

NEW ENANTIORNITHINE BIRD FROM THE MARINE UPPER CRETACEOUS OF ALABAMA

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In 1992, a field party led by Storrs L. Olson (National Museum of Natural History) recovered several bird bones from the marine Upper Cretaceous Mooreville Chalk Formation of western Alabama. In addition to a few remains of the ornithurine *Ichthyornis*, the only avian taxon previously reported for the Mesozoic of Alabama (Wetmore, 1962; Olson, 1975; Lamb, 1993, 1997; Lamb et al., 1993), the party collected several small bones, which proximity and taphonomic characteristics support that they belong to a single individual. The new specimen shares synapomorphies with Enantiornithes, a Cretaceous group of volant birds mostly known from continental deposits (Walker, 1981; Chiappe and Walker, in press). The occurrence of this new specimen in offshore deposits is thus significant. Most importantly, comparisons to other enantiornithines reveal characters justifying the erection of a new species, thus increasing the known taxonomic diversity of this major clade of basal birds.

DEPOSITIONAL SETTING

The Mooreville Chalk Formation consists of the upper Arcola Limestone Member and an unnamed lower member (Monroe, 1946). Faunal, lithologic, and trace fossil evidence suggests a near-shore depositional environment for the Mooreville Chalk Formation, perhaps just beyond the area of clastic deposition (Frey and Bromley, 1985). Stephenson and Monroe (1938, 1940) and Monroe (1968), among others, have suggested that few major rivers flowed into the Gulf of Mexico in western Alabama during the depositional time of the Mooreville Chalk Formation. This resulted in fairly clean, shallow waters of normal marine salinity within a warm climatic regime (Pryor, 1960).

During the deposition of the lower member of the Mooreville Chalk Formation, bottom waters appear to have been periodically dysoxic. Oxidic-dysoxic horizons, generally 1–2 m thick, are visible at various sites. Oxidic layers are characterized by noticeable concentrations of invertebrate mega-fossils (mainly crenulate oysters). Dysoxic layers are darker, contain abundant iron pyrite concretions, and typically lack invertebrate mega-fossils. Dysoxic layers are rich in fossil vertebrates. To date, all avian remains from the Mooreville Chalk Formation come from dysoxic horizons of its lower member.

In western Alabama, the Mooreville Chalk Formation ranges from latest Santonian to middle Campanian in age (Puckett, 1994). Using regional dip of approximately 6.5 m/km for the Mooreville Chalk Formation (Davis et al., 1975) and correlating from the contact of the underlying Eutaw Formation, exposed along Trussels Creek near Clinton (Greene County, Alabama), locality AGr-4 (the site that provided the specimen reported herein) lies in approximately the middle of the Mooreville Chalk Formation. This is slightly lower in the section than the area of nearby China Bluff to which Smith (1989) assigned an early–middle Campanian age based on calcareous nanno-fossils and planktonic foraminifera. Thus, the locality AGr-4 is of late-early to early-middle Campanian age.

During this time, AGr-4 was situated just within the southern edge of the Mississippi Embayment, along its eastern shore (Fig. 1). The embayment was bounded by the Appalachian Mountains on the east, and the Ozark Mountains on the west. AGr-4 is estimated to have been about 50 km offshore.

SYSTEMATIC PALEONTOLOGY

AVES
ORNITHOTHORACES
ENANTIORNITHES
EUEANTIORNITHES

HALIMORNIS THOMPSONI, gen. et sp. nov.
(Figs. 2–4)

Holotype—The new specimen is housed in two institutions. The first discovered elements are catalogued as D2K 035 (Discovery 2000, Birmingham). These elements include the proximal end of the right humerus (Fig. 2), the distal end of the right femur (Fig. 3), two trunk vertebrae, one caudal vertebra, and the pygostyle (Fig. 4). Subsequent excavation of the site produced a few other elements, which were catalogued as UAMNH PV996.1.1 (Alabama Museum of Natural History, Tuscaloosa). These include the shoulder half of the left scapula (Fig. 3), a thoracic vertebral centrum, and a thoracic neural arch (Fig. 4). All of these elements were found as a fan-shaped scatter on a slightly sloping surface, within an area smaller than 400 cm². Our understanding of the taphonomic conditions of the Mooreville Chalk Formation, and the fact that the greatest distance between any two elements was 32 cm, leads us to the conclusion that the bones unquestionably belong to a single individual. The two different collection numbers are a consequence of the inactivity of the former Red Mountain Museum collections (now Discovery 2000).

Locality and Horizon—AGr-4, approximately 11 km west of Clinton, Greene County, western Alabama (Fig. 1). Unnamed lower member, Mooreville Chalk Formation, Late Cretaceous (early–middle Campanian).

Etymology—*Halimornis thompsoni* from the Greek “*halimos*” (meaning “belonging to the sea,” in allusion to the marine deposits in which the specimen was found), and “*ornis*” (meaning bird); the specific name “*thompsoni*” is after Mrs. W. Thompson, the landlord of the area in which the specimen was found, in recognition of her many years of support of fossil collecting on her property.

Diagnosis—Enantiornithine bird with the bicipital crest of the humerus approaching the level of the humeral head and thus more proximally located than in any other enantiornithine, and an inflated area projecting laterally in the distal end of the femur. These characteristics are regarded as autapomorphies.

DESCRIPTION

The humerus preserves only the proximal end, with the pectoral crest missing (Fig. 2). In proximal view, the head is convex caudally and concave cranially, as in other basal birds (Chiappe, 1996a). The strong development of this condition, however, in which the head is divided into two portions that meet at a right angle (Fig. 2D), compares better to that of the Late Cretaceous *Enantiornis leali* and other enantiornithines from El Brete, Argentina (Walker, 1981; Chiappe, 1996a). In cranial view, the superior margin of the head is slightly concave in its central portion, approaching the more distinctly concave morphology of *Enantiornis leali* (Chiappe, 1996b), the Chinese Early Cretaceous *Sinornis santensis* (*Cathayornis yandica* [Zhou et al., 1992] is regarded as a junior synonym of *Sinornis santensis* [Serenio and Rao, 1992]—see Chiappe [1995]; Serenio et al. [in press]), and other enantiornithines

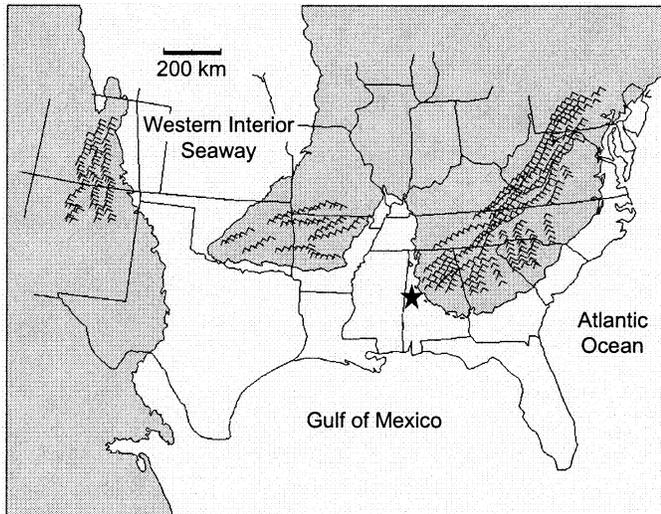


FIGURE 1. Map illustrating the fossil locality (modified from National Geographic 183 (1), Map supp. p. 2A).

(Chiappe, 1996a; Chiappe and Walker, in press). Cranially, and immediately distal to the head, there is a deep and circular depression (Fig. 2A). A similar cranioproximal fossa is present in Enantiornithes (Chiappe, 1996a, b; Chiappe and Walker, in press), and also in the flightless *Patagopteryx deferrariisi* from the Late Cretaceous of Patagonia (Alvarenga and Bonaparte, 1992; Chiappe, 1996a). The bicipital crest of *Halimornis thompsoni* is very pronounced and cranioventrally projected

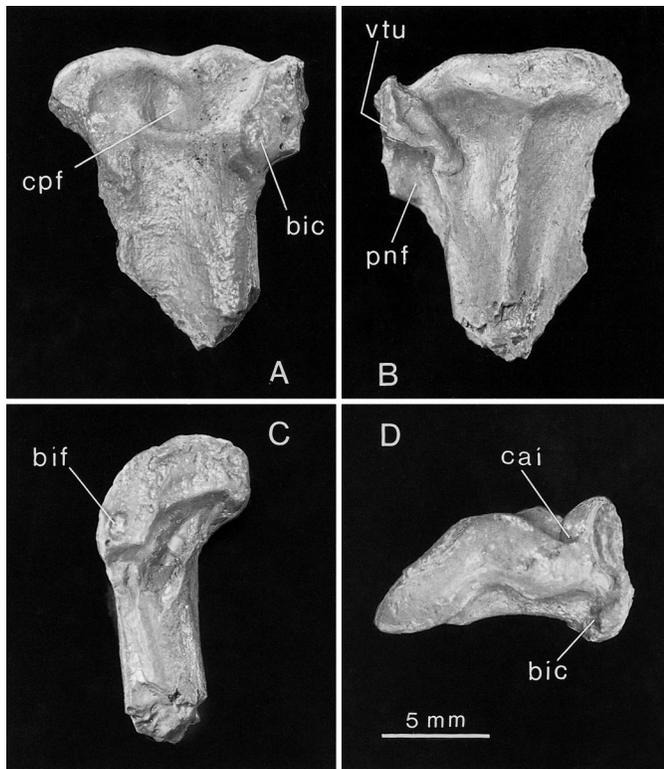


FIGURE 2. Proximal end of the right humerus (D2K 035) of *Halimornis thompsoni* in cranial (A), caudal (B), ventral (C), and proximal (D) views. **Abbreviations:** bic, bicipital crest; bif, muscular fossa (scar) on distal portion of bicipital crest; cai, capital incision; cpf, cranioproximal fossa; pnf, pneumotricipital fossa; vtu, ventral tubercle.

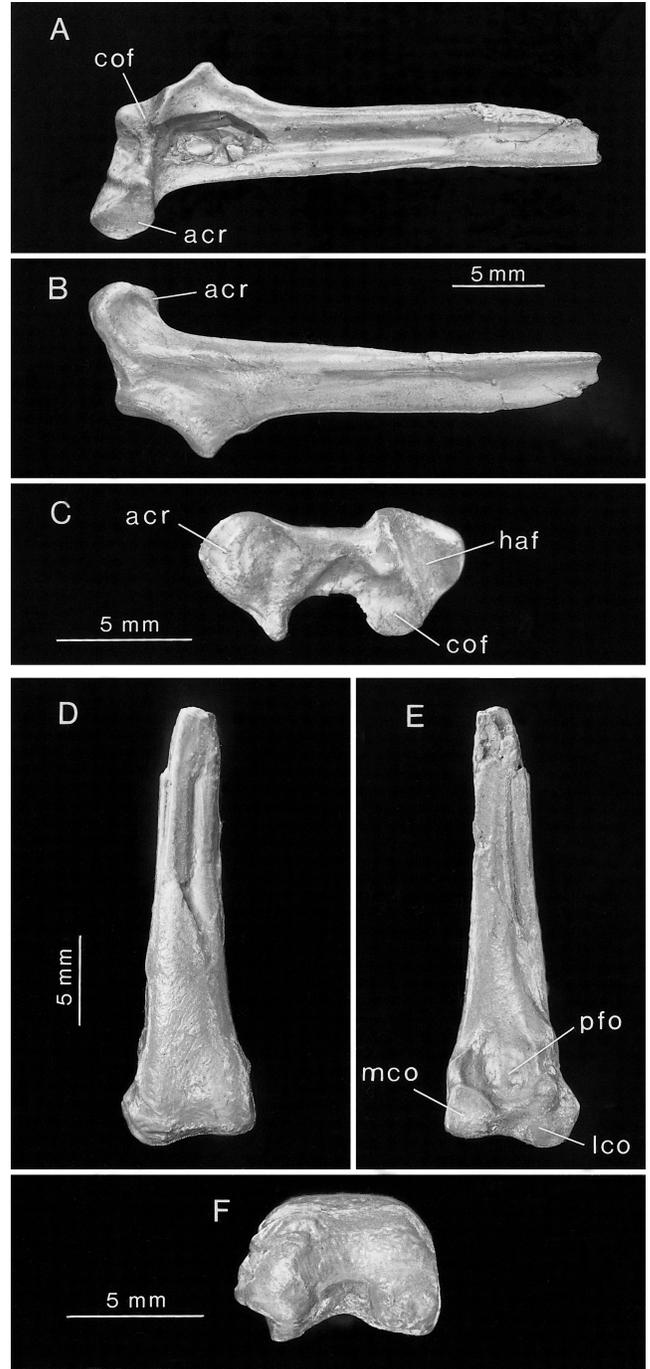


FIGURE 3. Shoulder half of left scapula (UAMNH PV996.1.1) (A–C) and distal end of right femur (D2K 035) (D–F) of *Halimornis thompsoni* in costal (A), lateral (B), proximal (C), cranial (D), caudal (E), and distal (F) views. **Abbreviations:** acr, acromion; cof, coracoidal articular facet; haf, humeral articular facet; lco, lateral condyle; mco, medial condyle; pfo, popliteal fossa.

(Fig. 2A, D), much as in Enantiornithes (Chiappe, 1996a, b). This crest has an elevated position, approaching the level of the humeral head. Proximal to this crest, there is a small, subtriangular depression that corresponds to the transverse groove of neornithine birds. The small development of this groove compares well to that of *Concornis lacustris* (Sanz et al., 1995), contrasting with the much greater transverse groove of other enantiornithines. In the ventral surface of the bicipital crest,

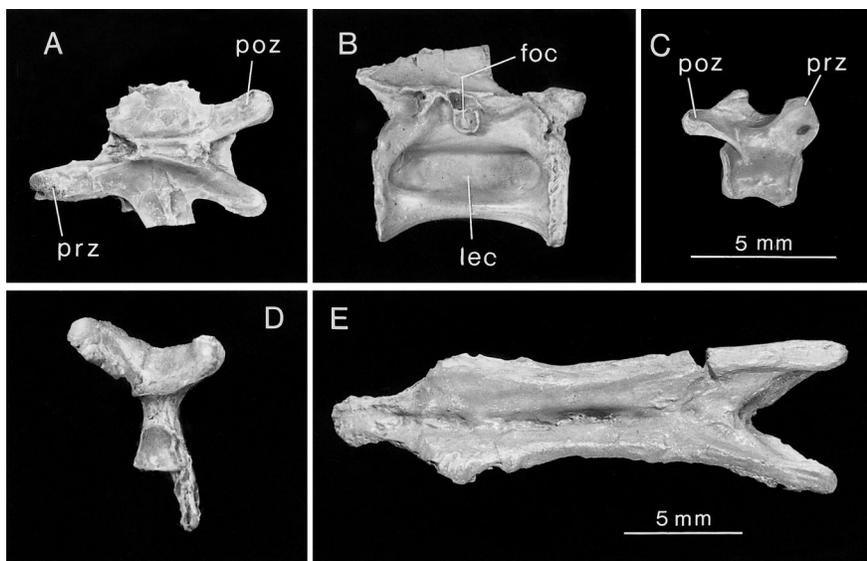


FIGURE 4. Thoracic and caudal vertebrae of *Halimornis thompsoni*. **A**, dorsal view of isolated neural arch of a thoracic vertebra (UAMNH PV996); **B**, right lateral view of caudal thoracic vertebra (D2K 035); **C**, right lateral view of a free caudal vertebra (D2K 035); **D**, **E**, cranial and dorsal view of pygostyle. **Abbreviations:** **foc**, costal fossa on parapophysis; **lec**, lateral excavation of centrum; **poz**, postzygapophysis; **prz**, prezygapophysis.

near the cranial border, there is a small, round fossa that most likely corresponds to a muscle scar (Fig. 2C). This scar is also present in a variety of enantiornithines (Chiappe, 1996a; Chiappe and Walker, in press) as well as in *Ichthyornis*. The ventral tubercle is strong and caudally directed, but it is not perforated, as in some other enantiornithines (e.g., *Enantiornis leali*). Distally, it is excavated by the pneumotricipital fossa, although a pneumatic foramen is absent.

The shoulder half of the left scapula is the only known portion of the thoracic girdle of *Halimornis thompsoni* (Fig. 3). The morphology of the scapula compares very well to that of other enantiornithines. The scapular blade is straight and of subequal width throughout its preserved segment.

On its medial margin, there is a distinct longitudinal groove (Fig. 3A) similar to that of *Enantiornis leali* and the Patagonian Late Cretaceous *Neuquenornis volans* (Chiappe and Calvo, 1994). The lateral surface of the blade also bears a longitudinal depression, although this is less pronounced than the medial one (Fig. 3B). The shoulder end of the scapula possesses a robust, subtriangular acromion (Fig. 3C). As in *Enantiornis leali* (Chiappe, 1996b; fig. 8C), the craniomedial area of the acromion forms a semilunate surface that may have articulated to the furcula, although in *Halimornis thompsoni* this surface is proportionally shorter and wider. Furthermore, this surface ends in a sharp, medially oriented tip that is absent in *Enantiornis leali*. The scapula of *Halimornis thompsoni* also differs from that of *Enantiornis leali* in that the acromion is separated from the articular facets for the coracoid and the humerus by a distinct neck (Fig. 3C). The scapula of *Halimornis thompsoni* lacks the circular pit of *Enantiornis leali*, located medially between the acromion and the articular facet for the coracoid (Chiappe, 1996b; Chiappe and Walker, in press); in *Halimornis thompsoni*, this area is excavated by a wide, semicircular notch (Fig. 3C). The humeral articular facet is subtriangular; it is more elongate and less concave than that of *Enantiornis leali*. As in the latter taxon, cranially and costally to the humeral articular facet, and located in a nearly perpendicular plane, there is a facet for the articulation to the coracoid (Fig. 3A, C). The facets for the humerus and coracoid are separated by a low ridge. Cranial to the humeral articular facet, this ridge converges with a distinct protuberance (Fig. 3C). Caudal to the vortex of the humeral articular facet, on the ventral margin of the scapular blade, there is a weak, subcircular tubercle (Fig. 3A, B).

Only the distal half of the right femur is known of the hindlimb; the shaft of the femur has been compressed after death (Fig. 3D, E). Cranially, the distal end lacks a patellar groove (Fig. 3D). The lateral condyle is slightly larger than the medial one. These two are connected to

each other distal to the shallow popliteal fossa (Fig. 3E). As in other basal avians, the lateral condyle lacks any evidence of a fossa for the femoral origin of *m. tibialis cranialis*. The weak tibiofibular crest of this condyle does not extend distally, being restricted by its caudal portion. Proximal to the tibiofibular crest, on the caudolateral border of the femur, there is an inflated area that slightly projects laterally; the caudally projected lateral crest of the distal end of the femur found in other enantiornithines (Chiappe and Walker, in press) is absent.

The three preserved thoracic centra are very similar and probably belong to the caudal part of the presacral series, since they show no trace of a ventral process (Fig. 4). The isolated neural arch compares well with the other vertebrae, although, since it is slightly wider than the others, it may come from a more cranial position within the thoracic series. Both cranial and caudal articular faces of the centra are slightly concave and subcircular. The centra are laterally compressed, although not as much as in the El Brete Enantiornithines (Chiappe and Walker, in press). Laterally, they are excavated by a deep, elliptical fossa (Fig. 4B). Comparable excavations are typical of Enantiornithes (Chiappe, 1996a; Sanz et al., 1995), but they are also present in a variety of other basal birds, including the Chinese Early Cretaceous confuciusornithids (Chiappe et al., 1999), *Hesperornis regalis*, and *Ichthyornis* (Marsh, 1880), as well as in various extant lineages (e.g., Procellariiformes, Turniciformes, and some Charadriiformes). The dorsal borders of these excavations bear strongly projected parapophyses that are located at the midpoint of the centrum (Fig. 4B); this condition is exclusively seen in Enantiornithes. The costal fossa of the parapophysis is round and it faces laterocaudally. As in other enantiornithines, a slender transverse process projects laterally from the centrum, caudally and dorsally to the parapophysis. A deep infrapostzygapophysial fossa excavates the caudal base of this process; in the only preserved neural arch, it does not connect to the vertebral foramen as it does in many extant lineages of birds. The vertebral foramen is ample, and the pre- and postzygapophyses are small. The prezygapophyses, longer than the postzygapophyses, are well separated from the cranial margin of the spinal process (Fig. 4A). Deep, triangular recesses for the attachment of interspinous ligaments excavate the area between the prezygapophyses and the postzygapophyses, cranial and caudal to the spinal process, respectively (Fig. 4A). As in confuciusornithids and all other ornithothoracines, *Halimornis thompsoni* lacks hyosphene-hypantrum accessory articulations.

The only free caudal vertebra preserved is complete, with the exception of the transverse processes (Fig. 4C). The articular facets are nearly flat. The spinal process is laterally compressed and it tapers dorsally in

lateral view. The dorsally projected prezygapophyses have nearly vertical articular facets. The articular facets of the postzygapophyses are also vertical. The postzygapophyses project caudally further back than the caudal face of the vertebral centrum (Fig. 4C).

The pygostyle (Fig. 4D, E) is laterally compressed. It is formed by at least eight vertebrae, as is evident from the number of foramina separating the different elements. The cranial articular facet is almost round. The dorsal margin forms an axial shelf with a median deep furrow (Fig. 4E). This condition is not seen in any neornithine lineage, but it compares well with the morphology of the pygostyle of the Chinese Early Cretaceous Enantiornithes *Sinornis santensis* (Zhou et al., 1992; Sereno et al., in press), as well as that of the confuciusornithids (Chiappe et al., 1999). Laterally, the dorsal shelf overhangs the synsacral centra. The cranial end of this shelf forms a robust fork that projects over the cranial articular facet; this fork is also present in the latter enantiornithine. Cranially, the base of the pygostyle has paired laminar processes (the right one is missing) that project ventrally (Fig. 4D).

DISCUSSION

The avian status of *Halimornis thompsoni* is indisputably indicated by the presence of a pygostyle, the caudal orientation of the ventral tubercle of the humerus, the non-sutured, movable articulation of the thoracic girdle, the wide vertebral foramen, and the distal delimitation of the fossa poplitea of the femur by an intercondylar ridge (Chiappe et al., 1996a).

Halimornis thompsoni shares several synapomorphies with Euenantiornithes, a subgroup of Enantiornithes defined as all taxa closer to *Sinornis santensis* than to *Iberomesornis romerali* (Chiappe and Walker, in press). These synapomorphies include the presence of: (1) a prominent longitudinal furrow on the medial surface of the scapular blade; (2) a cranioventrally projected bicipital crest of the humerus; (3) a median concavity of the superior margin of the humeral head; and (4) the median position of the parapophyses of the thoracic vertebrae. The presence of the prominent craniocaudally concavity-convexity of the humeral head, a fossa for muscular attachment on the ventral face of the bicipital crest of the humerus, wide lateral excavations on the thoracic centra, and a cranial fork in the pygostyle may also be synapomorphies of this clade (if so, some would be convergent to other birds).

The fragmentary nature of the single known specimen of *Halimornis thompsoni*, along with the incomplete knowledge of the interrelationships among enantiornithines complicates the assessment of its phylogenetic position beyond Euenantiornithes. An attempt to clarify the historical relationships among 16 valid euenantiornithine taxa, resulted in a complete lack of resolution, even though 36 variables were included in the analysis (Chiappe and Walker, in press). Understanding of the phylogenetic relationships of euenantiornithines is hindered by the incompleteness of many species, which are often known from a single bone, and the great morphological similarity of these birds (Chiappe and Walker, in press).

Halimornis thompsoni is the first enantiornithine to be discovered in deposits formed on the eastern margin of the Western Interior Seaway. This new species stands out among most other enantiornithines in that it comes from marine deposits. With the exception of *Nanantius eos* from the Albian Toolebuc Formation of Australia (Molnar, 1986), all other enantiornithine species so far described are known from continental (nonmarine) deposits. The occurrence of *Halimornis thompsoni* in a site located approximately 50 km offshore during the late-early to early-middle Campanian may indicate that this species frequented marine environments. This suggestion, combined with the misinterpretation of other marine avian remains (e.g., "*Ichthyornis*" *minusculus*, correctly identified as an enantiornithine by Kurochkin [1996]), suggests that the role played by Enantiornithes in Cretaceous marine ecosystems may have been more important than previously considered.

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