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Large euenantiornithine birds from the Cretaceous of southern France, North America and Argentina

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Abstract – We review historical approaches to the systematics of Enantiornithes, the dominant birds of the second half of the Mesozoic, and describe the forelimb remains of a new Cretaceous euenantiornithine. This taxon is known on the basis of fossil specimens collected from southern France, Argentina and the United States; such a wide geographical distribution is uncharacteristic for Enantiornithes as most taxa are known from single localities. Fossils from the Massecaps locality close to the village of Cruzy (Hérault, southern France), in combination with elements from New Mexico (USA) and from the Argentine locality of El Brete (Salta Province) testify to the global distribution of large flighted euenantiornithine birds in the Late Cretaceous. We discuss the systematics and taxonomy of additional isolated bones of Enantiornithes that were collected from the Argentine El Brete locality in the 1970s; the presence of these flying birds in Cretaceous rocks on both sides of the equator, in both northern and southern hemispheres, further demonstrates the ubiquity of this avian lineage by the latter stages of the Mesozoic.

Keywords: palaeontology, anatomy, Mesozoic, France, Argentina, New Mexico, flight.

1. Introduction

Over the last two decades the number of fossil birds known from the Cretaceous has ballooned; more fossils have been discovered and described since the early 1980s than were known for almost the entire preceding century (Chiappe, 1995; Kurochkin, 1995; Chiappe & Dyke, 2002; Fountaine *et al.* 2005) (Fig. 1). Because of this explosion in the known record, several new lineages of fossil birds have been discovered and documented, among them Enantiornithes (Walker, 1981; Kurochkin, 2001; Chiappe & Walker, 2002). This clade is now thought to have been the most diverse group of flying birds throughout the Cretaceous, comparable in morphological and taxonomic diversity to that of modern birds (Chiappe & Walker, 2002). The flight styles of these birds mirrored those seen amongst their modern counterparts (Neornithes) (Rayner & Dyke, 2002) and some were even flightless (Chiappe *et al.* 2006).

Our current understanding of the evolution of enantiornithine birds dates from the work of Walker (1981), who recognized novel morphologies in a collection of Late Cretaceous bones which had been shown to him by J. Bonaparte in the 1970s (Bonaparte was then working at the Universidad de Tucuman, Argentina). Bonaparte had collected a series of fossil bones between 1974 and 1976 (with help from J. Leal) from continental deposits of the Maastrichtian Lecho Formation in Salta Province, northwestern Argentina (Bonaparte *et al.* 1977; Bonaparte & Powell, 1980) (Fig. 2). Bonaparte took this collection of largely isolated bones to the USA where he showed them to the late Pierce Brodkorb; because Brodkorb told him that these elements 'did not belong to birds', he carried them on to London where they were examined in The Natural History Museum by Walker. A description and short analysis of some of the original El Brete collection followed (Walker, 1981); however, the bulk of this collection still remains undescribed, even though it has formed the basis for much subsequent descriptive and phylogenetic work on Enantiornithes (e.g. Brett-Surman & Paul, 1985; Chiappe, 1993, 1996; Chiappe & Walker, 2002). Walker (1981) based his diagnosis for 'Enantiornithes' on the anatomy of the forelimb and shoulder girdle; limited subsequent taxonomic work on the El Brete collection (Chiappe, 1993, 1996) focused instead on the hindlimb, in particular the anatomy of the tarsometatarsus.

In this paper we review previous taxonomic studies and note that Walker's original manuscript, later to form the basis for his 1981 publication, was much longer than in its final published form (Chiappe & Walker, 2002; cited in Chiappe, 1991, as 'in preparation'). We also provide a historical review of early ideas about enantiornithine taxonomy (1980s) and describe a new taxon that was originally identified (but never fully documented) by Walker in the 1980s. Some elements of

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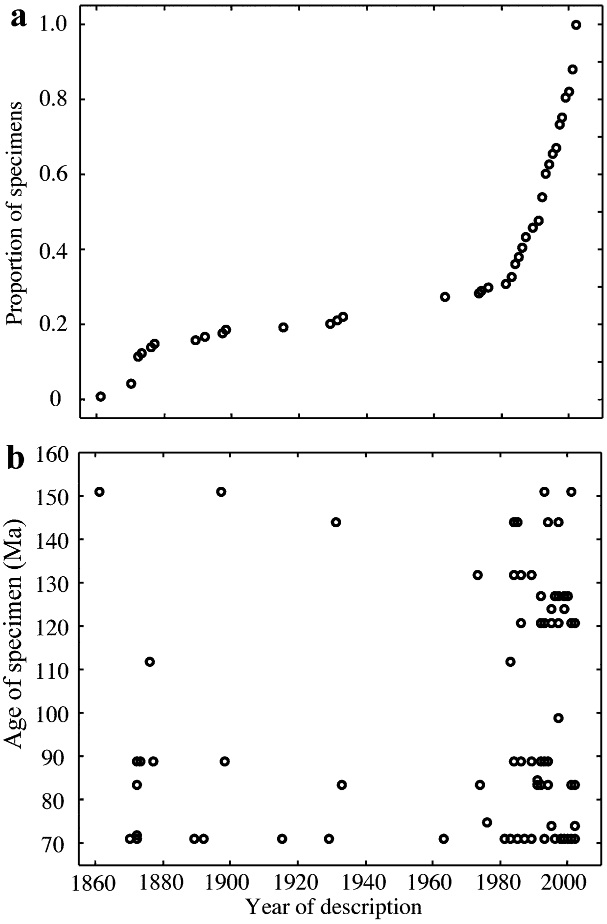

Figure 1. Collector curves to show increasing numbers of known Mesozoic birds since the 1980s: (a) increasing proportion of all known specimens, and (b) distribution of geological ages. From Fountaine *et al.* (2005).

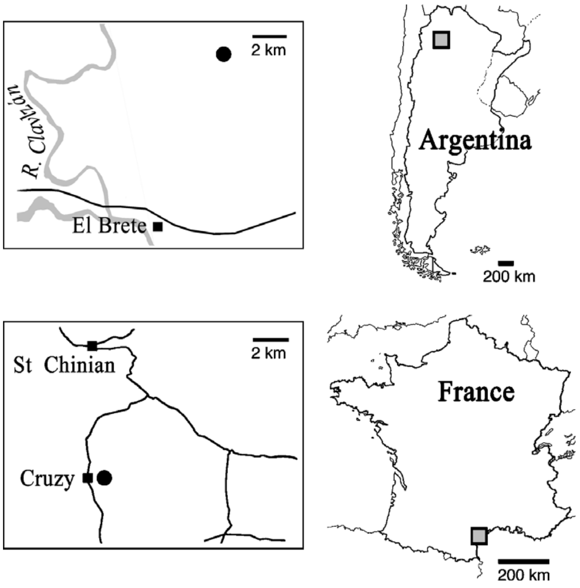

Figure 2. Maps showing the locations of El Brete (Argentina) and Massecaps (France). Regions of countries are shown as shaded boxes, localities as filled dots.

this new bird were figured by Walker (1981). Based on well-preserved humeri, this new Late Cretaceous bird is well represented in the original El Brete collections, and has more recently been discovered in sediments of the same age in southern France. Also collected in the mid-1970s, one additional bone also testifies to the presence of this taxon in the North American Late Cretaceous.

2. Material and methods

Repositories for specimens, and abbreviations used in the text, are indicated by the following acronyms: BMNH – The Natural History Museum, London, UK (Palaeontology Department collections); KU-NM – University of Kansas, Museum of Natural History, Lawrence, Kansas, USA; ACAP – Musée de Cruzy, Cruzy (l'Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois), Cruzy, France; PVL – Fundación-Instituto Miguel Lillo, Tucumán, Argentina. Although our illustrations are of original specimens (PVL), some of our anatomical descriptions are based on casts made in London in the 1980s (BMNH).

3. Historical review

In the late 1970s, pre-cladistic views of avian phylogeny and classification recognized three 'subclasses' of birds, termed 'Archaeornithes', 'Odontornithes' and 'Neornithes'. Examination of the morphology of the El Brete specimens, brought to London by J. Bonaparte, led Walker to name a new avian group, which he termed the subclass 'Enantiornithes' (Walker, 1981) to accommodate these (at the time) strange forms. Once published, not everyone agreed with this interpretation: at the time, considerable doubt was expressed verbally and in print concerning the 'avian affinities' of Enantiornithes (Steadman, 1983). Later, and as more material came to light, Walker's (1981) identification became more generally accepted in the literature (Elzanowski, 1981; Martin, 1983; Thulborn, 1984; Kurochkin, 1985; Olson, 1985; Cracraft, 1986; see review in Chiappe & Walker, 2002). Some authorities, however, remained unconvinced and still considered that at least part, if not all, of Walker's 'enantiornithine assemblage' was 'reptilian' (Steadman, 1983; Brett-Surman & Paul, 1985). The turning point came with subsequent reinterpretation of *Alexornis antecedens*, a sparrow-sized bird from the Cretaceous of Mexico that had been originally described as a 'coraciiform/piciform ancestor' by Brodkorb (1976). Walker (1981) noted similarities between the humerus of this taxon and elements from El Brete (which we discuss in this paper); critics of the 'enantiornithine' hypothesis had up until then not questioned the avian affinity of *Alexornis*, anatomically comprising little more than a scaled-down version of some of the bones from El Brete

(Walker, 1981). This connection was communicated to L. D. Martin by Walker, and eventually appeared in Martin (1983); Brodkorb (1976) had understandably mis-identified the scapula and coracoid of *Alexornis*.

Martin (1983), in the same paper, also suggested placing the 'ratite-like' *Gobipteryx* (Elzanowski, 1974, 1977), from the Cretaceous of Mongolia, within Enantiornithes. Martin (1983) referred specifically to the morphology of an undescribed lower jaw from Argentina, figured by Elzanowski (1977); this suggestion, like Martin's (1983) comment on *Alexornis*, was also criticized by Steadman (1983). Nevertheless, description of additional, incomplete, specimens of anatomically similar fossil birds followed in the 1980s; further isolated bones from the Cretaceous were next described and figured by Nessov (1984). Two small genera were recognized: *Zhyraornis kashkarovi*, which was thought closely related to the marine *Ichthyornis*; and *Kizylkumavis cretacea*, which Nessov (1984) likened to the similarly sized *Alexornis* (and thus to Enantiornithes). The distal part of a humerus that is the type and only known specimen of *Kizylkumavis* was considered enantiornithine by Walker in his original manuscript; it has a dorsoventrally curved distal end with poorly developed condyles on its cranial surface (Chiappe & Walker, 2002).

In general, a dearth of fossil birds, let alone specimens well-enough preserved to corroborate Walker's (1981) 'Enantiornithes', formed the research materials of the 1980s (Fig. 1) (Harrison & Walker, 1973; Brodkorb, 1978; Feduccia, 1980; Martin, 1983; Olson, 1985; see Feduccia, 2006). It is in this context that the approaches and methodologies used, as well as the conclusions reached, by early students of Enantiornithes must be viewed.

Walker (1981) hypothesized that: (1) Enantiornithes would prove to be widespread, that they likely enjoyed a global distribution in the Cretaceous; and that (2) Enantiornithes would prove to be the most abundant group of Mesozoic birds, but that their range would be restricted to the Cretaceous. Both of Walker's (1981) hypotheses have been borne out by subsequent fossil discoveries (Fig. 3) (Kurochkin, 1995, 1996; Feduccia, 1999, 2006; Zhang & Zhou, 2000; Zhang *et al.* 2000; Chiappe & Walker, 2002; Fountaine *et al.* 2005).

4. Geological setting and fossil associations

4.a. Southern France

The French specimen described here was collected during the course of systematic excavations at the Massecaps locality close to the village of Cruzy, Hérault, southern France (Fig. 2). Excavations in this area are conducted by the Centre National de la Recherche Scientifique (CNRS) and the Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois (ACAP); this Massecaps locality has yielded an abundant and diverse fauna of Late Cretaceous vertebrates, mostly represented by isolated elements, including lepisosteid fish, coelacanths, amphibians, turtles, varanoid lizards, mammals, dinosaurs and enantiornithine birds (Buffetaut, 1998, 2005; Buffetaut *et al.* 1999; Cavin *et al.* 2005). Remains of enantiornithines, consisting of a coracoid and a fragmentary femur, were first reported from Massecaps by Buffetaut (1998).

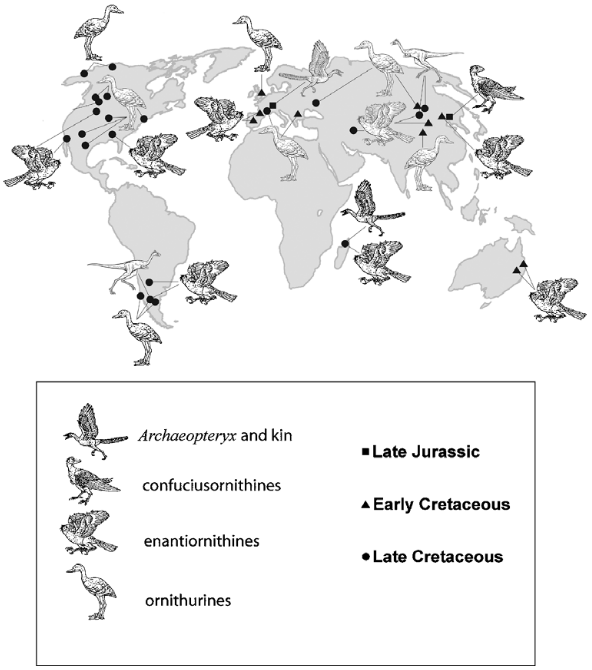

Figure 3. Map to show the known geographic distribution and relative ages of Enantiornithes alongside the other main lineages of Mesozoic birds (re-drawn from Chiappe & Dyke, 2002).

This region of France, a hilly area located between the coastal plain that borders the Mediterranean and the Palaeozoic massif of the Montagne Noire (Fig. 2), is the expression of a complex geological structure that was folded and faulted during the Cenozoic. In this area the Late Cretaceous is well represented by fluvial red beds that comprise conglomerates, sandstones and clays, and are overlain by freshwater limestones; these deposits are often referred to as the 'Grès à reptiles' (Buffetaut, 2005). Although precise dating of these sediments has proved difficult (Buffetaut, 2005), the vertebrate assemblage, especially from the Cruzy area, is consistent with a late Campanian–early Maastrichtian age. This has been corroborated by the presence of certain types of dinosaur eggs which suggest an early Maastrichtian age (Garcia & Valentin, 2001–2002).

4.b. Argentina

All the Argentine specimens were collected as mainly isolated elements from a small quarry (J. Bonaparte, pers. comm.) about 8 m wide, roughly in the mid-section of the Lecho Formation in Salta Province

(Walker, 1981). As reported in Chiappe (1991, 1993), the Lecho Formation is part of the Late Cretaceous Salta Group of sediments, part of the much larger Andean sedimentary basin (Bonaparte *et al.* 1977). All the bird bones examined by Walker in the BMNH were collected by J. Bonaparte and J. Leal from fine-grained sandstones within the Lecho Formation (Fig. 2); for more details relevant to the geological context of these specimens, see Chiappe (1991). Because of the non-associated nature of the bird bones from El Brete, direct anatomical comparisons other than on the basis of size cannot be corroborated. As noted by Walker (1981) and Chiappe (1993), this 'lack of association' means that fore- and hindlimb bones cannot definitively be associated with one another.

5. Systematic palaeontology

AVES Linnaeus, 1758
ORNITHOTHORACES Chiappe, 1996
ENANTIORNITHES Walker, 1981
EUENANTIORNITHES Chiappe, 2002
Genus *Martinavis* nov.

Type species. Martinavis cruzyensis, described below.

Etymology. The generic name is in honour of Larry D. Martin, in recognition of his contributions to the study of Mesozoic birds and for his support of Cyril Walker in the 1980s. Many of the original illustrations of the El Brete collection were rendered by KU-NM artists in the 1980s (Chiappe & Walker, 2002).

Diagnosis. An euenantiornithine bird that possesses the following unambiguous synapomorphies of the humerus (based on the phylogenetic analysis detailed in Chiappe, 2002, and Chiappe & Walker, 2002): dorsal margin concave in its central portion, rising both ventrally and dorsally on either side; bicipital crest prominent (well developed and broad); and ventral surface of bicipital crest bearing a small fossa for muscle attachment. In addition, this taxon 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); a well-marked depression underneath the proximal head of the humerus; weakly developed distal condyles; and a flat distal end that is not deflected dorsally (Chiappe & Walker, 2002). Additional characteristics of *Martinavis* include: wide pneumotricipital fossa; unperforated ventral tuberculum; flat and broad deltopectoral crest that joins the shaft smoothly and lacks any degree of ventral curvature; small and boss-like bicipital crest that is projected cranially; ventral martin of bicipital crest small with distally located fossa; ventral tuberculum does not bear proximodistal canal; distal end with poorly developed ventral condyle; ectepicondyle and entepicondyle lack marked tricipital grooves; ventral condyle enlarged and extended distally to below level of the dorsal and ventral condyles; external condyle transversely orientated.

Differential diagnosis. Martinavis comprises a taxon of euenatiornithine bird easily differentiated from the contemporaneous *Enantiornis* (from the same El Brete locality) on the basis of its more gracile humerus and in the morphology of its deltopectoral crest (Fig. 4). Distinct differences in comparison with other euenantiornithines include the fact that the surface between the shaft and the deltopectoral crest is smoothly angled (Fig. 4). This bird also has a bicipital crest that is not inclined caudally, a small entepicondyle, a laterally positioned ectepicondyle, and a transversely orientated external (dorsal) condyle. As we have noted above and has been discussed elsewhere (Walker, 1981; Chiappe, 1993), direct comparisons between bones referred here to *Martinavis* and the other El Brete euenantiornithines (apart from *Enantiornis*): *Lectavis*, *Yungavolucris* and *Soroavisaurus* (Chiappe, 1993), all based on tarsometatarsi, are impossible because these elements were not collected in association. Note that *Martinavis* is similar in its preserved morphology with *Gurilynia*, described from the Late Cretaceous of the Gobi Desert, Mongolia (Kurochkin, 1999); discussion of this will follow in a later paper.

Martinavis cruzyensis sp. nov.

Holotype. ACAP-M 1957, a complete uncrushed right humerus (Fig. 4a–d) preserved in three dimensions. In caudal view, the deltopectoral crest of this specimen is cracked at about its midpoint. This specimen is one of the largest euenantiornithine forelimb bones to be collected from the European Cretaceous and remarkably is almost identical to Argentine specimens from El Brete, collected some 20 years earlier (Fig. 4).

Etymology. For the village of Cruzy, Hérault, southern France, where this specimen was collected (Massecaps locality) (Fig. 2).

Type locality. Late Campanian–early Maastrichtian sediments (Massecaps locality), close to the village of Cruzy, Hérault, southern France (Fig. 2).

Diagnosis. Euenantiornithine bird exhibiting the following characters: bicipital crest of humerus strongly projected cranially; capital groove deeply depressed and wide; attachment site for m. pectoralis depressed and broad; absence of well-defined proximodistal groove on ventral tuberculum; internal (ventral) and external (dorsal) condyles greatly enlarged and expanded; ventral epicondyle enlarged and extended distally.

Martinavis vincei sp. nov.

Holotype. PVL 4054, complete left humerus (Fig. 4e).

Paratype. PVL 4059, distal end of left humerus (Fig. 4f).

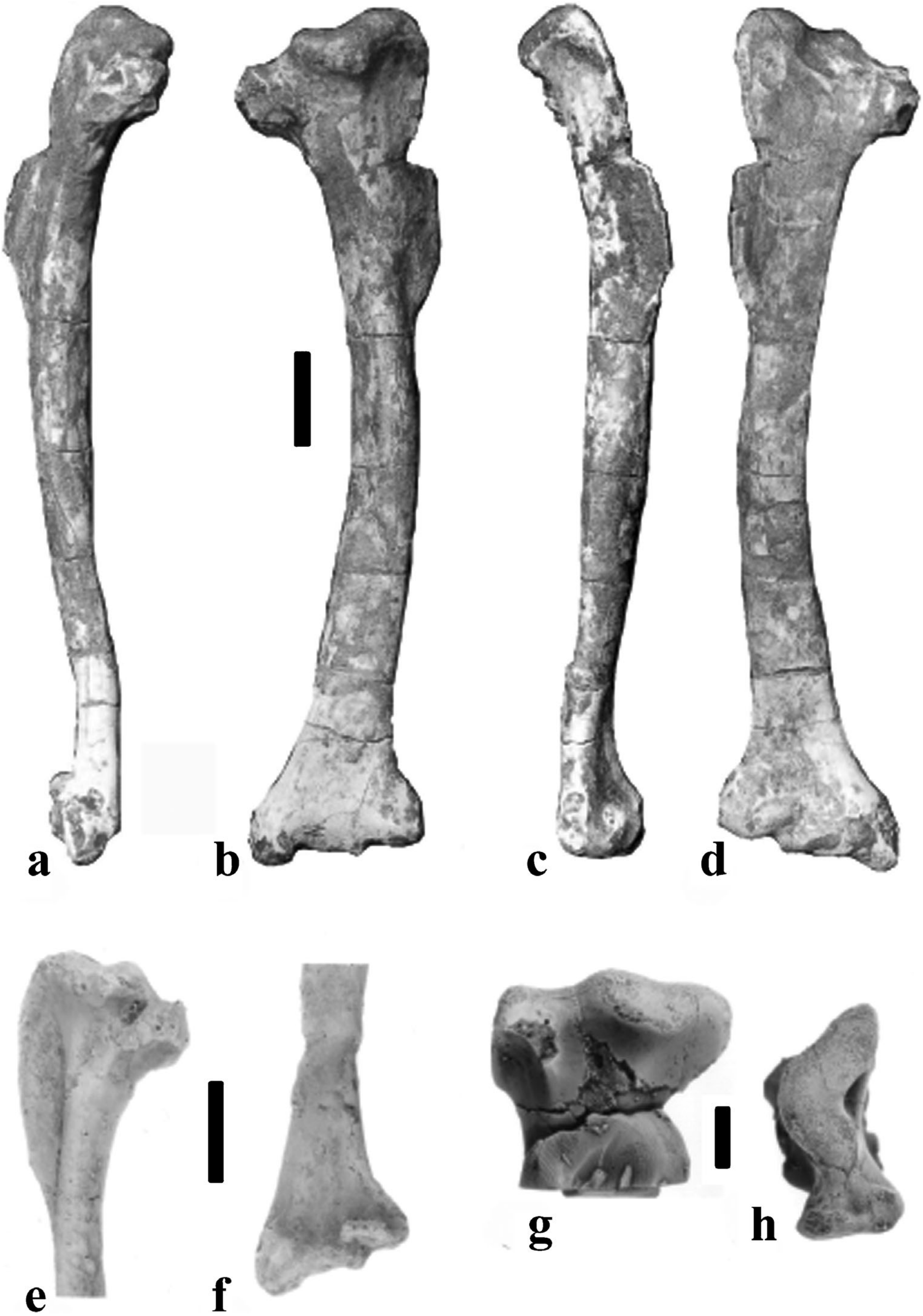

Figure 4. Humeri referred to *Martinavis* (see text for details): ACAP-M 1957, complete right humerus (holotype of *M. cruzyensis*) in left lateral (a), caudal (b), right lateral (c) and cranial (d) views; PVL 4054, portions of complete left humerus in caudal (e) and cranial (f) views; KU-NM-37, proximal end of left humerus in caudal (g) and proximal (h) views. For measurements see Table 1; scale bars are 10 mm.

Table 1. Measurements of humeri (in mm) referred to the euenantiornithine *Martinavis*

	PVL 4054 *M. vincei*	PVL 4059 *M. vincei*	PVL 4025 *Martinavis* sp.	PVL 4046 *Martinavis* sp.	PVL 4028 *Martinavis* sp.	KU-NM-37 *Martinavis* sp.	ACAP-M 1957 *M. cruzyensis*
Max. length	110		95.2				92
Width: bicipital crest to deltoid crest	22.2		20.9	14.8			21
Length: deltoid crest	25.4		25.4	7.1	6.3		28
Length: medial bicipital crest	10		9.7	6.7		16.6	11.2
Width: pneumotricipital fossa	9.7		8	4		17.7	7.3
Max. width distal end	20	20	20.8				21.2
Max. width olecranon fossa	7.9	7.9					7.6

See text for details and museum acronyms.

Etymology. For M. Vince who helped to collect the original El Brete material and was responsible for much of its preparation (J. Bonaparte, pers. comm. 1976).

Type locality. El Brete, Maastrichtian Lecho Formation, Salta Province Argentina (Bonaparte *et al.* 1977; Bonaparte & Powell, 1980; Chiappe, 1993) (Fig. 2).

Diagnosis. Euenantiornithine bird, comparable in size to *M. cruzyensis* (Table 1) but with a humerus that has a bicipital crest angled more cranially, a capital groove with a deeper depression, and more distally enlarged internal and external condyles (Fig. 4e, f).

Martinavis sp.

Referred specimens. PVL 4025, almost complete left humerus lacking the 'median ridge' that is crushed distally; PVL 4046, left humerus lacking its distal end; PVL 4028, left humerus lackings its distal end; KU-NM-37, proximal end of left humerus.

Localities. Argentina: PVL 4025 and 4046 were collected from the same locality as *M. vincei* (J. Bonaparte pers. comm.). USA: KU-NM-37 was collected from Campanian sediments at Lance's Quarry, in New Mexico, USA (L. D. Martin, pers. comm. 1980).

Remarks. Although PVL 4025 and PVL 4028 are smaller than the humeri referred above to either *M. vincei* or *M. cruzyensis* (Fig. 4; Table 1), we do not consider it prudent at present to allocate these specimens to distinct species. In addition to size, a number of subtle osteological differences are nevertheless evident in comparison, not only between these specimens, but also with ACAP-M 1957, and the types of *M. vincei* (PVL 4054 and PVL 4059) (Fig. 4). The bicipital crest of PVL 4025 is less cranially inclined than in the other elements referred to *Martinavis*, the distal extremity of the deltoid crest meets the shaft more abruptly, no depression is present in the capital groove, and the floor of the pneumatic fossa is depressed and broader. PVL 4028 is similar in size to PVL 4046 (Table 1), but differs in having a shorter deltopectoral crest and a deeper pneumatic fossa. The bicipital crest in this specimen is also more inclined cranially than in its counterpart PVL 4046 and the external tuberosity is more enlarged and bulbous (Fig. 4). In comparison, the most distinctive of these referred specimens is KU-NM-37, from the Campanian of New Mexico (Fig. 4). This incomplete element is indistinguishable from other bones referred here to *Martinavis*; it is from a large bird, slightly larger than the proximal part of humerus of the first named euenantiornithine from El Brete, *Enantiornis leali* (Walker, 1981; Table 1).

6. Description

Of the large sample of elements collected from El Brete, the humerus is the most diagnostic at present and thus is used to diagnose *Martinavis*. As noted above, we are unable to match the El Brete forelimb bones with any of the hindlimb elements already described (and named) by Chiappe (1993) and figured by Chiappe (1996) and Chiappe & Walker (2002). While it is certainly possible that *Martinavis* may prove to be a junior synonym of either *Soroavisaurus*, *Lectavis* or *Yungavolucris* (Chiappe, 1993), the discovery of additional articulated fossil birds will be required before this can be tested.

The general features of the *Martinavis* humerus exemplify the morphology of this bone in Enantiornithes in general and Euenantiornithes in particular; all of these birds are characterized by the presence of an 'L-shaped' (Walker, 1981) proximal articulation, a well-marked depression below the caput on the cranial surface (sulcus for the transverse ligament) and poorly developed distal condyles (Fig. 4). In all *Martinavis* specimens, as in all euenantiornithines, the head of the humerus is concave cranially and convex dorsally; the dorsal margin of this bone is particularly concave below the deltopectoral crest. The shaft of the humerus lacks marked curvature, although it is somewhat thicker and more robust in the specimen from Cruzy (ACAP-M 1957), compared to the bones from El Brete.

The pneumatic fossa of the proximal part of the humerus (crus dorsale fossae) in *Martinavis* is much wider than in its contemporary *Enantiornis* (Chiappe, 1996; Chiappe & Walker, 2002) and the ventral tuberculum is not perforate (Figs 4, 5). Both taxa lack a pneumatic foramen on the proximal part of the humerus.

The deltopectoral crest of the humerus in *Martinavis* is flat, broad and lacks any marked degree of cranial curvature, while the bicipital crest is smaller, boss-like and projected cranially. On the ventral margin of this crest there is a small distally located fossa, likely a site

Figure 5. Some of the skeletal elements (parts of PVL 4035 and 4020) previously referred to the El Brete euenantiornithine *Enantiornis leali* (Walker, 1981; Chiappe & Walker, 2002): proximal end of left humerus (PVL 4035) in cranial (a) and caudal (b) views; reconstructed complete left humerus of *Enantiornis leali* (PVL 4035 and 4020) in cranial (c), caudal (d), and right lateral (e) views. Scale bars are 10 mm.

for muscle attachment (region of m. pectoralis). The ventral tuberculum is well developed, projected caudally, and does not bear a well-defined proximodistal canal. The deltopectoral crest in *Martinavis* joins the shaft smoothly, as opposed to at an angle as is the case in *Enantiornis* (Walker, 1981; Chiappe, 1996; Chiappe & Walker, 2002). The bicipital crest is more cranially deflected in *Martinavis* than in *Enantiornis* (Fig. 5).

Distally the humerus of *Martinavis* is flared cranially and has a poorly developed ventral (internal) condyle. The ectepicondyle and entepicondyle are distinctly rounded and lack marked tricipital grooves; between the two distal condyles there is a deep, excavated olecranon fossa on the caudal surface (Fig. 4). The ventral epicondyle is enlarged, extending distally to below the level of the dorsal and ventral condyles. The internal condyle is not expanded and bulbous, as in modern birds (Neornithes: Clarke & Norell, 2002).

A number of fossil eggshell fragments from the same horizon and locality as *Martinavis cruzyensis* are currently under study by Gerald Grellet-Tinner (South Dakota School of Mines, Rapid City, South Dakota); preliminary analysis of these fragments supports their enantiornithine affinities, as well as the presence of additional birds and non-avian dinosaurs at Massecaps (Grellet-Tinner *et al.* unpub. data).

7. Discussion

7.a. El Brete euenatiornithines

Walker (1981) was the first to address the El Brete collection of euenantiornithine bones, presenting a series of osteological characters to define the taxon *Enantiornis leali* (Walker, 1981, table 2). Walker (1981) also intended to present the osteological evidence for the existence of a new clade of Cretaceous birds ('Enantiornithes'), a conclusion that met with extensive criticism in the 1980s (Steadman, 1983).

The holotype of the first of the El Brete euenantiornithines to be described, *Enantiornis leali*, is PVL 4035 (Walker, 1981; Chiappe, 1996; Chiappe & Walker, 2002). This is one of the very few El Brete specimens that consists of associated elements: portions of a left humerus (Fig. 5), coracoid and scapula. The coracoid of *Enantiornis leali* (PVL 4035) was figured in cranial view by Walker (1981) alongside the humerus (PVL 4054) which is now the holotype of *Martinavis vincei*. A scapula (PVL 4039) is very similar to PVL 4035, while a carpometacarpus (PVL 4049), right femur (PVL 4037), distal tibiotarsus (PVL 4033), and ilium and ischium (PVL 4042) are consistent in their size to the holotype of *E. leali*. Alongside these bones, a proximal tarsometatarsus (PVL 4021, now the holotype of *Lectavis bretincola*: Chiappe, 1993), a complete right tarsometatarsus (PVL 4053, now the holotype of *Yungavolucris brevipedalis*: Chiappe, 1993), and a complete tarsometatarsus (PVL 4048) (Walker, 1981) have also been described and await revision. We note that PVL 4049, PVL 4037 and PVL 4033 are consistent in size with the humeri of *Martinavis*.

In the early 1990s, Walker sent all materials pertaining to his work on the El Brete collections to L. M. Chiappe, then working at the American Museum of Natural History in New York. Chiappe (1991) described and figured a number of the El Brete specimens for the first time: PVL 4048 and PVL 4021 (Walker, 1981), alongside PVL 4052 (a complete left tarsometatarsus) and PVL 4043 (the proximal end of right humerus). Chiappe (1992, 1993) focused on the hindlimb morphology of these birds (*contra* Walker, 1981). In the context of the known morphology of the group, Chiappe (1992) presented a discussion of the tarsometatarsal morphology of the enantiornithine *Avisaurus*, describing the anatomy of this element based on specimens PVL 4048, PVL 4053 and PVL 4021. Chiappe (1992) also provided a sketch of PVL 4690, for the first time (Chiappe, 1992).

Chiappe (1993) published a review of known tarsometatarsal types based again on the El Brete collections, recognizing three taxa: *Yungavolucris brevipedalis, Lectavis bretincola* and *Soroavisaurus australis*. The squat tarsometatarsi from El Brete were used by Chiappe (1993) to diagnose *Yungavolucris brevipedalis* (PVL 4053 (holotype), PVL 4040, PVL 4052, PVL 4268 and PVL 4692 (referred specimens)). Of these elements PVL 4692 is extremely fragmentary, comprising just the distal trochlea of metatarsals II and III; the holotype (PVL 4053) and PVL 4692 were figured by Chiappe (1993). *Lectavis bretincola* was erected by Chiappe (1993) on the basis of a single specimen (PVL 4021), an elongate and slender associated left tarsometatarsus and tibiotarsus. PVL 4021 was illustrated by Chiappe (1993). Finally, Chiappe (1993) named *Soroavisaurus australis* on the basis of two isolated tarsometatarsi, PVL 4690 (holotype) and PVL 4048 (referred specimen including associated phalanges and claws). Both of these specimens were illustrated by Chiappe (1993); they were originally referred to the enantiornithine *Avisaurus* by Brett-Surman & Paul (1985) (see also Chiappe, 1992; Chiappe & Calvo, 1994).

All the bones of the holotype specimen of *Enantiornis leali* were figured by Chiappe (1996), and following Walker (1981), some additional specimens were referred to this taxon: PVL 4020 (an associated but crushed forelimb skeleton including a left scapula, coracoid, both ends of a humerus and an imperfect ulna as well as a right ulna and radius and proximal portion of a carpometacarpus and digits), PVL 4039, PVL 4055 (isolated scapulae), PVL 4023, and PVL 4181 (isolated ulnae).

To date, the most complete published compendium of euenantiornithine anatomy is that of Chiappe & Walker (2002), who reviewed the composition of the entire clade drawing heavily on the El Brete specimens, many of which were illustrated in this paper for the first time (PVL 4698, an isolated right mandibular ramus; PVL 4041 and 4051, series of thoracic vertebrae; PVL 4041 and PVL 4042, complete pelvises). Chiappe & Walker (2002) also figured PVL 4025 (referred here to *Martinavis*) and provided a sketch of PVL 4060 (a proximal end of a femur). Some of this newly figured material had been previously referred to *Enantiornis leali* (PVL 4055, an isolated scapula; PVL 4023, a complete ulna), but was not available to us for this study. In addition, Chiappe & Walker (2002) referred PVL 4049 (a complete carpometacarpus, also figured) to *E. leali* and referred PVL 4033 and PVL 4030 (two tibiotarsi; PVL 4030 figured for the first time) to *Soroavisaurus australis*.

As a result of this earlier work, we know that at least four taxa of euenantiornithines were present at El Brete: *Enantiornis* (Walker, 1981; Chiappe & Walker, 2002), *Martinavis* (this paper), and at least two of the three taxa described by Chiappe (1993). This conservatively assumes that one of Chiappe's (1993) taxa could turn out to be the same bird as either *Martinavis* or *Enantiornis*. On the other hand, as many as six euenantiornithines may be represented in the El Brete collections: all of the genera mentioned above as distinct taxa, as well as an additional morphotype identified by Walker (1981). Further discussion of this material, as well as additional post-cranial elements subjectively referrable to *Martinavis*, will form the subject of a later paper (Walker & Dyke, unpub. data).

7.b. Massecaps euenantiornithines

Buffetaut (1998) briefly reported two euenantiornithine bones from the Late Cretaceous Massecaps locality, near Cruzy in southern France (see also Buffetaut, 2005). These bones, a right coracoid and left femur, are large and were at the time the first records of Enantiornithes from the European Upper Cretaceous. Subsequently, additional specimens have been described from similarly aged (late Campanian to early Maastrichtian) strata in Provence, southern France (Buffetaut, Mechin & Mechin-Salessy, 2000) and from Santonian deposits in the Bakony Mountains, Hungary (Ösi, 2007). Buffetaut (1998) noted particular similarities between the Massecaps specimens and *Enantiornis* from El Brete: the coracoid (ACAP-M 192) is almost the same size as PVL 4035 and has a reduced acrocoracoid and robust head. Both specimens also have a pneumatic foramen located cranially with respect to the sternocoracoid impression (the 'dorsal fossa' of Buffetaut, 1998); in ACAP-M 192 and *Enantiornis* (PVL 4035) this foramen does not open into the fossa. The left femur (ACAP-M 193) from Massecaps is also very similar in size to other bones from El Brete (Buffetaut, 1998; Chiappe, 1996); the French element also has a well-developed trochanteric crest and is deeply excavated on its lateral face, as described in some of the El Brete specimens (Chiappe & Calvo, 1994; Chiappe & Walker, 2002). The clear degree of anatomical similarity between the Massecaps and El Brete euenantiornithines is further confirmed by the humeri described in this paper (Fig. 4). It cannot be excluded that the coracoid, femur and humerus from Massecaps all belong to the same individual, although this cannot be demonstrated other than on the basis of their relative proportions, as they were not found in articulation.

7.c. Distribution of euenantiornithines

Martinavis is one of very few reported Cretaceous vertebrate taxa known to have had a distribution spanning Europe, North and South America; in other words, we have demonstrated that very similar euenantiornithine taxa were present on both Laurasia and Gondwana in late Campanian–early Maastrichtian times. Most other enantiornithines, indeed Mesozoic birds in general (Kurochkin, 2001; Chiappe & Dyke, 2002; Fountaine *et al.* 2005), are known from a single locality; just the Late Cretaceous enantiornithines *Nanantius* (Queensland, Australia and the Gobi Desert, Mongolia: Molnar, 1986; Kurochkin, 1996), *Avisaurus* (El Brete, Argentina and the Two Medicine Formation, Montana: Brett-Surman & Paul, 1985; Varricchio & Chiappe, 1995) and *Martinavis* (Maasecaps, France and El Brete, Argentina) have so far been described with a distribution spanning both hemispheres. Subsequent work, however, has suggested that the Gobi Desert species of *Nanantius* (*N. valifanovi*: Kurochkin, 1996) is instead referrable to *Gobipteryx* (Chiappe, Norell & Clark, 2001), previously described from the Gobi Desert by Elzanowski (1974, 1977) (see also Kurochkin, 2004).

The status of *Avisaurus*, known only from isolated postcranial elements, is also uncertain because the El Brete tarsometatarsi referred to this taxon (PVL 4048, PVL 4053, PVL 4021, PVL 4690) are unassociated. The difference in geological age between the Albian

Nanantius eos from Australia and the Campanian *Nanantius valifanovi* from Mongolia is also worth noting and may not be suggestive of a congeneric status. The tarsometatarsus of *Avisaurus* is largely indistinguishable from similarly sized enantiornithines: indeed, one of the specimens from El Brete referred to *Avisaurus* (PVL 4048) was illustrated as an example of variation within the El Brete collection by Walker (1981) (and subsequently referred to *Soroavisaurus australis* by Chiappe, 1993). At the time, Walker (1981) had not intended to give a new name to this specimen; this was done by Brett-Surman & Paul (1985) and Chiappe (1993), despite the specimen's lack of association. We raise the possibility that *Avisaurus*, indeed *Soroavisaurus,* could be junior synonyms of *Enantiornis*.

Biogeographically, the occurrence of the same bird taxon in the Late Cretaceous of Europe, South and North America may appear surprising. However, the presence of faunal elements with 'Gondwanan' affinities in the Late Cretaceous vertebrate faunas of southwestern Europe has already been reported (Buffetaut, 1989), the most convincing cases probably being those of abelisaurid theropods (Buffetaut, Mechin & Mechin-Salessy, 1988) and mawsoniid coelacanths (Cavin *et al.* 2005), both of which occur at Massecaps together with *Martinavis*. Moreover, the dispersal abilities of a volant euenantiornithine such as *Martinavis* were probably good, which may further explain the wide geographical distribution of this genus. Dispersal, even migratory behaviour, might be envisaged for *Martinavis*, but such a hypothesis can hardly be tested on the basis of fossil evidence.

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