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Estimating the Ontogenetic Status of an Enantiornithine Bird from the Lower Barremian of El Montsec, Central Pyrenees, Spain

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ABSTRACT

An Enantiornithes specimen from El Montsec was initially described as an immature individual based upon qualitative traits such as its relatively large orbit and overall proportions of the skull and the postcranium. In this study we re-evaluate the precise determination of the ontogenetic stage of this individual, establishing a cross-talk among taphonomic, anatomic, and morphometric data. The exceptional preservation of the specimen has allowed pondering ontogenetic influence *versus* preservational bias in features like the external patterns of bone surfaces, instead of being aprioristically considered due to taphonomic alterations only. The rough texture of the periosteal bone associated with pores in the distal, proximal and mid-shaft areas of the humeral shaft, indicates a subadult stage when compared with long bones of modern birds. Forelimb proportions of embryo and juvenile Enanthiornithes are equivalent to those of adult individuals of other taxa within this clade, though this is not a reliable criterion for establishing a precise ontogenetic stage. The El Montsec specimen may be attributed a close adulthood, yet only if growth regimes in Enantiornithes are considered equivalent to those in Neornithes birds.

Key words: Enantiornithes, Growth, Early Cretaceous, Maturity, Morphometrics, Ontogeny, Taphonomy, Anatomy.

RESUMEN

Un ejemplar de Enantiornithes del Montsec fue inicialmente descrito como un individuo inmaduro sobre la base de caracteres cualitativos tales como su órbita relativamente grande y sus proporciones generales en cuerpo y cráneo. En este estudio se realiza una reevaluación del estado ontogenético preciso de este individuo, estableciendo una argumentación cruzada con datos tafonómicos, anatómicos y morfométricos. La preservación excepcional de este ejemplar ha permitido ponderar la influencia ontogenética *versus* el sesgo tafonómico en caracteres como los patrones externos de las superficies óseas, en lugar de considerarlos apriorísticamente como debidos únicamente a alteraciones tafonómicas. La textura rugosa del periostio, asociada a la presencia de poros en las áreas distal, proximal, y del centro de la epífisis humeral, sugiere un estado subadulto si se compara con los huesos largos de las aves modernas. Las proporciones del miembro anterior de embriones y adultos de enanthiornithes son equivalentes a las de adultos de otros taxa dentro de este clado, aunque ello no constituye un criterio fiable para establecer un estado ontogenético preciso. Se puede atribuir una edad relativa al ejemplar del Montsec cercana a la de un adulto, aunque únicamente si los regímenes de crecimiento de las enantiornites son considerados equivalentes a los de las aves neornites.

Palabras clave: Enantiornithes, crecimiento, Cretácico inferior, madurez, morfometría, outogenia, tafonomia, anatomía.

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Introduction

The determination of the precise ontogenetic stage in fossil vertebrates is far from straightforward. Absolute size is, among others, a species specific variable. Therefore, only complete series of distinct ontogenetic stages can directly relate size and age. Such series are extremely rare in the tetrapod fossil record. Palaeohistology, in turn, is a suitable way for providing direct evidence on the biological age of an individual; for instance, by using skeletochronological estimations with the "Lines of Arrested Growth" method (Castanet and Smirina, 1990). The efficacy of the technique, however, depends on the growth pattern and how bone modelling takes place in organisms (see Chinsamy *et al.,* 1994, 1995 and Cambra-Moo *et al.,* 2006 for avian enantiornithines, and Ricqlès, *et al.,* 2003 for *Confuciusornis sanctus*, and Ponton *et al.,* 2004 for actual birds). Unfortunately, it is a destructive technique.

Herein we develop the method for determining ontogenetic stages by networking hypotheses formulated from the three different approaches of Taphonomy, Anatomy, and Morphometrics initiated by Marugán-Lobón *et al.* (2002). The objective is the re-evalutation of the ontogenetic state of a small enantiornithine bird from the Lower Barremian of El Montsec that was initially considered as a very early juvenile (*nestling*; Sanz *et al.,* 1997). We base the procedure in what we have informally named "biological preservation": a preservational factor that depends on palaeobiological sources rather than on taphonomical processes alone. In this paper we seek for preservational features that might be due to the age of the individual, and that might have been previously misinterpreted as solely dependant on taphonomic alterations.

These features include the texture of bone surface, the absence of expected bone elements, limited bone deformations, and differences in tegument and soft tissues preservation along the body. Our aim herein is to evaluate the palaeobiological, namely ontogenetic, significance of bone surface texture (i.e., presence of striations and pitting), ossification (differential pattern of cartilage-bone ratio, and suture closure). For that purpose, we firstly characterize the taphonomical preservation of the fossil, evaluating its biostratinomic alterations. Secondly, we provide a morphological description of its bone surface texture and a comparison with Recent birds. Thirdly, we fine-tune the hypothesis by exploring the morphometrics of forelimb proportions in adults *versus* embryonic Neornithes, Enantiornithes, non-avian theropod dinosaurs, *Confuciusornis*, and *Archaeopteryx*, in order to assess a more precise ontogenetic stage to the El Montsec enantiornithe.

Taphonomical characterisation

The El Montsec fossil Lagerstattën

The laminated limestone deposits from El Montsec have formed Konservat-Lagerstättën with exceptionally preserved fossils. The fossil assemblages represent different terrestrial and aquatic (lacustrine and lagoonal) habitats. El Montsec has yield remains of plants (the macroflora includes Pteridophyta, Prespermathophyta, Spermathophyta, and angiosperms), invertebrates (Mollusca, Crustacea, Arachnida, and Insecta), and vertebrates (chondrichthyan and osteichthyan fishes, amphibians, and reptiles including Chelonia, Lepidosauromorpha and Archosauria, plus Aves) (Martínez-Delclós, 1991). Fossils from El Montsec are usually articulated and in anatomical connection. Plants for instance show stems with leaves and cones in connection, and even the distalmost parts of the fin rays in fishes are completely articulated. Most exceptional preservation in El Montsec consists of: soft bodies' organisms (e.g., larval and pupae states of insects), and soft tissues (e.g., in the abdominal cavity of fish —*Rubiesichthys*— or skin of anurans). Delicate structures has also been preserved such as capillary extremities of ranunculaceans, antennae of crustaceans, spinnerets in the spiders, ovipositors and compound eyes on insects, and copulative structures in male frogs (Martínez-Delclós *et al.,* 2004). Finally, patterns of coloration in wings, abdomen of insects, and pigmentation in the barbules of bird's feathers can also be preserved.

Taphonomy of specimen LP-4450-IEI

This enantiornithine bird was initially considered as Enantiornithes *indet.* by Sanz *et al.* (1997). The specimen is labelled LP-4450-IEI (Institut d'Estudis Illerdencs, Lleida; collection from La Pedrera fossil site); it is preserved in two slabs, as part and counterpart. Bone elements are articulated, but unfortunately the fossil was found *ex situ* and the slab is broken away, lacking the posterior part of the skeleton. The skull is laterally twisted, and slightly detached from the first vertebra. Nine cervical vertebrae (including the axis) are exposed, so that their ventral or dorsal views are recognized in each slab. The thoracic region of the vertebral column is composed by at least six elements: four dorsal vertebrae plus isolated ribs. Cervical and thoracic vertebrae have similar conditions of preservation. This indicates that there is no a differential pattern of cartilage-bone ratio between these regions. Most of the pectoral girdle and the forearms rest articulated beneath the body, whereas the scapula rests above the vertebral column. The left wing skeleton is flexed, and the hand, with its finger I, is medially oriented (fig. 1). The right forelimb is laterally directed and flexed. The furcula and both coracoids are preserved in nearly anatomical position, slightly detached.

The preserved tegument is observable as a light brown colored outline, covering the body, but not the skull. At the neck area a dense surface of cuticle is preserved. This area is externally bordered by a dark line that might include impressions from the trachea as well. Small feather-looking structures are placed along the neck, close to the cervical vertebrae. These feathers are filamentous structures up to 0.5 cm long. Such filamentous structures, similar to those described as "protofeathers"-like (Zhang & Zhou, 2000), overlap the vertebrae centra in dorsal view (fig. 1). Protofeathers on the right side are orthogonally extended, while, at the left side of the body, the tegumentary structures are obliquely oriented. Similar protofeathers are placed not only around the neck but probably throughout the carpus-metacarpus as well. In turn, a few true vane feathers rest close to the zeugopodial area. Filamentous protofeathers are three dimensionally preserved, especially those overlapping bone elements. Contrary to protofeathers, wing vaned feathers are preserved as impressions.

No severe biostratinomic alterations are observable in the specimen. The individual was buried at the most stable position after death, that is, prone. Some body volume is preserved, so that overlapping bones are not crushed and overlapped bones are not broken. This could be explained because carbonate from surrounding substrate matrix can quickly be incorporated into bones, thus infilling natural pores (Merino, 2000). This helps preventing from possible crush or collapse effect in bones (even in not fully ossified skull bones). Deformations in the skeleton of the specimen are observed in incompletely ossified regions of bones, such as furcula branches, sternal plates, and the distal part of the humerus.

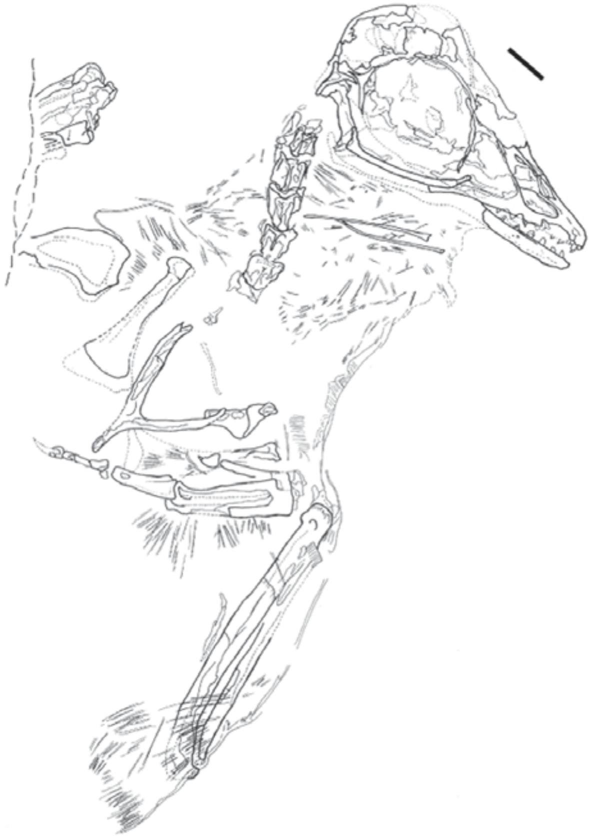

Fig. 1.—Light camera drawing from counterslab of specimen LP-4450-IEI (Lower Barremian, Central Pyrenees, Lleida province, Spain). Scheme includes soft tissues preserved (e.g., feathers, skin contour). Scale-bar 0.5 cm.

The high quality of the structures preserved in this specimen indicates that there was short or no transport at all, and rapid burial of the individual. The specimen does not show any skeletal torsion; backward neck curvature is also absent. In Recent birds, this indicates that the very earliest biostratinomic process have occurred out of water influence (Cambra-Moo, 2006). The posture of the specimen and the preservation of tegument indicate a subaerial decay process, although it is not discarded that the specimen was also embedded in a microbial mat. The only process that must have taken place previous to the embedding of the carcass by the microbial mats is skeletonization (loss of flesh), which should have been nearly or completely finished. The hypothesis of microbial mats occurrence does strengthen the explanation of how some soft body elements have been preserved (Gupta *et al.,* 2007). Furthermore, the El Montsec specimen shows a differential pattern of tegumentary preservation (i.e., feather imprints and three dimensional filaments). In fact, only by considering the presence of microbial mats can such a pattern of differential taphonomic preservation be explained (Davis and Briggs, 1999). Microbial mat encrustation must have minimized general biostratinomic alteration and permitted differential preservation to occur.

Taphonomical differential preservation in the tegument, as we have seen, is strikingly related with the presence of both true vane feathers and filamentous protofeathers, denoting the occurrence of two types of epithelial cover in this enantiornithine bird. The El Montsec specimen shares the derived condition of presence feathers and protofeathers with *Protopteryx* and *Longipteryx*.

Bone surface texture

In the preliminary description of the El Montsec specimen Sanz *et al.* (1997) evidenced the presence of clusters of tiny foramina in the periosteal bone surface of mandible, vertebrae and long bone shafts. This particular bone surface texture was related with the incomplete ossification of periosteal bone due to early ontogenetic stage. Evaluation of the bone porosity has been carried out in different groups of fossil vertebrates, and recently examined in recent avian and crocodylian skeletons; the relationships between bone surface texture and skeletal maturity has been denominated “textural-ageing”, and it is a way to differentiate general ontogenetic classes such as juvenile, subadult and adult in birds (see Tumarkin-Deratzian *et al.,* 2006 for an extended overview of this issue).

Detailed observation of the El Montsec enantiornithe bone textural pattern results on its location on the skull, axial skeleton, pectoral girdle, and forearm. Differential bone texture on the skull is located at the inner surface of the articular bone in the mandible (fig. 2A), at the dorsal side of frontal-parietal contact, and at the occipital region above the foramen magnum. Figure 2B represents microestructural bone surface details on the inner posterior mandibular region. Bone surface pattern shown in the figure depicts foramina surrounded by a trabecular structure of fibrolamellar bone. On the axial skeleton, pitting is observed at the articular area of the scapula and the anterior part of the ventral surface of the cervical centra. On the axial column, the pitting increases towards the posterior successive centra (fig. 2C). Finally, on the pectoral girdle and forearm it is found at the ventral face of the coracoid and on the humeral shaft.

In order to temptatively assess a relative age to the fossil enantiornithe, the bone texture of its humerus is compared with the corresponding region in modern avian species. The textural characteristics of the humeral shaft match one of the types observed in the Recent anatid *Branta canadensis* (Tumarkin-Deratzian *et al.,* 2006). This pattern of distribution and shape of foramina in Recent birds, found at the proximal and distal regions and along the midshaft of the humerus is very similar to the one found on specimen LP-4450-IEI. On figure 3, the distal humeral region shows a rough texture with pores that penetrate the shaft obliquely with short longitudinal trails. At the midshaft, pores are mostly perpendicular to the shaft and smaller in diameter. This pattern suggests that the enantiornithine humeral shaft is of Type III in Tumarkin-Deratzian *et al.* (2006), considering that in their Type II the entire shaft is textured, while in the specimen there is a smooth area between the midshaft and the distal and proximal regions.

Morphometrics

The morphometrics of the forelimb (humerus, radius, and carpometacarpus lengths to their total sum, in order to yield their corresponding proportions) were treated with a Principal Components Analysis. There are two distinct subsamples within the pool (N = 694 individuals), one of adults and one of embryos, plus two putative juveniles enantiornithines (one, the El Montsec specimen, the other *Liaoxiornis* from Hou and Chen, 1999). The subsample of embryos (n = 8) contains seven neornithes and one enantiornithe (Zou and Zhang, 2004). The adult subsample contains 24 non-avian theropod dinosaurs, six *Archaeopteryx* specimens, two *Confuciusornis* specimens, 14 enantiornithe and 640 neornithe birds (see caption of fig. 4 for sources).

The PCA ordination yields one first eigenvector explaining a 60.15% of forelimb variance negatively correlated with the humerus (–0.99), and very close, though with different sign, the radius (0.81; table 1). The second eigenvector (39.84%) correlates forelimb variance with the proportion of the carpometacarpus (0.92), and negatively with the radius (–0.58).

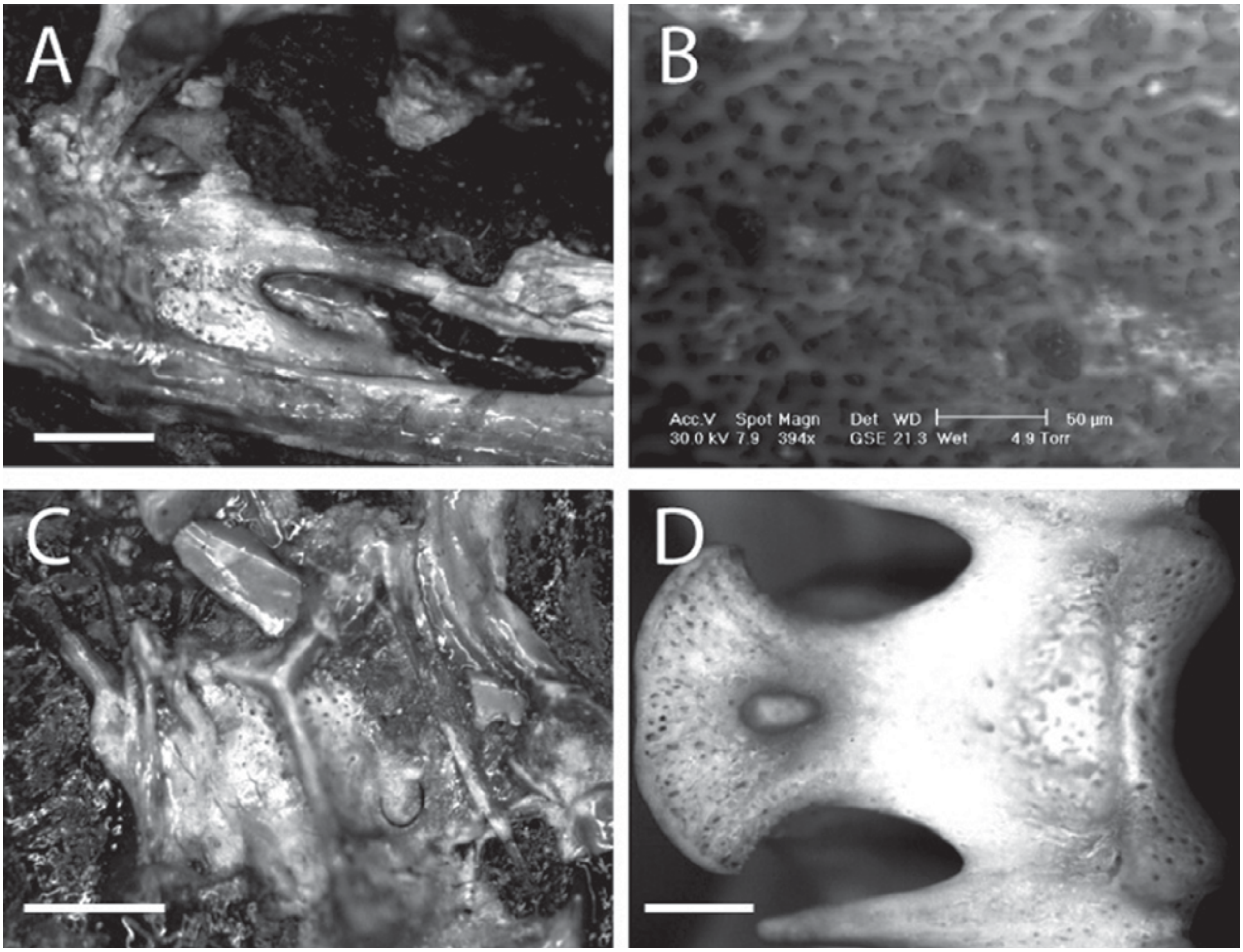

Fig. 2.—Bone surface pattern on El Montsec specimen. A) Inner surface of the articular bone showing pattern of foramina. B) ESEM (XL30) photograph showing ultraestructural details in the mandible bone surface. C and D) Ventral view of cervical vertebrae in LP-4450-IEI (Montsec) specimen and juvenile of *Falco tinnunculus* (MNCN 264416) respectively. In A, C, and D scale-bar is 1mm.

The distribution of neornithe birds extends throughout all the possible combinations of forelimb proportions in the PCA scatter-plot (figs. 4 and 5). In the distribution, non-avian theropod dinosaurs overlap with paleognath neornithes, since both have forelimbs with proportionally larger humeri and proportionally shorter radii (see also Middleton and Gatesy, 2000). *Enantiornithes* cluster together and overlap with other neornithe taxa, with which they share the presence of proportionally shorter humeri, larger radii, and proportionally shorter carpometacarpii. Both basal birds, *Archaeopteryx* and *Confuciusornis*, lie very close to an intermediate position between fossil non-avian theropods and enanthiornithe birds, thus both genera present average forelimb proportions different from the rest of the pool sample.

Table 1.—**Variance explained by PCA factors and their correlation with original variables (forelimb proportions)**

	% Explained Variance	
PC	% Variance	% total
1	60.1534	60.1534
2	39.8465	99.9999
3	4.38E-14	100
	PC 1	PC 2
% Humerus	–0.9936	–0.1128
% Radius	0.815	–0.5794
% Carpometacarpus	0.3912	0.9202

Interestingly, each embryo clusters near its corresponding clade. For instance, embryonic *Struthio* fall near adult *Struthio* (i.e. Paleognaths on figs. 4 and 5), and embryonic enantiornithes fall near each

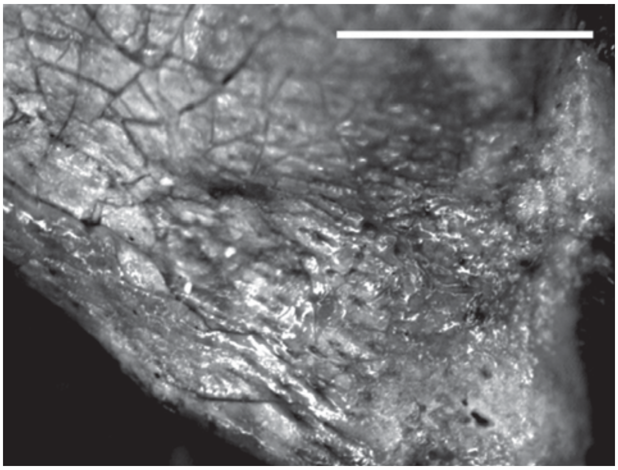

Fig. 3.—Distal area of humerus in specimen LP-4450-IEI. Rough texture of bone surface with pores going obliquely through the cortical. Short longitudinal trails can be recognized at the epiphysis.

corresponding adult enantiornithe. Therefore, forelimb proportions seem to have an important phylogenetic signature, since the position of all embryos in comparison with their corresponding adults in the clusters is grouping clades within morphospace.

Discussion

We have approached the re-evaluation of the relative age of this enantiornithine bird from El Montsec by networking the results provided by three different approaches: taphonomical (preservation features and processes), anatomical (mostly bone surface pitting), and morphometric (metrical analysis of forelimb proportions).

Taphonomically, the El Montsec specimen is remarkable by its excellent preservation; soft tissues, delicate anatomical skeletal features, and histological patterns are finely preserved in the specimen. This exceptional taphonomical preservation allows to observe microstructural details of bones (fig. 2, A and B). It seems that the bone surface texture of the El Montsec bird is not a taphonomical alteration, and is more likely related with its bone growth pattern (fig. 2, C and D). We have observed relationships between striations/pitting and bone immaturity in several parts of the skeleton (fig. 3). At the same time, limited bone deformations have been observed in those parts where the bone has a spongy texture.

From its general qualitative attributes, the El Montsec specimen might seem to have a juvenile stage; for instance, the presence of partial sutural lines on the skull and the relative proportion of the orbit and the rostrum is evident. *Liaoxiornis* has as well juvenile qualitative attributes (Hou and Chen, 1999). Morphometrically, the bird from El Montsec and *Liaoxiornis* present very similar forelimb proportions (fig. 4). Unfortunately, however, forelimb proportion itself does not provide information about the relative age of the El Montsec specimen, since both the putative juveniles (such as *Liaoxiornis*) and the embryo from Liaoning (V14238) have typical enanthionithine forelimb geometries. It is worth stressing, nonetheless, that exploring other aspects of the skeletal morphology will most likely add information for addressing this issue.

The characters of the bone surface as an indication of relative age, which has been named "textural-ageing" by Tumarkin-Deratzian *et al.,* (2006), provides the best estimation of the ontogenetic status for the El Montsec fossil specimen. The surface pattern of the humeral shaft indicates that the skeletal maturity of this element is that of a subadult stage. This assessment is, however, conditioned by the relationships between textural changes and growth regimes, and thus, we work with the assumption that Enantiornithes have a similar growth pattern than Neornithes. The subadult condition of this specimen, as suggested by the condition of the humeral shaft, is reinforced by the presence of a nearly fully ossified humeral distal condyle, in such a way that the growth line at the humeral epiphysis can be readily traced (fig. 3). Consequently, both early juvenile and fully adult stages can be disregarded on the basis of these features.

A caveat would be, however, that very little is known about the growth dynamics of Enantiornithes. If early growth regime were accelerated in enantiornithines, referenced from neornithes, then textural-ageing standardizations for the El Montsec specimen would overestimate its age. It would otherwise be a juvenile as was previously assessed by Sanz *et al.* (1997). Morphometric results are more consistent with this estimation, since El Montsec forelimb proportions are comparable to other juvenile Enantiornithes such as *Liaoxornis*.

In conclusion, if growth regimes in enantiornithines are considered equivalent to those of neornithes, the relative age of the El Montsec specimen could be a subadult, close to adulthood. If, on contrary, the growth regime of basal birds is accelerated, the El Montsec specimen would otherwise be a juvenile individual.

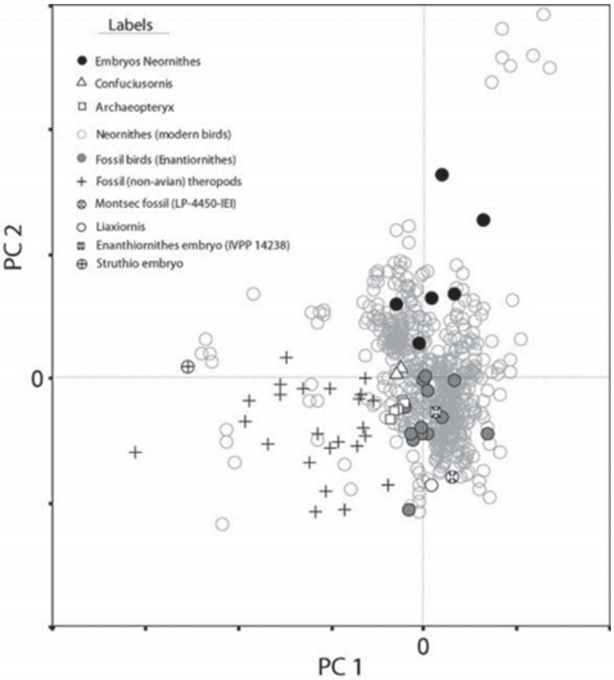

Fig. 4.—PCA of forelimb proportions of $N = 693$ theropod dinosaurs. The autopod is referred as *carpometacarpus* although in non-avian theropod dinosaurs this proportion corresponds with metacarpal II (Middleton and Gatesy, 2000). Data was collected from literature and corresponds to 24 non-avian theropods (21 species), 6 *Archaeopteryx*, 640 Neornithes (Middleton and Gatesy, 2000), two *Confuciusornis* (GMV-2131, GMV-2132; Chiappe *et al.,* 1999), 14 Enantiornithes: *Cathayornis, Concornis, Noguerornis,* one unnamed enantiornithine (Middleton and Gatesy, 2000), *Sinornis*, *Cathayornis* (Sereno *et al.,* 2002), *Eoalulavis* (Sanz *et al.,* 2002), *Liaoxiornis* (Hou and Chen, 1999), *Eoenantiornis* (Zhou *et al.,* 2005), *Protopteryx* (Zhang and Zhou, 2000), *Eocathayornis* (Zhou, 2002), *Jeholornis* (Zhou and Zhang, 2002) and *Shenzhouraptor* (Ji *et al.,* 2002), 7 Neornithes embryos (*Regulus regulus, Phaeton rubicauda, Oceanodroma leucorhoa, Sterna forsteri, Podiceps cristatus, Sturnus vulgaris*; Starck, 1998; *Struthio camelus*; specimen prepared at the Unidad de Paleontología, UAM), one Enantiornithes embryo (Zhou and Zhang, 2004) and the fossil Montsec specimen (LP-4450-IEI, Institut D'estudis Ilerdencs).

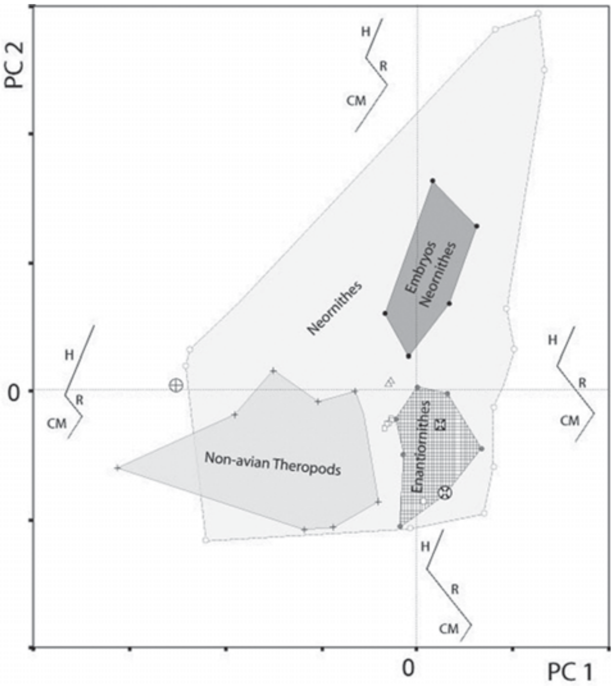

Fig. 5.—Forelimb morphospace in where it is represented the percentage of H (humerus), R (radius) and CM (*carpometacarpus*). In the morphospace has been outlined the distribution of non-avian theropods, the avian clades Neornithes and Enantiornithes, and a group of neornithine embryos. Symbols identified the same taxon as in figure 4.

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