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Brief report

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A euenantiornithine bird from the Late Cretaceous Haţeg Basin of Romania

XIA WANG, GARETH J. DYKE, VLAD CODREA, PASCAL GODEFROIT, and THIERRY SMITH

We present the first record of a euenantiornithine bird from Romania. A small collection of fossil remains from the Maastrichtian add to the known distribution of large euenantiornithines and descriptions of birds from the Haţeg Basin augment the known vertebrate fauna from this famous region of Transylvania. The new specimens referred here to an indeterminate taxon of euenantiornithine further demonstrate that the larger members of this diverse Cretaceous lineage were globally distributed, as many birds are today.

Introduction

Enantiornithine birds are now known to be the most diverse of the lineages of avians from the Cretaceous (Walker et al. 2007). These taxa were first recognized by Walker (1981), who noted a series of novel morphologies in a collection of Late Cretaceous bones from the Argentine locality of El Brete (Walker and Dyke 2010). He named one taxon (*Enantiornis* Walker, 1981). More than a decade later, Sanz and Buscalioni (1992) reported the first European records of enantiornithines, describing *Iberomesornis*, *Concornis*, and *Eoaluavis* from the Early Cretaceous of Spain in a subsequent series of papers (Sanz and Buscalioni 1992; Sanz et al. 1995, 1996). Buffetaut (1998) then presented the first European records from the Late Cretaceous, a coracoid and femur from the village of Cruzy in the south of France. Additional specimens, also from the south of France, of similar age including some very large possible enantiornithines have now been reported (Buffetaut et al. 2000; Walker et al. 2007). Elsewhere in Europe, fragmentary specimens from the Santonian have been described from Hungary (Ősi 2008; Dyke and Ősi 2010) and from the Maastrichtian type-section at Maastricht, the Netherlands (Dyke et al. 2002, 2008). A putative enantiornithine known from an endocranial cast has also been reported from the Cenomanian of the Volgograd Region of European Russia (Kurochkin et al. 2006).

Although Cretaceous-aged deposits in Romania are well-known, only a handful of fragmentary avian bones have ever been described (Hope 2002; Dyke et al. 2011), alongside a single element from the Haţeg Basin recently reported to be ornithurine (Wang et al. 2011). Although spectacularly diverse from elsewhere, no enantiornithines have yet been reported from the paleontologically important Haţeg Basin, otherwise very well-known for a well-preserved and diverse vertebrate fauna (e.g., Bojar et al. 2010; Grigorescu 2010). Here, we present the first certain fossil evidence for the presence of enantiornithine birds in Romanian sediments, a nearly complete right humerus and the proximal end of a left humerus from the Late Cretaceous of the Haţeg Basin. These bones (NVEN 1 and NVEN 2) were collected from the Maastrichtian at Nalaţ-Vad, a locality near to the town of Haţeg on the banks of the river Râul Mare and are from the Sânpetru Formation (Smith et al. 2002; Fig.1). These sediments are of fluvial origin and combine coarse-grained channel deposits channelized into fine-grained floodplain deposits with calcrete palaeosols that accumulated around the early/late Maastrichtian boundary (Van Itterbeeck et al. 2004, 2005). Our use of osteological terminology follows Baumel and Witmer (1993).

Institutional abbreviation.—NVEN, Laboratory of Vertebrate Paleontology, Universitatea Babes-Bolyai, Cluj-Napoca, Romania.

Other abbreviations.—EN, Enantiornithine; NV, Nalaţ-Vad.

Systematic paleontology

Aves Linnaeus, 1758 (sensu Chiappe, 1992)

Ornithothoraces Chiappe and Calvo, 1994 (sensu Sereno, 1998)

Enantiornithes Walker, 1981

Euenantiornithes Chiappe, 2002

Genus and species indet.

Fig. 2.

Material.—NVEN 1, complete right humerus (Fig. 2A); NVEN 2, proximal end of left humerus (Fig. 2B).

Description and comparison.—The two humeri (NVEN 1 and 2) are identical to one another, and thus pertain to the same taxon. Our description here is based on the more complete humerus (NVEN 1) which is long (53 mm), robust, and slightly twisted so that its proximal and distal ends are expanded in different planes. This bone is longer than the majority of Early Cretaceous enantiornithines, but shorter than *Pengornis* (64.3 mm), the largest Early Cretaceous taxon from China, *Concornis* (68.1 mm) from the Early Cretaceous of Spain, and *Martinavis* (90–110 mm) from the Late Cretaceous of southern France, America and Argentina (Walker et al. 2007). The shape of the Romanian humerus is also not as sigmoid as is in *Cathayornis*, *Concornis*, and *Eoenantiornis* (Fig. 3E, F) (Sanz et al. 1995; Zhou 2002; Zhou et al. 2005, 2008; Walker et al. 2007); indeed, the length and degree

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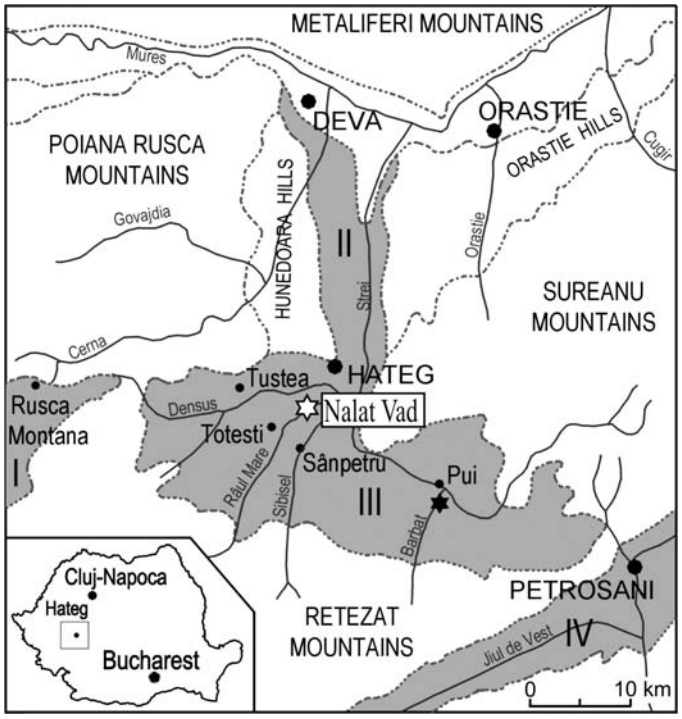


Fig.1. Geography of the Haţeg Basin, Western Romania, showing the position (star) of the microvertebrate bone bed that yielded the specimens discussed in this paper. Grey areas show post Late Cretaceous tectogenesis ("Laramian") sedimentary basins: I, Rusca Montana Basin; II, Strei Basin; III, Haţeg Basin; IV, Petrosani Basin.

of torsion observed in NVEN 1 is most similar to *Pengornis* (Zhou et al. 2008). The caudal surface of NVEN 1 is convex, while the cranial surface is relatively flat and not strongly concave as in *Enantiornis*, *Martinavis*, and *Gurilynia* (Fig. 3A, B) (Walker 1981; Kurochkin 1999; Walker et al. 2007). A globose morphology similar to ornithurines was reported for the humerus of *Pengornis* (Fig. 3C) (Zhou et al. 2008).

In cranial view (Fig. $2A_1$), the proximal margin of NVEN 1 is typically enantiornithine (Chiappe and Walker 2002) (Fig. 2B): concave in its midline and rising dorsally and ventrally, rather than being convex as is the case in the phylogenetically more derived ornithurine birds (Hope 2002). A globose humeral head is also seen in *Pengornis* and *Martinavis* (Walker et al. 2007). Distal to the head (Fig. $2A_1$, B_1), the proximocranial surface of the bone bears a deep impression from the M. coracobrachialis on its midline, as is also present in *Cathayornis* and *Enantiornis* (Fig. 3B) (Walker 1981; Zhou 2002). Proximoventral to this impression (Fig. $2A_1$, B_1), a long and imperforated sulcus ligamentous transversus is present, as in some of the El Brete specimens (Walker and Dyke 2010); in *Concornis*, *Halimornis*, and *Pengornis* this sulcus is shorter and shallower (Sanz et al. 1995; Chiappe et al. 2002; Zhou et al. 2008). The robust crista bicipitalis of specimen NVEN 1 is knoblike and prominently projected cranioventrally (Fig. $2A_1$, B_1). In contrast, the degree of projection of this crista is low in *Rapaxavis* and high in *Enantiornis* and *Concornis* (Fig. 3B, E) (Walker 1981; Sanz et al. 1995; Morschhauser et al. 2009). A small, pit-shaped, fossa similar to that seen in *Enantiornis*, *Halimornis*, *Eoalulavis*, *Concornis*, and even some basal ornithurine birds like *Apsaravis* (Walker 1981; Sanz et al. 1995, 1996; Norell and Clarke 2001; Chiappe et al. 2002) is located distally on the ventral margin of this crest, presumably the attachment site of a tendon of the M. biceps brachii, the aponeurosis of which covers the bicipital region in modern birds (Clarke 2004). In the flightless enantiornithine *Elsornis* this fossa is much larger (Chiappe et al. 2007).

The crista deltopectoralis is large and extends through the proximal third of the humerus (Fig. $2A_2$). Distally, it tapers gradually as in *Eoenantiornis*, *Pengornis,* and *Martinavis*, although in some enantiornithines this crest ends more abruptly (e.g., *Concornis*, *Enantiornis*). In contrast to the majority of euenantiornithines, however, where the crista deltopectoralis is flat, joins the shaft smoothly, and lacks any angle (Walker et al. 2007), the crista deltopectoralis of NVEN 1 projects cranially, a condition common in Neornithes (Hope 2002). Interestingly, in *Eoenantiornis* and *Pengornis* this crest is projected dorsally rather than cranially (Zhou et al. 2005, 2008). Ventral to its proximal half, there is an elliptical muscle scar on this crista that could be the attachment of the M. coracobrachialis cranialis, as also present in *Gurilynia* and *Eoalulavis* (Sanz et al. 1996; Kurochkin 1999). Located proximoventrally to this scar there is a round, shallow fossa distal to the humeral head; a similar fossa is seen on the humeri of other enantiornithines as well as in the basal ornithuromorph *Patagopteryx deferrariisi* (Chiappe 1996).

In caudal view (Fig. $2A_2$, B_2), the tuberculum ventrale is well-developed and prominent, deeper and more prominently projected caudally than seen in similarly-sized El Brete specimens (Walker and Dyke 2010). A large, round and imperforated fossa pneumotricipitalis, presumably the site for muscle attachment on the caudal surface of the crista bicipitalis is also present, but is deeper than the condition in most euenantiornithines (Chiappe and Walker 2002). The tuberculum dorsale is small and rises above the level of the head. The incisura capitis is deep and wide.

On its distal end (Fig. $2A_3$), this humerus is craniocaudally compressed and transversely expanded, as in other euenantiornithines (Chiappe and Walker 2002). The condylus ventralis is weakly developed and transversally located, not expanded and bulbous as in modern birds (Clarke and Norell 2002). In contrast, the condylus dorsalis of NVEN 1 is rectangular and horizontally oriented, as is typical of all known enantiornithine birds (Chiappe 1996). The epicondylus ventralis is enlarged and projects caudally, extending distally to below the level of the condyles to make the distal margin of this bone incline laterally while the epicondylus dorsalis is enlarged and extended cranially. Unlike *Alexornis*, *Martinavis vincei*, and *Eoalulavis* (Sanz et al. 1996; Walker et al. 2007; O'Connor 2009), the distal margin of NVEN 1 is angled slightly relative to the long-axis of the humerus shaft and there is no well-developed processus flexorius. A depressed fossa musculus brachialis is present but a distinctive scar for this muscle attachment is absent, as is characteristic of other enantiornithines (Chiappe and Walker 2002). On the craniodorsal margin, the tuberculum supracondylare ventralis and processus supracondylaris dorsalis are well-developed. In caudal view, no marked sulcus humeralis tricipitalis can be seen, although a wide, deep

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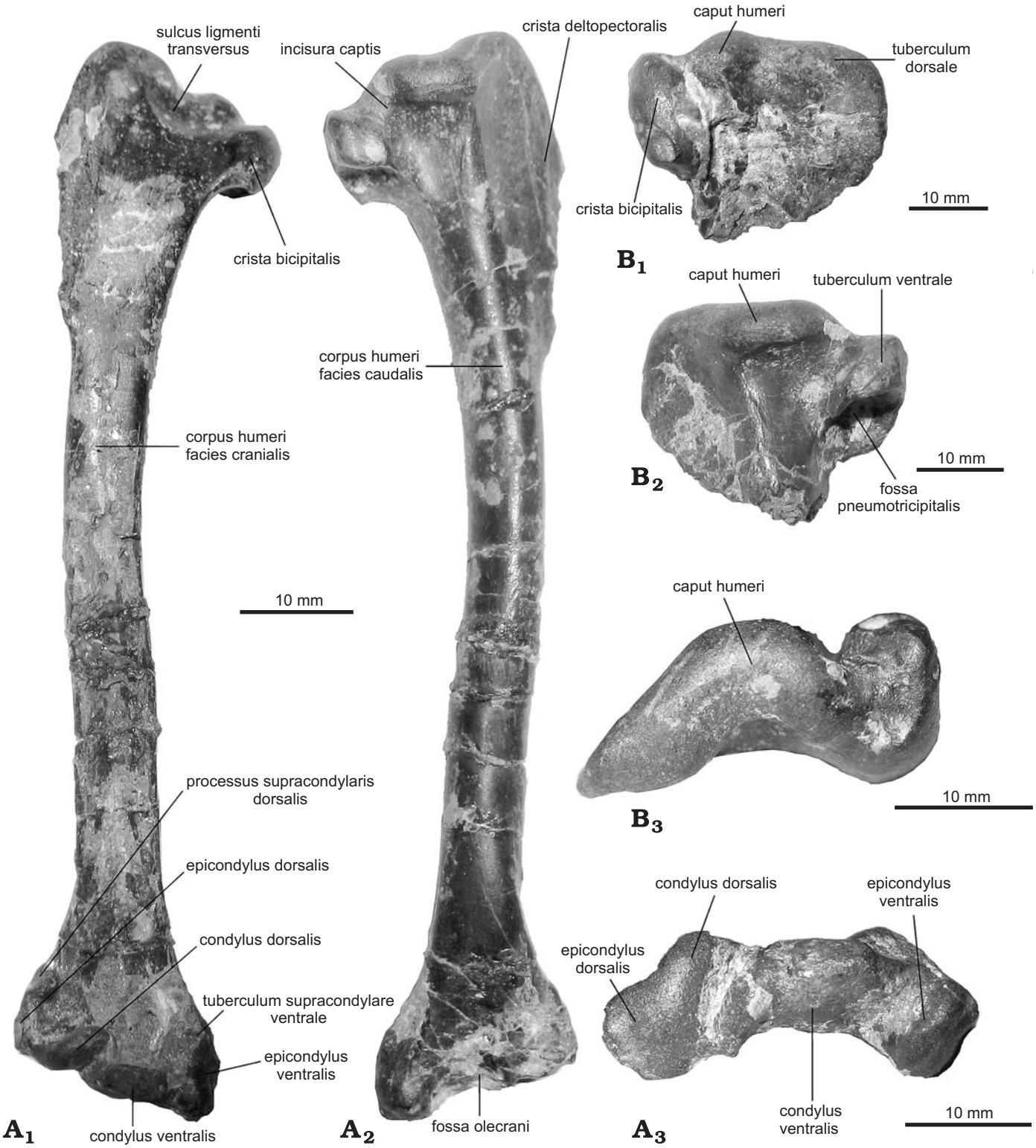


Fig. 2. Enantiornithine bird humeri from Romania, Hațeg Basin, Upper Cretaceous. **A**. NVEN 1, right humerus in cranial (A_1), caudal (A_2), and distal (A_3) views. **B**. NVEN 2, left proximal humerus in cranial (B_1), caudal (B_2), and proximal (B_3) views.

fossa olecrani is excavated between two distal condyles, both features typical of enantiornithines.

Measurements.—NVEN 1 maximum length, 53.3 mm; length of crista deltopectoralis, 17.2 mm; length of medial crista bicipitalis, 5.1 mm; width of fossa pneumotricipitalis, 4.5 mm; width of crista bicipitalis to crista deltopectoralis, 11.8 mm; medial/lateral thickness of median side of shaft, 5.0 mm; width of fossa musculus brachialis 3.9 mm; width of fossa olecrani, 3.8 mm; maximum width across distal end, 11.2 mm.

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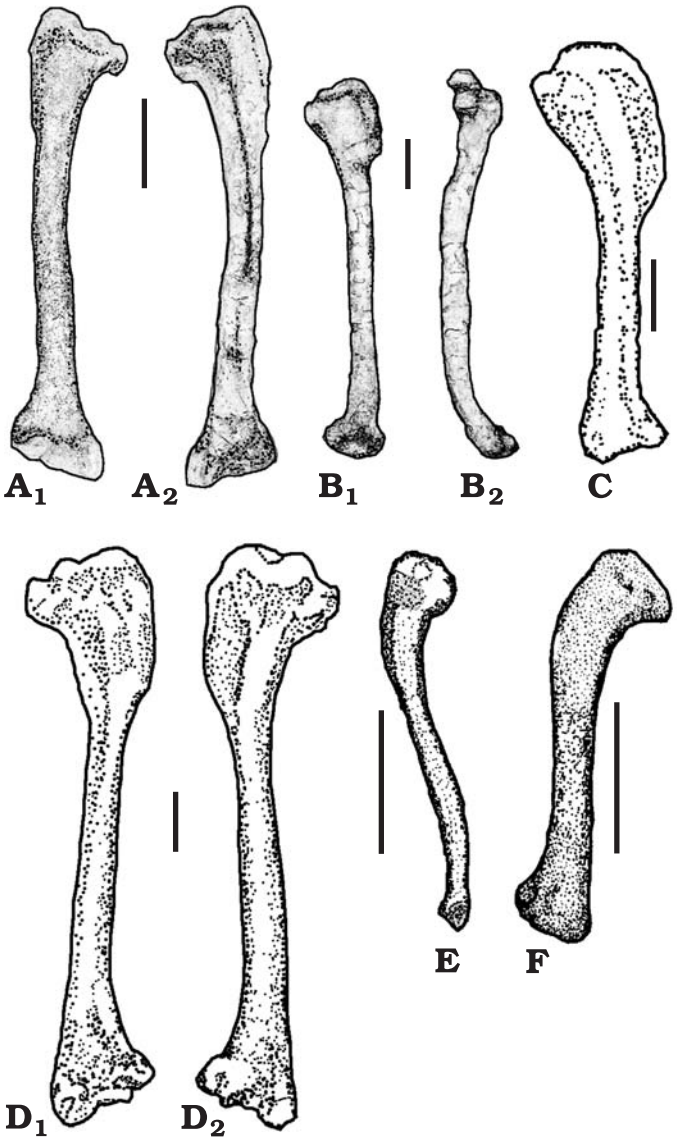


Fig. 3. Drawings of enantionithine humeri for comparison. **A**. NVEN 1, right humerus in cranial (A_1) and caudal (A_2) views. **B**. *Enantiornis leali* Walker, Buffetaut, and Dyke, 2007, in cranial (B_1) and caudal (B_2) views. **C**. *Pengornis houi* Zhou, Clarke, and Zhang, 2008, right humerus in caudal view. **D**. *Martinavis vincei* Walker and Dyke, 2010, left humerus in cranial (D_1) and caudal (D_2) views. **E**.*Concornis lacustri* Sanz, Chiappe, and Buscalioni, 1995, right humerus in cranial view. **F**. *Eoenantiornis buhleri* Hou, Martin, Zhou, and Feduccia, 2000, left humerus in caudal view. Scale bars 10 mm.

Stratigraphic and geographic range.—Maastrichtian, Sânpetru Formation, at Nalaț-Vad, near to the town of Hațeg.

Discussion

The general features of NVEN 1 exemplify the morphology of the humerus in enantiornithines in general and euenantiornithines in particular (Chiappe and Walker 2002; O'Connor 2009). NVEN 1 possesses the following unambiguous synapomorphies of euenantiornithine birds (based on the phylogenetic analyses of Chiappe and Walker 2002 and O'Connor 2009): dorsal margin of the humeral head concave in its central portion, rising both ventrally and dorsally on either side; crista bicipitalis prominent and cranioventrally projecting; ventral surface of crista bicipitalis bearing a small fossa for muscle attachment; and distal end of humerus very compressed craniocaudally. In addition, NVEN 1 shares with other members of Enantiornithes the presence of: an "L-shaped" articulation between the proximal part of the humerus and the coracoid (seen in proximal view: Walker 1981) (Fig. $2B_3$); a well-marked depression underneath the proximal head of the humerus; weakly developed distal condylus ventralis; epicondylus ventralis and epicondylus dorsalis lacking marked sulcus humeralis tricipitalis; condylus dorsalis horizontally orientated (Chiappe and Walker 2002). Additional characteristics that distinguish specimen NVEN 1 from other known enantiornithines include: wide and deep fossa pneumotricipitalis; crista deltopectoralis large and curved slightly cranially; tuberculum ventrale deep and prominently projected caudally; and a distinct fossa musculus brachialis.

The NVEN 1 humerus is very similar to specimens referred to the genus *Martinavis* (especially *M. vincei*), to date reported from the Late Cretaceous of France, America, and Argentina (Walker et al. 2007; Walker and Dyke 2010), except for its much smaller size, larger and more cranially projected crista deltopectoralis, and more caudally curved tuberculum ventrale. However, considering this large difference in relative size (NVEN 1 is about only half the size of *Martinavis vincei* and one third smaller than *Martinavis minor*) and also the fact that no sign of immaturity on this bone is detected, it is likely this size difference precludes individual variation. Consequently, NVEN 1 is likely not referable to a previously named species of *Martinavis*. Although morphological differences are seen on this new specimen, it is only a humerus and so we refrain from naming it at this point: the discovery of additional material might well require this action in the future.

The Romanian enantiornithine fossil bones we describe from the Hațeg Basin augment the known record of these birds and further demonstrate that members of this lineage were important components of latest Cretaceous vertebrate faunas. Although for some time the fossil record of these birds was little known from Central Europe (Chiappe and Dyke 2002; Fountaine et al. 2005), new discoveries both in Hungary (Dyke and Ősi 2010) and now in Romania have filled in important biogeographical gaps in our knowledge. These new enantiornithine records also provide further evidence for faunal element dispersal between Gondwana and Laurasia as it is highly likely that the larger taxa of Cretaceous enantiornithines were globally distributed, as many birds are today. *Martinavis* is one such taxon that has been hypothesized to have had a wide, perhaps global, distribution during the Cretaceous (Walker et al. 2007). If referred to this taxon, the new Romanian material described here further corroborates this pattern.

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