoracoidal tubercle, a feature also restricted to some enantiornithines (O'Connor, 2009). In all of these features, RAM 14306 matches described enantiornithine coracoids and differs from coracoids of non-enantiornithine birds (e.g., Chiappe and Walker, 2002; Hope, 2002; Longrich et al., 2011). Thus, RAM 14306 is here assigned to Enantiornithes. However, given the incomplete nature of the specimen and pending description of a partial enantiornithine skeleton from the Kaiparowits Formation assigned to *Avisaurus* (Hutchison 1993), we refrain from erecting a new taxon.

5. Discussion

RAM 14306 represents the first described specimen of a bird from the Kaiparowits Formation, and thus is an important addition to the faunal list for this unit. Although the occurrence is not surprising given the occurrence of birds in coeval deposits from western North America, it does indicate potential for future discoveries.

Interestingly, despite a relatively well-represented avian sample, enantiornithines are not yet known in the Dinosaur Park Formation of Alberta (Longrich, 2009), which is partially equivalent in age to the Kaiparowits Formation (Roberts et al., 2005). This may reflect

ecological differences between the two areas, although additional study and sampling are needed to investigate this issue. Regional endemism, as suggested for some non-avian dinosaurs (Sampson et al., 2010) probably is not a strong possibility. Most enantiornithines were presumably volant, so endemism by virtue of geographic barriers is unlikely, as additionally demonstrated by the occurrence of other enantiornithines near Alberta (see below).

In addition to the Kaiparowits Formation, enantiornithines have been reported from the Campanian of North America in New Mexico (Walker et al., 2007), Montana (Varricchio and Chiappe, 1995), Alabama (Chiappe et al., 2002), Baja California (Brodkorb, 1976; Chiappe, 1992) and British Columbia (Dyke et al., 2011; Morrison et al., 2005). Only *Alexornis antecedens* from Baja California (illustrated and described in Brodkorb, 1976; referred to Enantiornithes by Chiappe, 1992) and an isolated specimen from British Columbia (Morrison et al., 2005) preserve a coracoid. This element in the holotype of *A. antecedens* is less complete than the coracoid in RAM 14306, but comes from an individual of much smaller body size (approximately one-third the size of RAM 14306, estimating from Brodkorb, 1976: fig. 1) and with a much less bulbous scapular facet. An isolated coracoid from British Columbia (Morrison et al., 2005) is approximately half the size of RAM 14306, with a more protruding scapular facet as well as appearing to lack a prominent acrocoracoidal tubercle (Morrison et al., 2005: fig. 3B). Thus, these specimens probably come from different taxa.

Enantiornithine humeri, radii and tarsometatarsals from Campanian-aged deposits of New Mexico, Montana, and British Columbia indicate relatively large individuals for Mesozoic birds (Dyke et al., 2011; Morrison et al. 2005; Varricchio and Chiappe, 1995), perhaps comparable in size to RAM 14306. They may pertain to the same taxon, but the lack of overlapping material prevents a rigorous test of this hypothesis. A coracoid from the late Maastrichtian-aged Hell Creek Formation (YPM 57235; cf. *A. archibaldi*) was estimated to come from an individual weighing approximately 5 kg (Longrich et al., 2011: supplemental information). This specimen is also of similar size to RAM 14306 (humeral articular facet length of 16 mm in YPM 57235 vs. 19 mm in RAM 14306), although it differs the two specimens differ in other anatomical details (as outlined above). These fossils, along with finds from South America and Europe (Chiappe, 1993, 1996; Walker et al., 2007; Walker and Dyke, 2010; Wang et al., 2011) indicate that large enantiornithine birds were a widespread component of terrestrial ecosystems during the Late Cretaceous.

Acknowledgements

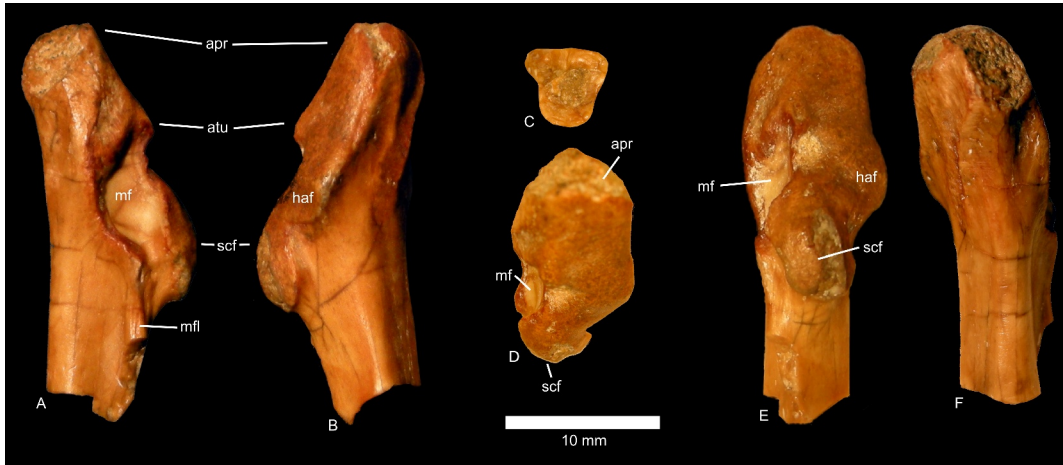
Fieldwork was conducted under Paleontological Resources Use Permit UT06-001S from the United States Bureau of Land Management, Utah. We thank Alan Titus at Grand Staircase-Escalante National Monument, and Scott Foss with the Bureau of Land Management, Utah, for their assistance with permitting and field logistics. Discussions with Luis Chiappe, Nicholas Longrich, Jingmai O'Connor, and Lindsay Zanno were helpful in confirming the identity of the specimen. Don Lofgren and numerous volunteers from The Webb Schools are gratefully acknowledged for their efforts in collecting fossil material, the David B. Jones Foundation and the Mary Stuart Rogers Foundation are thanked for funding, and Ashley Fragomeni is thanked for curatorial assistance. Comments by an anonymous reviewer and Luis Chiappe also were helpful in improving the manuscript.

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Fig. 1. *Enantiornithes* gen. et sp. indet., partial right coracoid RAM 14306 in: A, medial view; B, lateral view; C, cross-section of shaft (dorsal end at top); D, shoulder view; E, dorsal view; F, ventral view. Abbreviations: apr, acrocoracoidal process; atu, acrocoracoidal tubercle; haf, humeral articular facet; mf, medial fossa; mfl, medial flange; scf, scapular facet of coracoid.



Supplementary Data. Topologies of phylogenetic trees showing the position of RAM 14306 within Aves, as discussed in the text.

Figure S1. Strict consensus tree resulting from phylogenetic analysis of the position of RAM 14306 within Aves, using the matrix of Ji et al. 2011, with the re-addition of *Rapaxavis pani* and *Longicrusavis houi* from O'Connor et al. (2010).

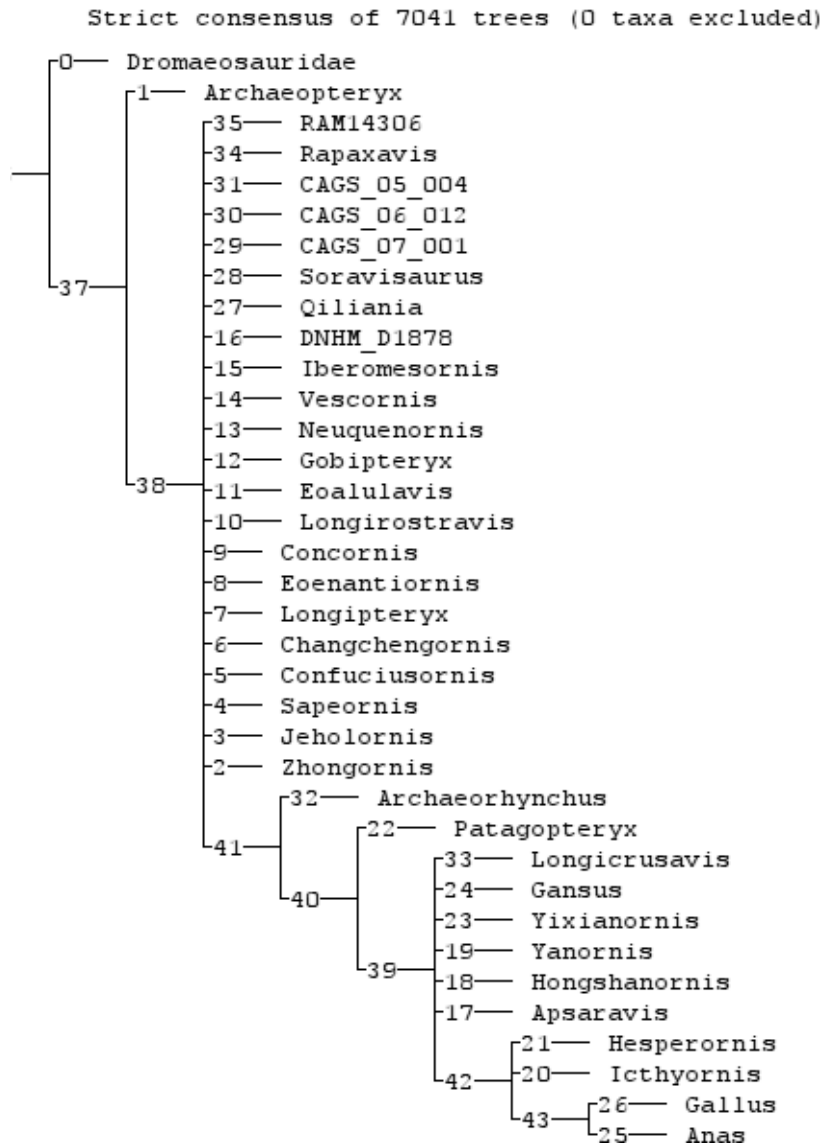


Figure S2. Strict consensus tree resulting from phylogenetic analysis of the position of RAM 14306 within Aves, using the matrix of Ji et al. 2011, with *Rapaxavis pani* and *Longicrusavis houi* excluded.

