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SHORT COMMUNICATION

AN ENANTIORNITHINE BIRD FROM THE LOWER MIDDLE CENOMANIAN OF TEXAS

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The fossil record of North American Cretaceous birds has improved little over the past two decades, even as a great diversity of fossil avians has been uncovered in Cretaceous sediments of Asia, Europe, and South America during the same time span. The best-represented Cretaceous North American birds are *Ichthyornis* and a small number of hesperornithine taxa, mostly from Upper Cretaceous marine sediments (Marsh, 1880; Clarke, 2004). In contrast, the most diverse and common Cretaceous fossil birds known from other continents belong to the more basal clade Enantiornithes. Enantiornithes was first recognized as a group of morphologically distinct birds based upon numerous remains collected from Maastrichtian terrestrial deposits of Argentina (Walker, 1981). A great diversity of enantiornithine taxa were recognized during the past two and a half decades, with most reported from Asia, Europe, and South America (Chiappe and Walker, 2002). Many taxa, especially those from China and Spain, were represented by relatively complete skeletons, thus providing some of the best morphological data known for these Cretaceous birds.

The North American record of enantiornithine birds has lagged behind discoveries on other continents. *Alexornis antecedens* was reported from the Bocana Roja Formation (Campanian) of the Baja California of Mexico (Brodkorb, 1976), and was later assigned to Enantiornithes by Chiappe (1991). *Avisaurus archibaldi* was first described as a small, bird-like dinosaur from the Hell Creek Formation (Maastrichtian) (Brett-Surman and Paul, 1985), but was subsequently identified as an enantiornithine (Chiappe, 1992). *Avisaurus gloriae* was described later from the Two Medicine Formation (Campanian) of Montana (Varricchio and Chiappe, 1995). The most complete North American enantiornithine specimen to date was collected from the Kaiparowits Formation (Campanian) of Utah, and the yet to be described specimen was informally referred to *Avisaurus* (Hutchinson, 1993). *Halimornis thompsoni* was erected based upon bones from offshore marine deposits of the Mooreville Chalk Formation (Campanian) of Alabama (Chiappe et al., 2002), and additional elements referable to Enantiornithes were described from the marine Northumberland Formation (Campanian) of British Columbia (Morrison et al., 2005). The proximal end of a humerus from Campanian sediments of New Mexico was recently referred to the enantiornithine taxon *Martinavis* sp. (Walker et al., 2007).

We report the discovery of enantiornithine bird fossils from the middle Cenomanian Woodbine Formation of north-central Texas (Fig. 1). The fossils were found near the Grapevine Lake Dam Spillway, U.S. Army Corps of Engineers controlled property, northeast Tarrant County, Texas (Fig. 1A). The bird bones described here were found spread out on the surface within centimeters of each other and came from near the top of an isolated, sandy channel and levee deposit cut into gray, marine mudstone of the Lewisville Member of the Woodbine Formation (Fig. 1B) (Dodge, 1969). Other fossils from the channel deposit include numerous isolated remains of sharks, bony fishes, turtles, crocodilians, dinosaurs, and abundant carbonized and petrified wood. Preservation quality of the vertebrate fossils from the site is poor, because of heavy gypsum invasion of elements and weathering of the bones. The sedimentology and particularly the mix of marine and terrestrial fossils indicate a coastal marine depositional setting. The uppermost part of the overlying Arlington Member (Dodge, 1969) of the Woodbine Formation produces invertebrates consistent with the *Conlinoceras tarrantense* Zone ammonite fauna (Lee, 1997a, 1997bb; Jacobs and Winkler, 1998). The age of the base of this ammonite zone is variably set at 96.01 Ma (Gradstein et al., 2005) to 95.73 ± 0.61 Ma (Cobban et al., 2006), making the type horizon no younger than early middle Cenomanian.

The bird fossils are very incomplete and poorly preserved, yet exhibit at least one unambiguous enantiornithine character. The fossils bear unique, diagnostic apomorphies that justify erecting a new taxon. The new specimen extends the North American record of Enantiornithes back by approximately 10 million years. This provides an additional data point for enantiornithine diversity that straddles the Lower Cretaceous avifaunas of Asia and Europe and the highest stages of the Upper Cretaceous in North America.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758 (sensu Chiappe, 1992)

ORNITHURAE Haeckel, 1866 (sensu Gauthier, 1986; Sereno, 1998)

ORNITHOTHORACES Chiappe & Calvo, 1994 (sensu Sereno, 1998)

ENANTIORNITHES Walker, 1981 (sensu Sereno, 1998)

FLEXOMORNIS HOWEI nov.

Holotype—DMNH (Museum of Nature and Science, Dallas) 18137, a right scapula missing the tip of the acromion process.

Referred Material—Several additional elements also catalogued as DMNH 18137 include a partial carpometacarpus, proximal tibia, and several indeterminate but avian-like bone fragments. All additional pieces were found within a square meter surrounding the holotype. The close proximity of the avian fossils to one another and absence of any other avian remains from the vicinity is evidence that these elements belong to a single individual.

Locality and Horizon—Lewisville Member of the Woodbine Formation (lower middle Cenomanian), near the Grapevine Lake Dam Spillway, northeast Tarrant County, Texas, U.S.A. More specific locality information is on file at the Museum of Nature and Science, Dallas.

Etymology—*Flexomornis*, from *flex* (Latin for bend, curve, or turn), *om* (Greek for shoulder), and *ornis* (Greek for bird); *howei* in recognition of Kris Howe, the local fossil enthusiast who brought the site and its vertebrate fossils to our attention.

Diagnosis—A relatively large enantiornithine bird that differs from other members of the lineage in having a scapular blade that is dorsoventrally broad and mediolaterally laminar, lacks a medial longitudinal groove, and has a distinct ventral-ward bend in the blade axis in mediolateral view. Another potentially diagnostic apomorphy for the taxon is the presence of crests along the

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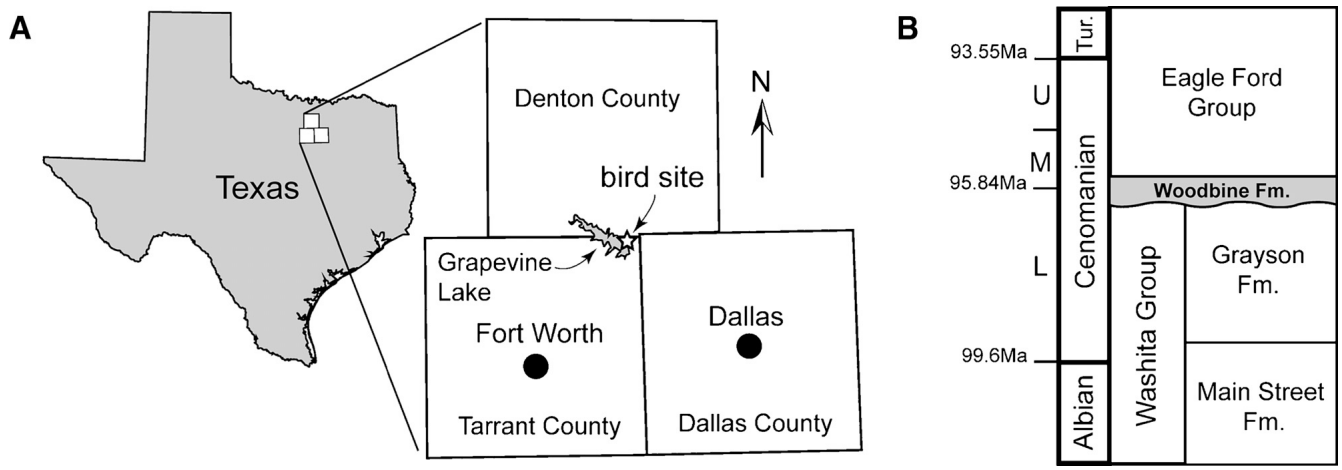

FIGURE 1. **A**, Map of Texas, U.S.A., highlighting counties adjacent to Grapevine Lake and showing proximity to cities of Dallas and Forth Worth. Bird fossil locality indicated by open star at southern end of Grapevine Lake. **B**, stratigraphic column showing position of Woodbine Formation relative to timescale and adjacent geologic units. Time scale based on Gradstein et al. (2005).

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craniodorsal margins of the minor and major metacarpals. There is not enough additional information preserved in the specimens to justify placing the new taxon in an extensive phylogenetic analysis of Enantiornithes at this time.

Description—The holotype scapula measures 63.8 mm from the broken base of the missing acromion process to the distal tip of the blade, and 61.4 mm from the proximal lip of the humeral facet to the distal tip of the blade (Fig. 2A–F). The proximal end has a pronounced, saddle-shaped humeral facet that faces more ventrally than laterally. The base of a stout acromion process projects craniodorsal to the facet, but most of the process is missing. A sub-triangular depression, the coracoidal articular facet of the scapula, is located medial (= costal) to the humeral articulation with a weak ridge separating the two (Fig. 2C–F). A scapulacoracoid contact consisting of a concave coracoidal facet on the scapula and a complementary convex scapular articulation on the coracoid is a diagnostic character of Enantiornithes (Zhang and Zhou, 2000; Chiappe and Walker, 2002; Zhou et al., 2008). This ubiquitous structure is reversed from the state in Neornithes and other avians in which the scapula bears a small tubercle to engage a concavity on the coracoid.

The blade of the scapula is not straight in mediolateral view, but has a pronounced ventral-ward angle, or bend a little more than one third of the way toward the distal end (Fig. 2A, B, E, F). There is no sign of post-depositional deformation of the bone, indicating the bend is not an artifact of preservation. The blade is dorsoventrally broad, nearly as wide as the craniocaudal span of the humeral facet. It is very thin mediolaterally, and gradually tapers to the distal tip. This contrasts with the condition in most other enantiornithines and other basal birds, in which the scapula is straight and dorsoventrally narrow (Chiappe and Walker, 2002). An exception among Enantiornithes may be *Protopteryx fengningensis* from the Lower Cretaceous of China, in which the distal end of the scapula is reportedly curved and thin as in more derived birds (Zhou, 2002). The ventrally directed bend, or kink, in the scapular blade is similar to that in *Elsornis keni* from the Djadokhta Formation (Campanian) of the Gobi Desert (Chiappe et al., 2007). A section of the medial surface of the scapula of DMNH 18137 is missing near the proximal end, but otherwise the medial surface is relatively intact and well preserved. It is clear that the medial surface is only weakly concave in its proximal half, and it lacks the distinct longitudinal furrow cited as a potential synapomorphy of Euenantiornithes (Chiappe and Walker, 2002).

The carpometacarpus is incomplete. The alular metacarpal and distal ends of the major and minor metacarpals are not preserved (Fig. 2G, H). Proximally, the distal carpals and major and minor metacarpals are fully fused. The preserved metacarpal shafts are both weakly bowed, resulting in a concave cranial margin and convex caudal margin for the carpometacarpus. There is a thin crest along the craniodorsal margin of both the major and minor metacarpals. The crest is most pronounced on the minor metacarpal. The similarity in size, shape, and location of the crests on both metacarpals argues against them being artifacts of crushing or other postmortem damage. The presence of these crests is a diagnostic character of *Flexomornis*.

The partial right tibiotarsus is approximately circular to ellipsoidal in proximal view, a condition typical of enantiornithines (Fig. 2I) (Chiappe and Walker, 2002). There is a rudimentary cnemial crest on the cranial surface that extends distally only a short distance (Fig. 2J–M). The presence of a small cnemial crest on the tibiotarsus is also consistent with other enantiornithines (Chiappe and Walker, 2002). A flange-like fibular crest extends down the lateral and craniolateral margin of the bone for its preserved length. The tibiotarsus tapers in diameter distally from the proximal end to the level at which the specimen is broken, suggesting the missing distal part of the shaft was narrow.

Several additional pieces of bone were collected from the immediate vicinity of the holotype and the other pieces described above. These include parts of very thin-walled bones that fall into a size range consistent with the major elements described here, but the preservation quality of the material is very poor. One of the larger pieces may be the distal end of a humerus. The element has very thin walls and is crushed nearly flat. Unfortunately the bone is also heavily damaged by gypsum crystallization, and it cannot at this time be identified with greater certainty.

Discussion

Comparisons to *Elsornis keni*—The scapula of *Flexomornis howei* differs from that of most other enantiornithines and basal ornithurans in that it is dorsoventrally broad, laminar, has a knife-edged form, and most notably has a marked ventral-ward bend. This pronounced ventral bend or 'kink' in the scapula is also present in *Elsornis keni*, an enantiornithine from the Djadokhta

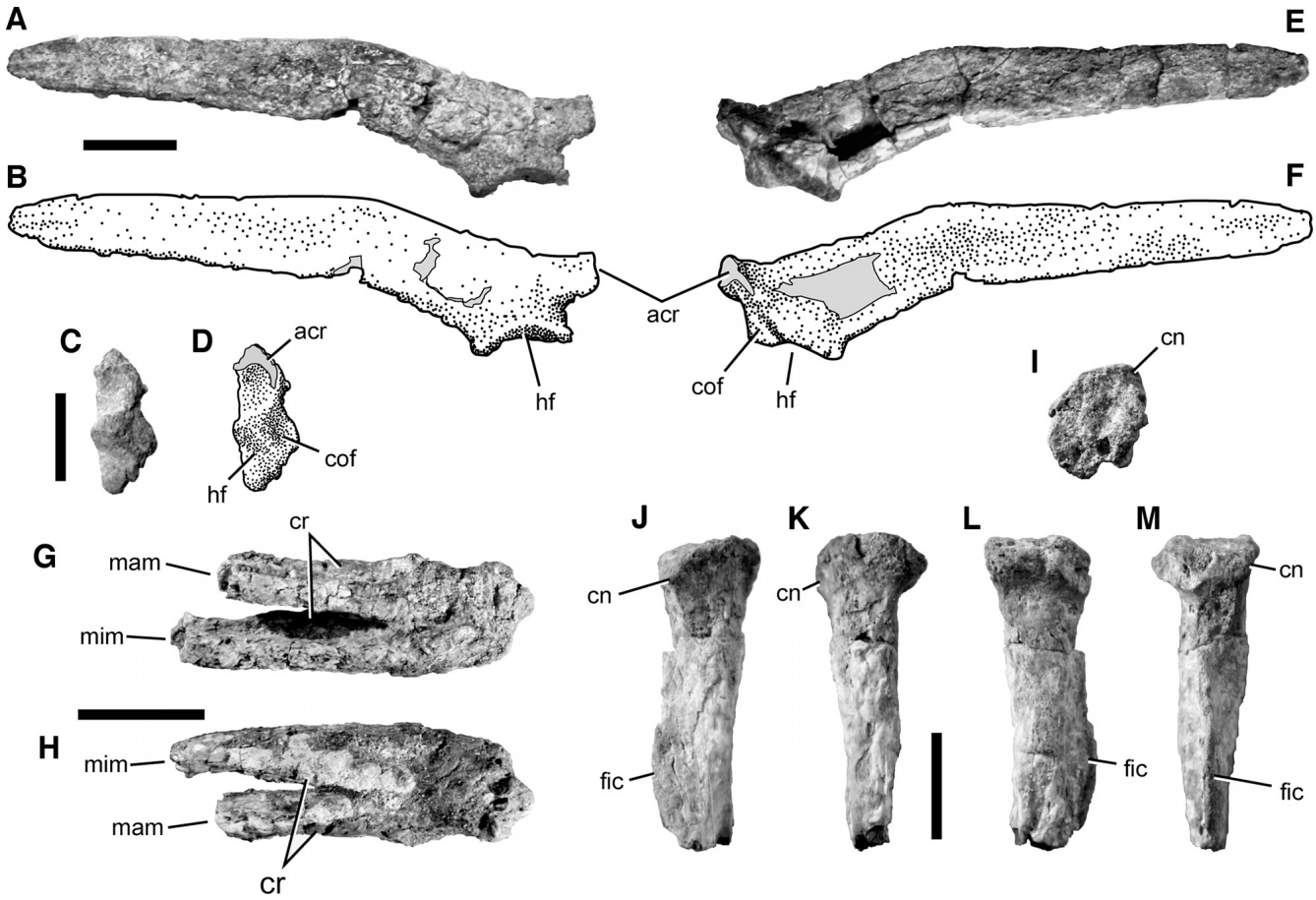

FIGURE 2. DMNH 18137, holotype of *Flexomornis howei* and associated specimens bearing same catalog number. **A**–**F**, holotype right scapula in lateral (**A**, **B**), proximal (**C**, **D**), and medial (**E**, **F**) views. **G**, **H,** partial right carpometacarpus in ventral/palmer (**G**), and dorsal (**H)** views. **I**–**M**, proximal end of tibiotarsus in proximal (**I**) anterior (**J**), medial (**K**), posterior (**L**), and lateral (**M)** views. **Abbreviations**: **acr**, acromion process; **cn**, cnemial crest; **cof**, coracoidal facet; **cr**, crest along metacarpal dorsomedial margin; **fic**, fibular crest; **hf**, humeral facet; **mam**, major metacarpal; **mim**, minor metacarpal. Gray areas indicate broken bone surfaces. Scale bars equal 1 cm.

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Formation (Campanian), of the Gobi Desert of Mongolia (Chiappe et al., 2007). In *Elsornis*, the bend is positioned at a point approximately one third of the distance between the proximal and distal ends of the scapula, whereas the bend is slightly more distally located in the scapula of *F. howei*. The presence of a ventral-ward kink in the scapular blade appears to be unique to these two taxa among known enantiornithines. There remain substantial differences in the morphologies of the two scapulae. The scapula of *E. keni* is more delicately constructed than in *Flexomornis*, particularly distal to the kink where the scapular blade is dorsoventrally narrower. The scapula of *F. howei* remains broad distal to the kink, tapering down only slightly to its tip. *Flexomornis* does not have a longitudinal groove along the medial surface of the scapular blade, unlike *Elsornis* and other enantiornithines. *Elsornis* also has a longitudinal groove on the lateral surface of the scapular blade, a feature not present in *F. howei* (Chiappe and Walker, 2002; Chiappe et al., 2007).

An additional similarity between *Flexomornis howei* and *Elsornis keni* is the presence of a craniocaudally bowed carpometacarpus (Chiappe et al., 2007). The shafts of the major and minor metacarpals are weakly curved in both taxa, resulting in a cranially concave margin to the profile of the carpometacarpus. This was cited as a unique apomorphy of *Elsornis keni* by Chiappe et al. (2007), because the cranial margin of the element is nearly straight in all other enantiornithines (Chiappe and Walker, 2002). The thin craniodorsal crests on the major and minor metacarpals of *F. howei* are not present in *E. keni*. Too little of the distal ends of the metacarpals are preserved in *F. howei* to determine if there is an exceptionally long distal metacarpal symphysis between them as is diagnostic of *E. keni* (Chiappe et al., 2007).

The ventrally angled scapular shaft and craniocaudally bowed carpometacarpus in these two taxa suggest the possibility of similar function or mechanics for the shoulder joint and forelimb. Chiappe et al. (2007) postulated that *Elsornis keni* may have been a flightless bird, the first flightless enantiornithine so recognized. The assertion was based upon the relatively short proportions of ulna length compared to humerus length and overall forelimb length, which plotted in the range of modern paleognaths (Chiappe et al., 2007). It is tempting to speculate that *Flexomornis howei* represents another flightless enantiornithine, based upon the similarities of the scapula and manus with those of *E. keni*. In the absence of the remaining forelimb elements for comparison, such a claim is likely premature.

There is the chance that the shared apomorphies of the scapula and carpometacarpus in these taxa have phylogenetic significance, perhaps indicating a close relationship to the exclusion of other enantiornithines. Given the temporal and

paleogeographical distances separating the two taxa, such a relationship would have intriguing implications and would illustrate how little we know of enantiornithine diversity and distribution. Alternative explanations such as convergence, or a greater distribution of these morphologies among yet unknown taxa, could also explain the similarity in these elements. It is beyond the scope of this paper to conduct an extensive analysis of enantiornithine phylogeny, and we refrain from further speculation concerning the in-group relationships between *Flexomornis howei* and other enantiornithines.

Cenomanian and Older North American Birds—The inferred minimum age of the type locality (96.01 Ma [Gradstein et al., 2005], 95.73 ± 0.61 Ma [Cobban et al., 2006]) is slightly older than middle Cenomanian marine bonebeds in Saskatchewan, Canada (95.17 ± 0.31 Ma), from which abundant remains of ornithurine birds were collected (Tokaryk et al., 1997; Cumbaa et al., 2006). Most of the specimens from the Canadian sites are those of the hesperornithine *Pasquiaornis* (*P. hardei* and *P. tankei*), with additional remains referred to *Ichthyornis* (Tokaryk et al., 1997). A single broken metatarsal piece from one of these sites was questionably identified as that of an enantiornithine based upon the lack of distal fusion between it and the other metatarsals (Tokaryk et al., 1997), a plesiomorphic condition retained in enantiornithine birds. Given that retention of this primitive condition is not in itself proof of an enantiornithine present in the Saskatchewan localities, we follow previous works (Tokaryk et al., 1997; Cumbaa et al., 2006) and only tentatively entertain the possibility that this element may be from an enantiornithine.

Several bird-like teeth were reported from the Mussentuchit Member of the Cedar Mountain Formation (Upper Aptian-Lower Cenomanian) of Utah (Cifelli et al., 1997, 1999). These teeth were identified as being similar to those of hesperornithines (Cifelli et al., 1999), although recent work suggested these specimens were more similar to hypsilophodontid premaxillary teeth (Garrison et al., 2007). Ash beds in the vicinity of the site (Cifelli no. 2 Quarry) that produced the purported bird teeth and an associated vertebrate fauna (termed the Mussentuchit Local Fauna) were dated from 98.2 ± 0.6 Ma to 96.7 ± 0.5 Ma (Garrison et al., 2007), establishing the Mussentuchit member as early Cenomanian in age. The fossil-bearing site is near the top of this section, close to ash beds dating to approximately 97 Ma.

If the isolated teeth from the Mussentuchit Member of the Cedar Mountain Formation are those of birds, they represent the oldest North American bird fossils yet known (we do not consider the Upper Triassic *Protoavis texenis* Chatterjee, 1991, an avialan theropod), and are at least one million years older than *Flexomornis howei*. If the Cedar Mountain teeth prove to be nonavian, then *F. howei* would represent the oldest (approximately 96 Ma) North American bird yet known. Regardless of the status of the Cedar Mountain Formation specimens, the postcranial remains of *Flexomornis howei* currently represent the earliest diagnostic enantiornithine fossils from North America.

Numerous enantiornithine taxa are known from Lower Cretaceous deposits of Asia (Zhang and Zhou, 2000; Chiappe and Walker, 2002; Zhou, 2002; Zhou et al., 2008) and Europe (Sanz and Buscalioni, 1992; Sanz et al., 1995; Chiappe and Walker, 2002). North American enantiornithines were previously known with certainty only from Campanian and Maastrichtian rocks (Brett-Surman and Paul, 1985; Varrichio and Chiappe, 1995; Chiappe and Walker, 2002; Chiappe et al., 2002; Morrison et al., 2005, Walker et al., 2007). The presence of *Flexomornis* in the lower middle Cenomanian essentially halves the gap between the Upper Cretaceous enantiornithines of North America and the numerous Lower Cretaceous taxa from Asia and Europe. The unambiguous enantiornithine status of *F. howei* strongly suggests that additional diagnostic identifiable remains of enantiornithines and other basal birds will eventually be found in Lower Cretaceous sediments of North America. Lower Cretaceous vertebrate fossil-bearing formations such as the lower members of the Cedar Mountain Formation of Utah, the Cloverly Formation of the mid and northern Rockies, and Antlers Formation of Texas and Oklahoma are all North American units that could produce bird remains. Further, given that this specimen highlights the still incomplete nature of the fossil record for the enantiornithine clade, some caution should be used when developing detailed biogeographic models to explain the known global enantiornithine distribution.

The discovery of *Flexomornis howei* in the coastal marine Woodbine Formation sediments of Texas demonstrates that North American enantiornithine birds already occupied marine and near-marine environments by the earliest Late Cretaceous. The association between this early Late Cretaceous enantiornithine and a coastal marine habitat is not a surprise. Enantiornithines were already reported from coastal and offshore marine deposits of Alabama and British Columbia (Chiappe et al., 2002; Morrison et al., 2005). It can be assumed then that enantiornithines were long-lasting members of marine and coastal communities in North America, occupying these habitats side-by-side with more derived ornithurine birds.

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