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## The Osteology of *Concornis lacustris* (Aves: Enantiornithes) from the Lower Cretaceous of Spain and a Reexamination of its Phylogenetic Relationships

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### ABSTRACT

Additional preparation of the holotype of *Concornis lacustris* from the Lower Cretaceous (Barremian) deposits of Las Hoyas (Spain) has provided abundant new osteological data. This specimen is superbly preserved and anatomical details are available for most skeletal regions except the skull and neck. The forelimb has "modern" proportions but it retains large claws. The sternum is carinate and deeply notched. The carina, however, does not reach the cranial margin but is developed in the caudal half of the sternum. The dorsal, synsacral and caudal vertebrae are amphicoelous. The

dorsal vertebrae have deep lateral grooves and parapophyses in a central position. The ischium has large obturator and dorsal processes; the pubes form a distal symphysis. The hind limb is gracile, elongate, and longer than the forelimb.

Cladistic analysis of various ornithothoracine taxa supports the allocation of *Concornis lacustris* within the Enantiornithes, a major clade of Cretaceous birds mostly recognized from continental deposits. This new interpretation is substantially supported by 12 synapomorphies shared by *C. lacustris* and the remaining enantiornithines.

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Within the Enantiornithes, tarsometatarsal data support a sister-group relationship between *C. lacustris* and the Avisauridae.

*Concornis lacustris* is the oldest enantiornithine bird from the Western Hemisphere. The interpre-

tation of this species as an enantiornithine emphasizes the wide geographical and stratigraphical distribution of this clade during the Cretaceous, and its large taxonomic diversity.

## RESUMEN

La nueva preparación del holotipo de *Concornis lacustris* del Cretácico inferior (Barremiano) de Las Hoyas (España) ha provisto nueva y abundante información osteológica. Este ejemplar, que se encuentra excepcionalmente preservado, provee detalles anatómicos para la mayor parte del esqueleto con la excepción del cráneo y cuello. El miembro anterior tiene proporciones de aspecto "moderno" si bien retiene garras bien desarrolladas. El esternón es aquillado y profundamente escotado. Curiosamente, la quilla esternal no alcanza el margen craneal sino que se encuentra desarrollada en la mitad caudal del esternón. Las vértebras dorsales, sinsacrales y caudales son anficélicas. Las vértebras dorsales poseen surcos laterales profundos y parapófisis ubicadas en el centro del cuerpo vertebral. Los procesos obturador y dorsal del isquión son grandes, y los pubis forman una sínfisis distal. El miembro posterior es grácil, elongado, y más largo que el miembro anterior.

El análisis cladístico de los distintos taxones de Ornithothoraces sustenta la asignación de *Concornis lacustris* a los Enantiornithes, un importante clado de aves cretácicas registrado principalmente en depósitos continentales. Esta nueva interpretación está sustentada por 12 sinapomorfías compartidas entre *C. lacustris* y los restantes Enantiornithes. Dentro de los Enantiornithes, la información del tarsometatarso sugiere que *C. lacustris* es el grupo hermano de Avisauridae.

*Concornis lacustris* es el Enantiornithes más antiguo del hemisferio occidental. La asignación de esta especie a los Enantiornithes enfatiza nuevamente la amplia distribución geográfica y estratigráfica de este grupo durante el Cretácico. A su vez, esta interpretación resalta la notable diversidad taxonómica alcanzada por los Enantiornithes.

## INTRODUCTION

The Las Hoyas fossil site is located in the Serranía de Cuenca (Iberian Ranges), province of Cuenca, Spain (fig. 1). Stratigraphically it belongs to the Lower Cretaceous (Barremian) "Calizas de La Huerquina" Formation of lacustrine and palustrine origin (Fregenal-Martínez, 1991; Fregenal-Martínez and Meléndez, 1993). The fossil site of Las Hoyas has provided thousands of fossil remains of plants, invertebrates, and vertebrates (Sanz et al., 1988, 1990). Among the latter, articulated skeletons of salamanders, frogs, lizards, crocodiles, nonavian dinosaurs, and in particular birds, are bringing to light the fossil record of these groups during the Early Cretaceous. The limestones of Las Hoyas are an example of the so-called *Konservat-lagerstätten*, in which even delicate structures such as feathers and insect wings, are preserved.

In the past decade an increasing number

of Mesozoic birds have provided critical new evidence for interpreting the early history of birds (Walker, 1981; Kurochkin, 1985; Sanz et al., 1988a; Alvarenga and Bonaparte, 1992; Chiappe, 1991, 1992a; Sanz and Buscalioni, 1992; Zhou et al., 1992; Sereno and Rao, 1992; Perle et al., 1993, 1994; Chiappe and Calvo, 1994). In this sense, the fossil site of Las Hoyas has contributed the important discoveries of *Iberomesornis romerali* (Sanz and Bonaparte, 1992) and the well-preserved *Concornis lacustris* (Sanz and Buscalioni, 1992) (fig. 2). Additional preparation of the latter specimen has revealed unexpected new anatomical information that supports a new hypothesis of its phylogenetic relationships. The aim of this paper is to redescribe the holotype specimen of *Concornis lacustris* and discuss its phylogenetic relationships in the light of the new anatomical information.

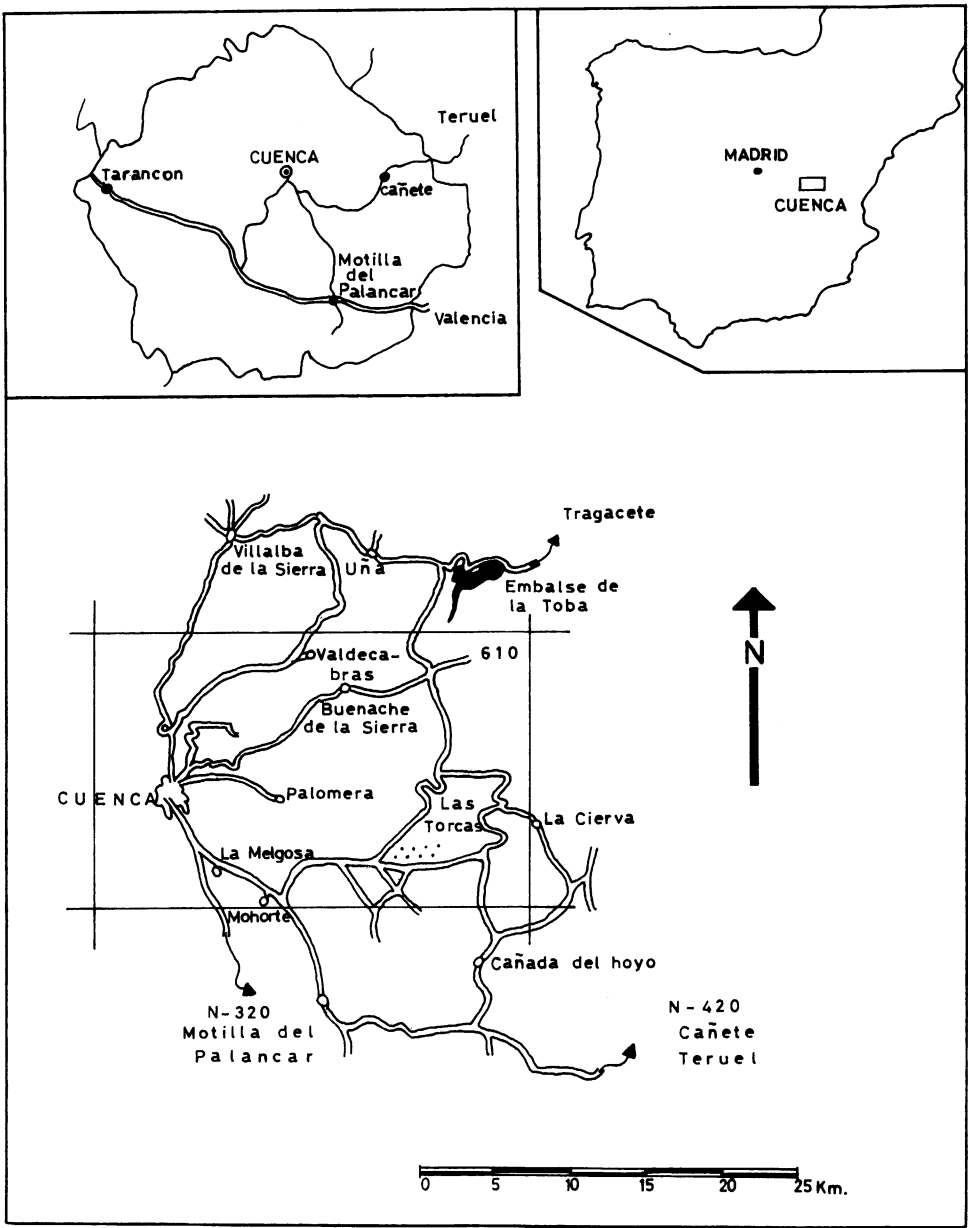


Fig. 1. Map indicating the area of Serrania de Cuenca (Spain) in which the quarry of Las Hoyas is situated.

MATERIALS AND METHODS

The original description of *Concornis lacustris* (Sanz and Buscalioni, 1992) was based on the unprepared specimen, so as not to destroy the wing feathers. The unprepared specimen comprised two main slabs of the

same block. After Sanz and Buscalioni's (1992) publication, the smaller slab (thoracic girdle) was glued to the main one in its original position. The matrix was then removed by mechanical and chemical techniques. With a few exceptions, most enantiornithine taxa are known from fragmentary re-

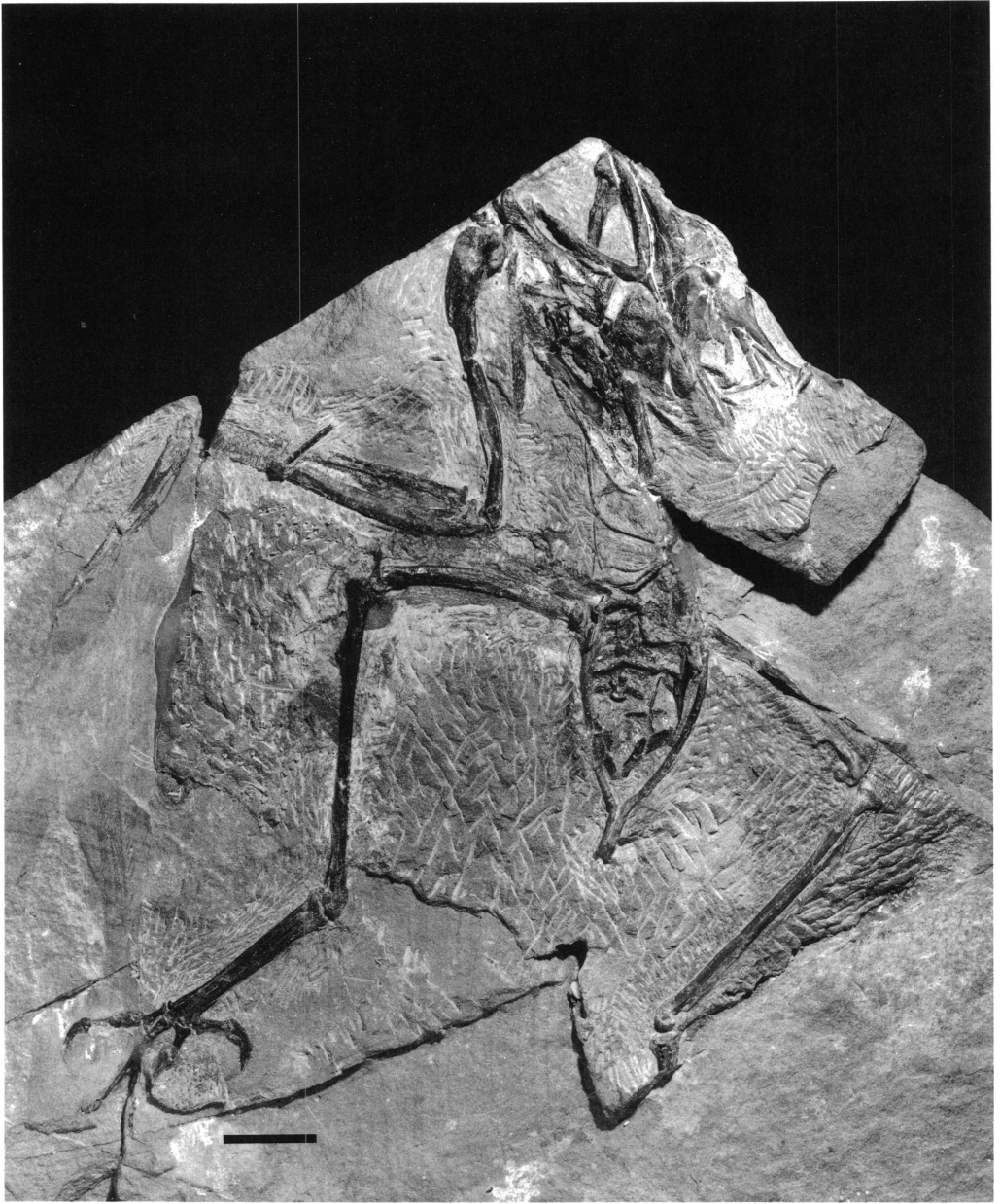


Fig. 2. *Concornis lacustris* (LH-2814) from the Lower Cretaceous of Spain. Specimen after preparation. Scale bar = 10 mm.

mains (see for example Chiappe, 1993). More complete new specimens are not yet described. This fact complicates our understanding of the phylogenetic relationships within this group. Chiappe (1992a, in press

a; see also Chiappe and Calvo, 1994) diagnosed the Enantiornithes on the basis of several derived characters shared by all specimens then known (see these papers for the geographical and stratigraphical distribution

of this clade). The present cladistic analysis (appendix 2) combines some of these with other characters used in a recent study of the phylogenetic relationships of the major groups of Cretaceous birds (Chiappe, 1992b, in press a, b; Chiappe and Calvo, 1994). The remaining diagnostic characters of Enantiornithes were not included because they are uncertain (not preserved) in *Concornis lacustris* and absent or uncertain in the remaining ingroup taxa. In the data matrix of appendix 2, character states scored for the Enantiornithes denote the condition present in all previously known enantiornithine taxa. Several characters of *Iberomesornis romerali* were re-scored after further preparation of the holotype specimen. Both data matrices were analyzed using the implicit enumeration (ie) command of the "Hennig 86" program (Farris, 1988). Derived characters exclusive to a single ingroup taxon were excluded from the data matrices in order to avoid their influence on the consistency indices (Carpenter, 1988; Wiley et al., 1991). The species concept used in this paper follows the phylogenetic species concept of Nixon and Wheeler (1990, 1992). Hence, the diagnosis of *C. lacustris* is based on a unique combination of characters that differentiates this taxon from all others.

The anatomical nomenclature used here generally follows Baumel and Witmer (1993) using the English equivalents of the Latin terminology.

## SYSTEMATIC PALEONTOLOGY

AVES LINNAEUS, 1758

ORNITHOTHORACES CHIAPPE AND CALVO, 1994

ENANTIORNITHES WALKER, 1981

*Concornis lacustris* Sanz  
and Buscalioni, 1992

**HOLOTYPE:** LH-2814 (LH refers to the collection from Las Hoyas), housed in the Unidad de Paleontología, Universidad Autónoma de Madrid, Spain. The specimen includes most postcranial elements in articulation, including the right forelimb and thoracic girdle; the sternum; some dorsal, synsacral, and caudal vertebrae; pubis; ischium; and hind limbs (figs. 2, 3).

**LOCALITY AND HORIZON:** Las Hoyas, La Cierva township, Province of Cuenca, Spain (fig. 1). "Calizas de La Huérguina" Formation, Barremian, Lower Cretaceous.

**DIAGNOSIS:** Enantiornithine bird with the following autapomorphies: ribbonlike ischium, transverse ginglymoid articulation of trochlea of metatarsal I, and strongly curved and laterally excavated distal end of metatarsal IV. The latter two features make this taxon different from all other enantiornithines for which the tarsometatarsus is known [e.g., *Lectavis bretincola* (Chiappe, 1993), *Yungavolucris brevipedalis* (Chiappe, 1993), *Soroavisaurus australis* (Chiappe, 1993), *Neuquenornis volans* (Chiappe and Calvo, 1994), *Avisaurus archibaldi* (Brett-Surman and Paul, 1985), and *A. glorioae* (Varricchio and Chiappe, 1995); see Chiappe (1993) for autapomorphic characters of these taxa]. In addition, *Concornis lacustris* differs from the Argentine *Enantiornis leali* (Walker, 1981) in that the latter species is very robust and large, and has a large and shallow transverse ligamental groove in the humerus. *C. lacustris* is clearly separable from *N. volans* by the presence of a long hypocleidum in the furcula, a sternal carina that develops only in the caudal half of the sternum, a straight metatarsal I, much stronger lateral grooves on the dorsal centra, a major metacarpal more robust than the minor one, and a much broader intermetacarpal space. The last character also distinguishes *C. lacustris* from the Chinese enantiornithine *Cathayornis yandica*, in which the intermetacarpal space is extremely narrow. *C. lacustris* also differs from this species by having larger claws in the forelimb and by the dorsal centra, which are not excavated by two small depressions (cranial and caudal).

## DESCRIPTION

The holotype and single specimen of *Concornis lacustris* is fairly complete, providing osteological details from most skeletal regions except the skull and neck (figs. 2, 3). The specimen lies in ventral aspect with its limbs partially flexed. The preservation is excellent as exemplified by the presence of feather impressions (Sanz and Buscalioni, 1992). The

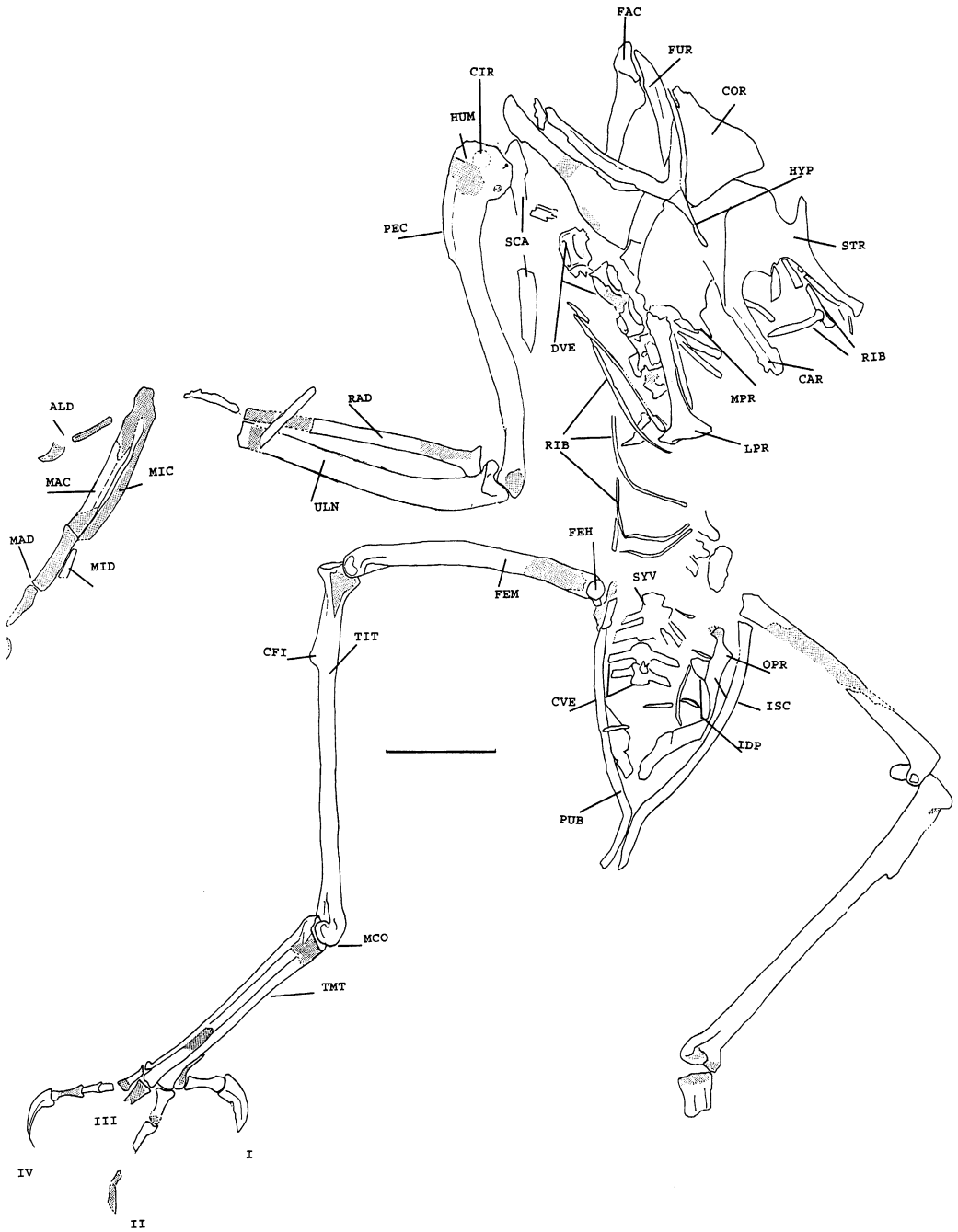


Fig. 3. Diagram of *Concornis lacustris* (LH-2814). Stippled areas indicate broken portions. Scale bar = 10 mm.

skeletal elements have suffered a slight dorsoventral compression with some areas (e.g., thorax and pelvis) sloping toward the left side of the specimen. No other major displacements are present.

#### AXIAL SKELETON

The new preparation has revealed fragments of four dorsal vertebrae, the most caudal portion of the synsacrum, and the first two caudal vertebrae.

**DORSAL VERTEBRAE:** The preserved trunk elements are regarded as midposterior dorsals on the basis of the absence of ventral processes. The four vertebrae are well preserved: the anterior three are exposed in ventral view and the last one in lateral view. The articular surfaces are amphicoelous. The vertebral bodies are laterally compressed. As in other enantiornithines (e.g., *Neuquenornis volans*, *Cathayornis yandica*, El Brete specimens), these bodies are excavated by deep longitudinal depressions and their parapophyses (costal foveae) are developed in a central position (figs. 4, 5).

**SYNSACRAL VERTEBRAE:** The last two vertebrae of the synsacrum are preserved, and bear elongate transverse processes, which retain their individuality and are caudally directed (fig. 3). The last process is narrower than the preceding one. This trend continues in the caudal vertebrae.

**CAUDAL VERTEBRAE:** The caudal centra seem to be amphicoelous. These vertebrae have elongate and narrow transverse processes that, like those of the synsacral vertebrae, are directed caudally (fig. 3). At the cranial border of the second caudal there is a bifurcated, ventrally projected ossification that probably represents the hemal arch, as in some extant birds (e.g., Accipitridae).

**RIBS:** Fragments of several ribs are preserved, although none of them are articulated with the vertebrae. Three of these ribs are fairly complete, and lack uncinat processes.

#### THORACIC GIRDLE AND STERNUM

**CORACOID:** Both coracoids are preserved, exposed in ventral view (figs. 6, 7). The additional preparation has revealed the shoulder end of the right coracoid, while that of

the left one is missing. The coracoid of *Concornis lacustris* is elongate and lacks lateral and procoracoid processes (Sanz and Buscalioni, 1992). The sternal half is broad and it has a convex ventral surface. Missing parts of the right coracoid show that the sternal half is thin. This fact and the convexity of the ventral surface suggest a dorsal fossa like those of other enantiornithines (Chiappe and Calvo, 1994), although this is not verifiable from the present preparation. As pointed out by Sanz and Buscalioni (1992), the lateral margin of the sternal half of the coracoid is remarkably convex, as in the Enantiornithes (figs. 6, 7). The medial margin is concave. The sternal border is slightly concave, but lacks the remarkable concavity shown by certain enantiornithines (Walker, 1981; Chiappe and Calvo, 1994). The shoulder area is very slender, and its ventral surface forms a ridge. Medially, the supracoracoid nerve foramen opens into a medial groove and is separated from the dorsal surface by a thick bar, a condition also found in Enantiornithes (Chiappe, 1992a) (fig. 7). Laterally, the shoulder end slopes dorsosternally also as in the enantiornithines.

**SCAPULA:** The new preparation has revealed the shoulder portions of both scapulae and part of the body of the right one (fig. 3). Unfortunately, the preserved areas contain little significant information. The scapular shaft is straight, lacking a sagittal curvature. On the shoulder end of the left scapula there is a subrectangular articular area interpreted here as the articular facet for the furcula.

**FURCULA:** The furcula is almost complete and is exposed cranially (figs. 6, 7). It is very robust, and as in the Patagonian enantiornithine *Neuquenornis volans* (Chiappe and Calvo, 1994) is laterally excavated with the cranial margin projected externally. At the shoulder end, below the articular area, it is laterally compressed with no external projection. The clavicular rami are separated from each other by an angle of 60° (Sanz and Buscalioni, 1992). The hypocleideum tapers distally, and its cranial face bears a weak crest. In contrast to *N. volans*, the hypocleideum of *Concornis lacustris* is very long as in the Chinese enantiornithine *Cathayornis yandica* (Zhou et al., 1992).

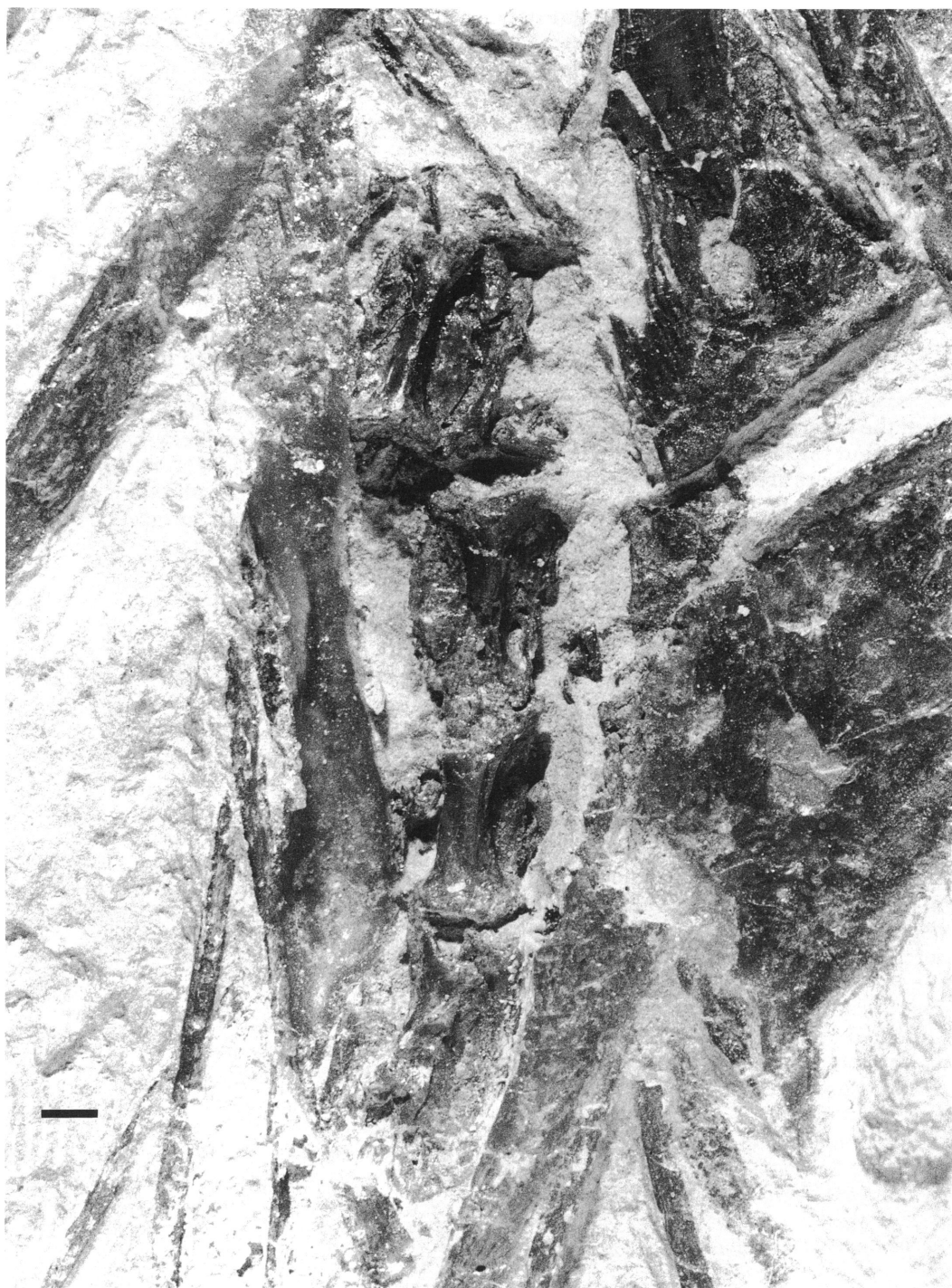


Fig. 4. Dorsal vertebrae of *Concornis lacustris* (LH-2814). Scale bar = 1 mm.



**STERNUM:** In addition to the cranial area described in the original study, the new preparation has revealed the caudal part of the sternum. The sternum is carinate (figs. 6, 7). The carina, however, is not developed in the cranial part of the sternum, but starts near the midpoint (Sanz and Buscalioni, 1992). Anterior to the carina, the sternum has a broad, flat surface, although the extension of this area might be exaggerated by postmortem compression (Sanz and Buscalioni, 1992). The cranial margin of the sternum is round. Lateral crests are well developed in front of the carina. As mentioned by Sanz and Buscalioni (1992), three foramina perforate the right side of the sternal body, and two perforate the left one. The caudal half of the sternum is deeply notched, exhibiting lateral and medial processes. The lateral process is stout, elongate, and has a remarkable distal expansion (figs. 6, 7). The morphology of this sternal process is very similar to those of *Neuquenornis volans* and *Cathayornis yandica*. The medial process is only preserved at its base. The latter process, however, appears to be less robust than the lateral one (Sanz and Buscalioni, 1992). At the level of the origin of the carina, there is another process branching off craniodorsally from the base of the lateral process. Cranial to this process there is a short notch interpreted as the articular area of the ribs (fig. 7). If this is correct, this area was very short, representing approximately 15% of the sternal length.

#### THORACIC LIMB

**HUMERUS:** Additional preparation has revealed the right humerus, exposed in cranial view (fig. 6). It is as long as or slightly shorter than the ulna (figs. 2, 3). Although the humerus is crushed, some extent of disphasing between the axial planes of both extremities is visible, a primitive condition known to occur in Enantiornithes and other basal birds (Chiappe, 1992b). At the proximal end, the pectoral crest does not curve cranially. In proximal view, the head is cranially concave and caudally convex. Distal to the head, in cranial aspect, there is a circular depression also found in Enantiornithes and the Patagonian bird *Patagopteryx deferrariisi* (Chiappe, 1992b) (fig. 7). Of interest

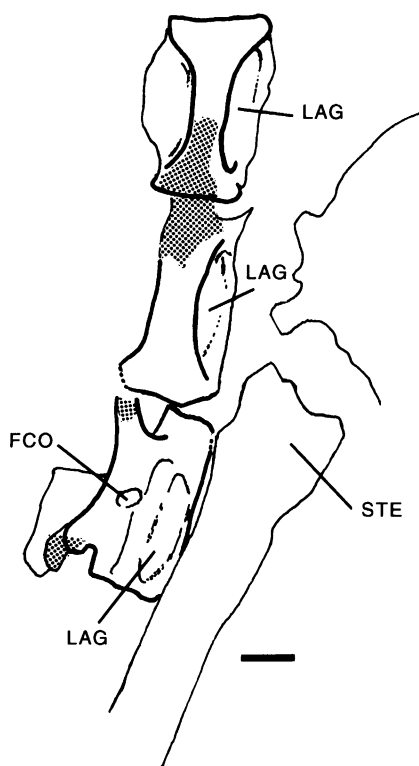


Fig. 5. Diagram of dorsal vertebrae of the enantiornithine *Concornis lacustris* (LH-2814). Stippled areas indicate broken portions. Scale bar = 1.2 mm.

is the strong development and cranioventral projection of the bicipital area, a derived condition of the Enantiornithes (Chiappe, 1992a). On the ventral face of the distal portion of this crest, there is a small, shallow depression also characteristic of the latter taxon (fig. 7). The proximal border of the bicipital crest bears a small but deep, subtriangular transverse ligamental groove. The development of this groove is considerably smaller than in the El Brete enantiornithines. In caudal aspect, the ventral tubercle is directed caudally. At the distal end, the condyles are not preserved, although it is evident that they were located on the cranial aspect. The distal extremity is craniocaudally compressed, and its cranial surface does not show any evidence of the fossa for the brachial muscle.

**ULNA:** Only the proximal half of the right ulna is preserved, and it is exposed cranio-

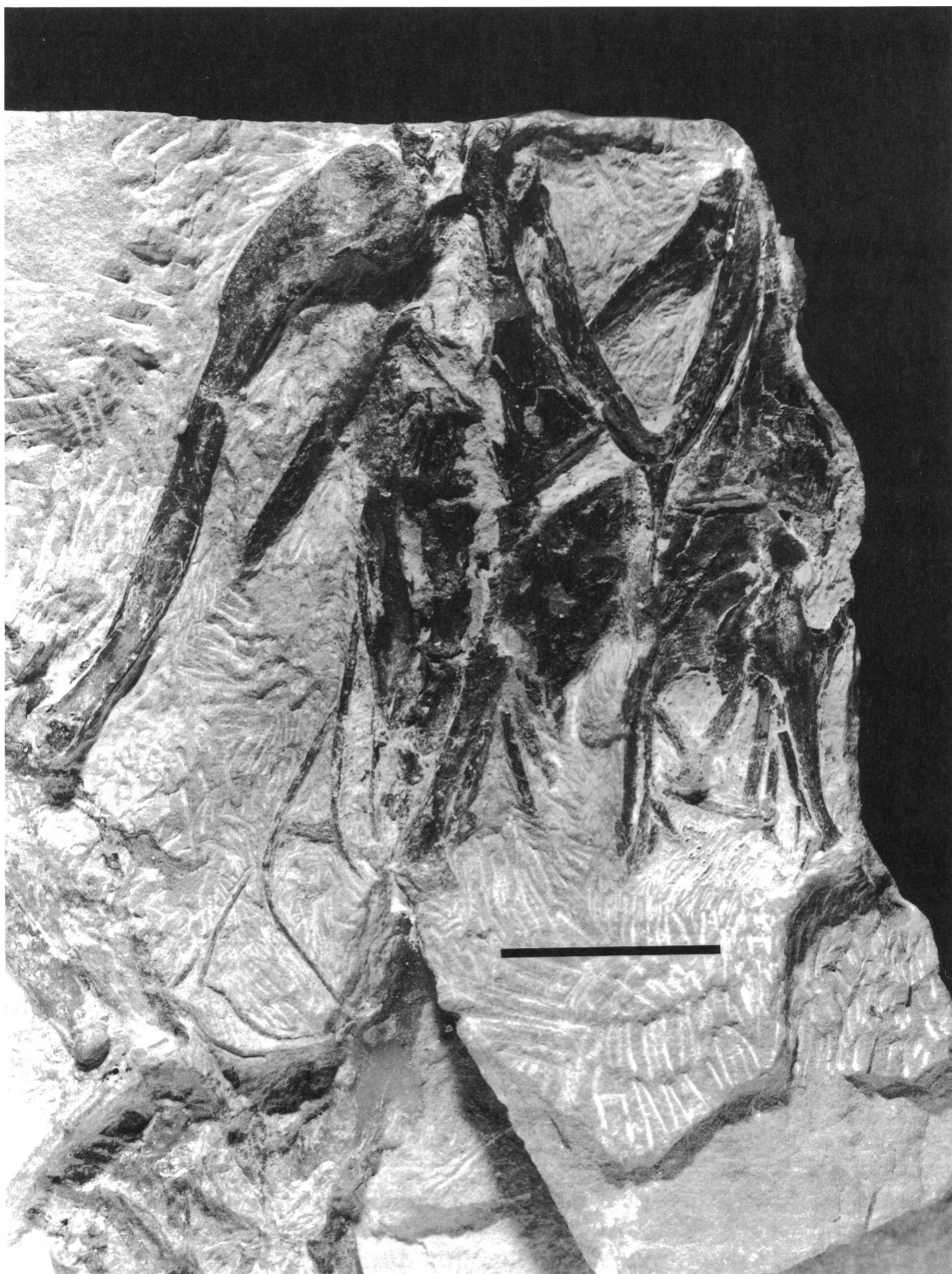


Fig. 6. Thoracic region of *Concornis lacustris* (LH-2814). Scale bar = 10 mm.

ventrally (figs. 2, 3). The ulna is significantly broader and more robust than the radius, with an approximate proportion of 2:1 with respect to the radial shaft (Sanz and Buscalioni, 1992). In the proximal articular area, the dorsal cotyla is convex, although less so than in

the El Brete enantiornithines. The dorsal cotyla is separated from the ventral cotyla and the olecranon by a shallow depression (figs. 8, 9), a condition also shared by other enantiornithines (Walker, 1981). The dorsal cotyla is strongly projected dorsocaudally. The

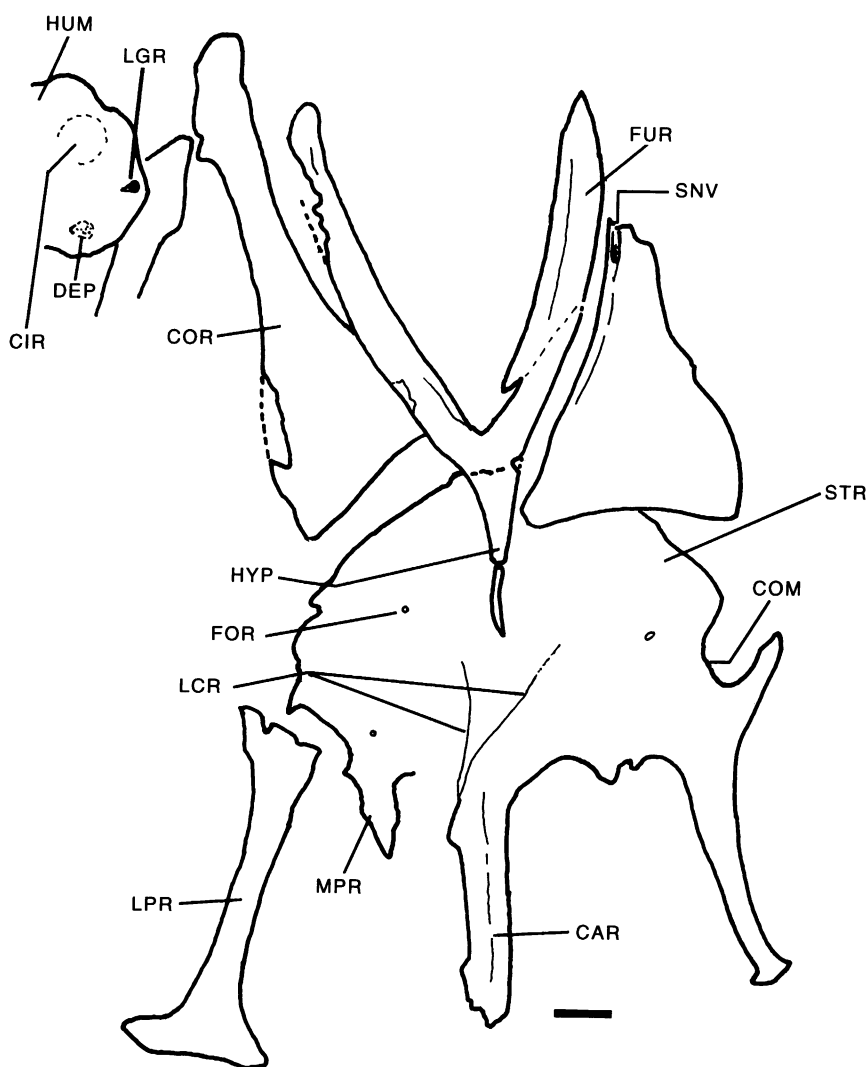


Fig. 7. Diagram of thoracic region of *Concornis lacustris* (LH-2814). Scale bar = 1.2 mm.

ventral cotyla is concave, and in its development the olecranon resembles that of the El Brete enantiornithines. The cranial surface immediately distal to the articular surface is not well preserved, although there is a distinct, round bicipital tubercle (fig. 9).

**RADIUS:** The right radius is missing its distal end (figs. 2, 3). It is significantly more slender than the ulna. Unfortunately, it is not possible to confirm the presence of the axial groove typical of the radial shaft of other Enantiornithes.

#### METACARPALS AND MANUAL PHALANGES:

The hand of *Concornis lacustris* is slightly shorter than the forearm (figs. 2, 3). The major metacarpal is the only one preserved, although some information about the other elements is available from their impressions. The major metacarpal is the most robust. It is straight, of uniform width, and its ventral surface is convex. On the basis of its impression, the dorsal surface of the minor metacarpal was sharp. The intermetacarpal space between these metacarpals is narrow (Sanz and Buscalioni, 1992), although wider than in *Neuquenornis volans*. The major and mi-



Fig. 8. Distal end of humerus and proximal end of ulna-radius of *Concornis lacustris* (LH-2814). Scale bar = 1 mm.

nor metacarpals appear to be fused distally. The proximal area, however, is damaged and the fusion between metacarpals and distal carpals remain uncertain. The alular metacarpal is not preserved. The distance between the proximal phalanx of this digit and the proximal end of the metacarpals suggests, however, that it must have been short, as in other enantiornithines and more advanced birds.

The alular digit is preserved as an impression and bears two phalanges (fig. 3). The proximal phalanx is slender and elongate; the distal phalanx is a claw. The major digit has three phalanges, all preserved as impressions. The proximal phalanx seems to be the largest, as in *Cathayornis yandica*; it differs from the primitive condition present in *Archaeopteryx lithographica* and *Patagopteryx deferrariisi* in

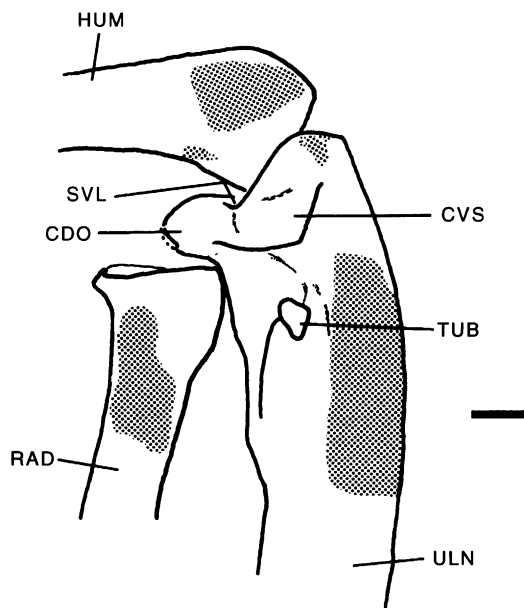


Fig. 9. Diagram of distal end of humerus and proximal end of ulna-radius of *Concornis lacustris* (LH-2814). Stippled areas indicate broken portions. Scale bar = 1.2 mm.

which the intermediate phalanx is the largest of the three. This phalanx, however, is slender, lacking the craniocaudal expansion typical of modern birds. A longitudinal ridge of matrix suggests the presence of an axial groove on its dorsal surface. The distal phalanx of this digit (fig. 3) is also a claw as in *C. yandica*. In the minor digit, only a single phalanx is preserved, also as an impression. This phalanx is slender and tiny. Hence, in contrast to previous considerations (Sanz and Buscalioni, 1992), the hand of *Concornis lacustris* has claws and its phalangeal formula is 2-3-1?-x-x.

#### PELVIC GIRDLE

**PUBIS:** Both pubes are preserved in ventral view (fig. 10). Their most proximal portions are missing. The pubis of *Concornis lacustris* is slender, elongate, and suboval in cross section. It was probably oriented posteriorly, although it is not possible to ascertain the degree of reversion. Distally, the apices of both pubes contact each other, forming a short symphysis (fig. 10). The distal end of the sym-



Fig. 10. Pelvic girdle of *Concornis lacustris* (LH-2814). Scale bar = 5 mm.

physis is missing, hence the presence or absence of a pubic foot remains uncertain.

**ISCHIUM:** The left ischium is fairly complete, while the right one is only represented by a distal fragment. The ischium is approximately 25% shorter than the pubis. It is laminar and laterally compressed. The proximal portion is dorsoventrally broad. Distally, the ischium narrows and in its distal two-thirds it has a ribbonlike aspect (fig. 10). Like the pubis, the ischium seems to be externally convex along almost all its length. The preserved proximal portion is difficult to interpret. There is an ample ventral process with a sharp end that is interpreted as a prominent obturator process. Internal to the dorsal border, at the proximal end, there is a fragment of bone representing an ischiadic dorsal process. The existence of such a process is not unexpected considering its presence in the ischium of the El Brete enantiornithines. Distally the terminal processes of both ischia are not in contact.

**ILIUM:** Unfortunately, there is no available information.

#### PELVIC LIMB

**FEMUR:** Both femora are preserved (fig. 3). The right is exposed in medial view and the left one craniomedially. The femur is robust and considerably shorter than the tibiotarsus. The femoral shaft is slightly curved, with the cranial surface convex. The femoral head is oval and well projected medially. A depression for the insertion of the round ligament appears to be absent. The lateral margin of the most proximal end of the left femur inclines medially as in the El Brete enantiornithines. This morphology may suggest the presence of the enantiornithine hypertrophied posterior trochanter (Chiappe, 1992a; Chiappe and Calvo, 1994), although this condition is not exposed. The distal end lacks a prominent patellar groove. The medial surface of the distal end is excavated by a sem-

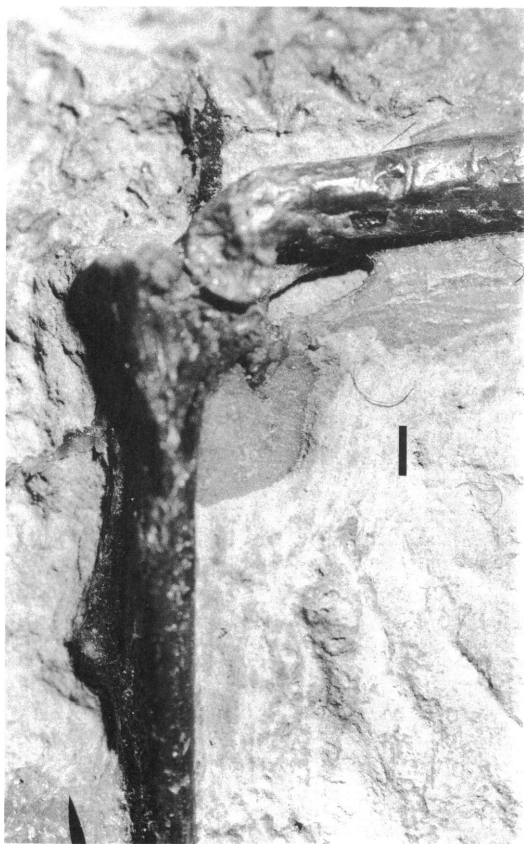


Fig. 11. Distal end of right femur and proximal end of tibiotarsus of *Concornis lacustris* (LH-2814). Note detail of caudal projection of lateral margin of femur, and the fibular crest. Scale bar = 1 mm.

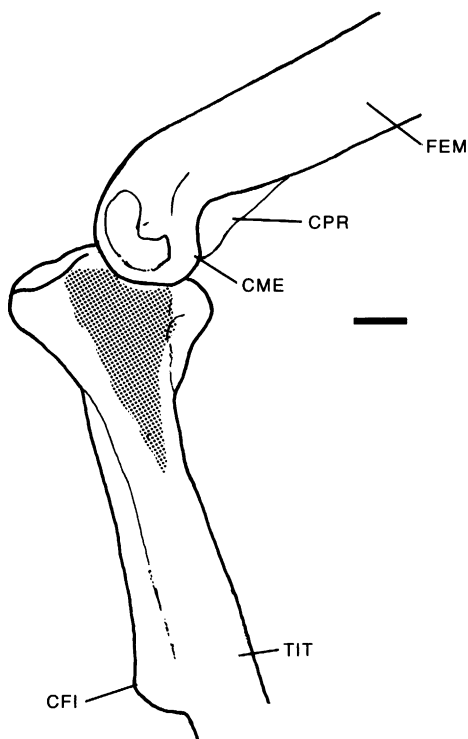


Fig. 12. Diagram of distal end of right femur and proximal end of tibiotarsus of *Concornis lacustris* (LH-2814). Stippled areas indicate broken portions. Scale bar = 1.2 mm.

ilunate depression with the concave border oriented proximally. The lateral margin of the distal end, proximal to the lateral condyle, projects caudally (figs. 11, 12) as in the El Brete enantiornithines and *Neuquenornis volans*.

**TIBIOTARSUS:** Both tibiotarsi are preserved, and exposed in craniomedial view. The tibiotarsus is gracile (fig. 3). Its fibular crest is short and strongly developed (figs. 11, 12). The degree of lateral projection of this crest increases distally, ending abruptly in a stout tubercle. The proximal surface of the tibiotarsus is round as in most enantiornithines [with the exception of the Argentine *Lectavis brenticola* (Chiappe, 1993)]. The articular surface of the proximal end slopes laterocrani-

ally. In the proximal end there is a single, weak, mediocranial cnemial crest as in the Australian enantiornithine *Nanantius eos* (Molnar, 1986), *Neuquenornis volans*, and the forms from El Brete.

Distally, the proximal tarsals are completely fused to the tibia. There is no evidence of a distinct ascending process or sutures between the tibia and the proximal tarsals. The medial condyle is transversely broad (fig. 13) as in other Enantiornithes (Walker, 1981; Molnar, 1986; Chiappe, 1993), although not strongly projected cranially as in *Lectavis brenticola*. In both tibiotarsi there is a proximodistally elongate depression on the cranial surface of the distal end. In the right element it forms a sort of fossa, although this may be an artifact of preservation. The midshaft section is subcircular and not craniocaudally compressed as in *L. brenticola*.

**TARSOMETATARSUS:** The right tarsometatarsus



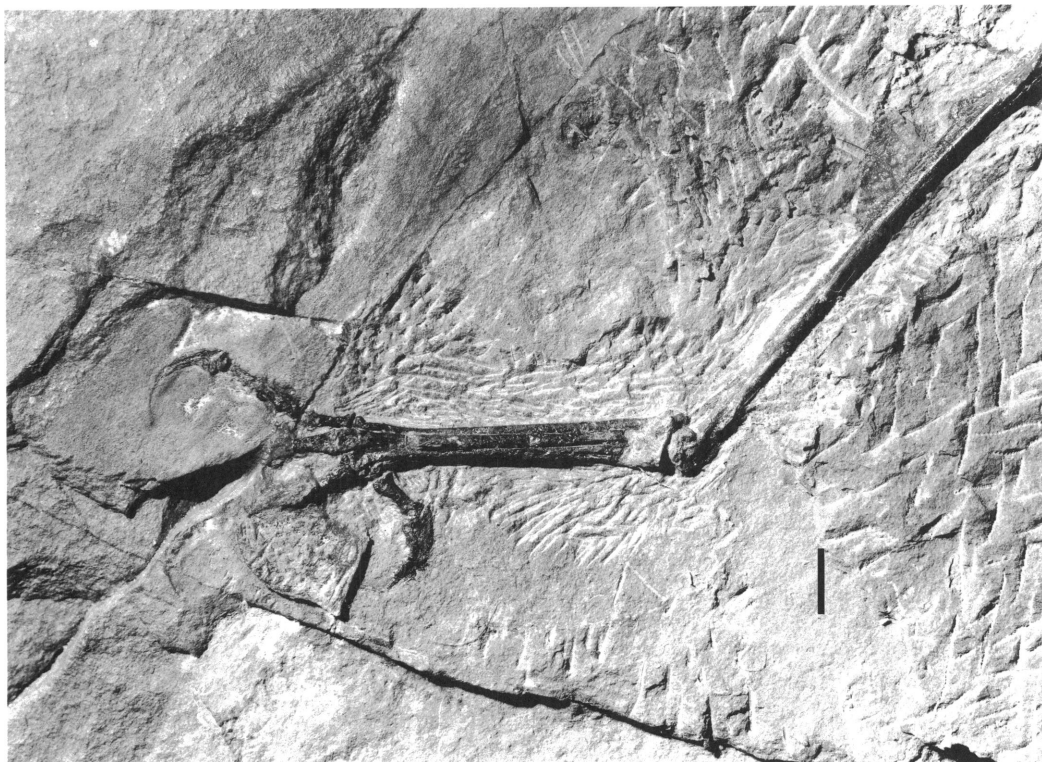


Fig. 13. Tarsometatarsus of *Concornis lacustris* (LH-2814). Scale bar = 5 mm.

tarsus is preserved and exposed in dorsal view (fig. 13). The left one is only represented by its most proximal end. The tarsometatarsus is significantly shorter than the tibiotarsus. Metatarsals II–IV are straight throughout their length. They are firmly united to each other but only fused proximally (Sanz and Buscailoni, 1992). At the proximal end, the intercylar eminence is not developed. The proximal articular surface does not slope dorsally as in several avisaurid enantiornithines (e.g., *Soroavisaurus australis*, *Avisaurus archibaldi*; Chiappe, 1993). Metatarsals II–IV are located in the same plane, although metatarsal III is located slightly forward to the other two. Metatarsal III is the longest (fig. 13). The central portion of the shaft of metatarsal III is strongly convex, as in Avisauridae (Chiappe, 1992a, 1993). The trochlea of metatarsal III is badly preserved; nevertheless, it is evident that it is narrower than that of metatarsal II as in other enantiornithines. In dorsal view, metatarsals II and III are the most conspic-

uous. Metatarsal IV is slightly more slender. At the distal end, its lateral surface is somewhat excavated. The trochlea of metatarsal IV is significantly more reduced than those of metatarsals II and III, and it is strongly curved laterally. Unfortunately, the presence or absence of the dorsolateral tubercle, which is present in the metatarsal II of other Enantiornithes (Chiappe, 1993), is not discernible. Distally, metatarsals II–IV are firmly united in broad contact, unlike those in *S. australis* in which the distal end of metatarsal II is widely separated from metatarsal III. In *Concornis lacustris*, the distal end of metatarsal II is nearly straight, lacking the strong medial curvature found in some avisaurids (Chiappe, 1993). As in the latter taxa, metatarsal I is not reverted but articulates with the medial margin of metatarsal II. Metatarsal I is straight, lacking the J-like morphology present in *S. australis* and *Neuquenornis volans* (Chiappe, 1993). The dorsal portion of this metatarsal is not completely preserved.

The plantar area of its trochlea is broad and is separated from the dorsal area by a constriction. This morphology defines a transverse ginglymoid articulation.

**PEDAL PHALANGES:** Only the right foot preserves its phalanges. Digits I and IV are complete and the I is reverted (fig. 13). It is robust and possesses a well-developed distal (ungual) phalanx. The intermediate phalanges of digit IV are relatively long. The distal phalanges lack a pronounced flexor tubercle (Sanz and Buscalioni, 1992).

### PHYLOGENETIC DISCUSSION

Sanz and Buscalioni (1992) recognized that *Concornis lacustris* was different from and more derived than *Iberomesornis romerali*, but their study only arrived at a tentative hypothesis of relationship. This preliminary study interpreted *C. lacustris* as the sister group of Ornithurae, although the inclusion of two more taxa (*Ambiortus dementjevi* and Enantiornithes) in the cladistic analysis resulted in a large number of different topologies (Sanz and Buscalioni, 1992). The new osteological information allows a more detailed analysis of the phylogenetic relationships of *C. lacustris* within the context of the most relevant ornithothoracine taxa.

Appendix 2 shows the 84 characters used to analyze the relationships of the Ornithothoraces (see Chiappe, 1992b, in press a, b; Chiappe and Calvo, 1994). Three most parsimonious trees (consistency index 0.84; retention index 0.87; length 101) resulted from the analysis of this data matrix. These three topologies vary in the relationships among the ornithurine taxa used in the analysis (Hesperornithiformes, Ichthyornithiformes, and Neornithes), and therefore they are irrelevant for establishing the phylogenetic relationships of *Concornis lacustris*.

The strict consensus cladogram of figure 14 shows that *Concornis lacustris* is closely related to all other enantiornithines. All these taxa share the following 12 unambiguous synapomorphies: humerus with a prominent, cranioventrally projected, bicipital crest (character 72), and a small fossa for muscular attachment on the lateral surface of this crest (character 83); ulna with convex dorsal cotyle, separated from the olecranon by a groove

(character 73); coracoid with convex lateral margin (character 74), and with the supra-coracoid nerve foramen opening into an elongate medial furrow and separated from the medial margin by a thick bony bar (character 75); dorsal vertebrae with strong lateral grooves on the centra (character 76), and the parapophyses (costal foveae) located in the central part of the centrum (character 77); lateral border of the distal end of the femur projecting caudally (character 78); wide and bulbous medial condyle of the distal end of the tibiotarsus (character 79); tarsometatarsus with metatarsal IV significantly smaller than metatarsals II and III (character 80), and trochlea of metatarsal II broader than those of metatarsals III and IV (character 81); furcula laterally excavated (character 84). The presence of a round articular surface at the proximal end of the tibiotarsus (character 82) supports this relationship as well, although this character has an ambiguous optimization in the present analysis. In addition to these synapomorphies, *C. lacustris* shares the distal expansion of the lateral process of the sternum with the enantiornithines *Neuquenornis volans* and *Cathayornis yandica*. This character was not included in the cladistic analysis because the sternum is poorly preserved in several ingroup taxa (e.g., *Iberomesornis romerali*, *Patagopteryx deferrariisi*) and because its ancestral condition is uncertain as well.

As mentioned above (see Materials and Methods), the interrelationships within the Enantiornithes are not well understood, a reality that stems from the fact that most enantiornithine species are known from isolated bones or fragmentary specimens (Walker, 1981; Molnar, 1986; Chiappe, 1993), or that formal and detailed descriptions are still pending (Hutchinson, 1993; Dong, 1993). Besides *Concornis lacustris*, *Neuquenornis volans* and *Cathayornis yandica* are the only enantiornithines known (or at least published) from fairly complete specimens. Chiappe (1993) presented the first attempt to understand the interrelationships among different species of Enantiornithes using data from the tarsometatarsus. In the present paper the available information from the tarsometatarsus of *C. lacustris* was incorporated into these data (Appendix 3). Three most par-



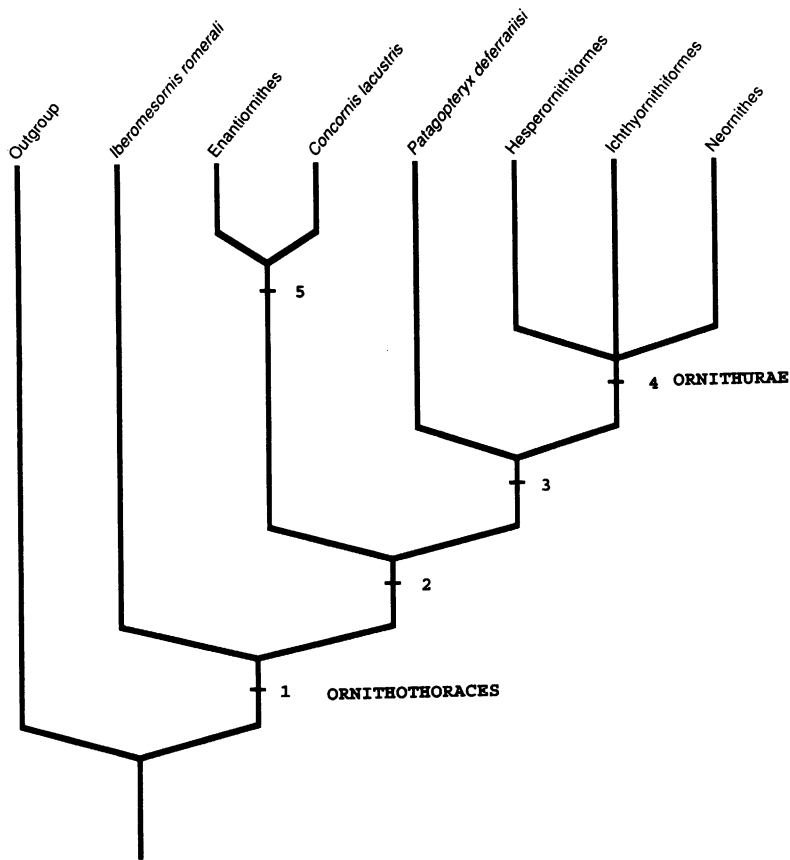


Fig. 14. Strict consensus cladogram (consistency index 0.84; retention index 0.87; length 101) illustrating the phylogenetic relationships of *Concornis lacustris* to other Mesozoic taxa (see Appendix 2 for list of characters). Characters diagnosing different nodes are: **Node 1**, Ornithothoraces: 13, 14, 19, 24, 28, 32\*, 34, 40. **Node 2**: 1\*, 2\*, 3\*, 5\*, 8\*, 16\*, 17, 18, 22\*, 25, 26\*, 27\*, 30\*, 31\*, 36\*, 37, 38, 39\*, 41\*, 42\*, 43\*, 46\*, 49\*, 55\*, 57\*, 58\*, 60, 64\*, 65, 68\*. **Node 3**: 10\*, 11\*, 29, 33, 48, 50, 52\*, 53\*, 59, 62, 66, 71. **Node 4**, Ornithurae: 4\*, 6\*, 7\*, 9, 12, 15, 20\*, 21, 23, 35, 44, 45, 47\*, 51, 54\*, 56, 58\*, 61, 63, 67\*, 69, 70. **Node 5**: 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82\*, 83, 84. Asterisked characters have an ambiguous optimization.

simonious cladograms (consistency index 0.83; length 12) resulted from this analysis, and their strict consensus tree is illustrated in figure 15. The three fundamental cladograms depict the alternative relations among the Argentine *Lectavis bretincola* and *Yungavolucris brevipedalis*, and a clade formed by *C. lacustris* and the Avisauridae. The sister group relationship of the latter two taxa is supported unambiguously in these three cladograms by the strong transverse convexity of the dorsal surface of the midshaft of metatarsal III (see Appendix 3, character 8).

Our phylogenetic study indicates that *Concornis lacustris* shares a large number of synapomorphies with other enantiornithine birds (fig. 14). Though restricted to tarsometatarsal data, this study regards *C. lacustris* as the sister taxon of the Avisauridae (fig. 15), an enantiornithine clade known from the Late Cretaceous of Argentina and the United States (Chiappe, 1993). The common presence of numerous derived characters, along with its nested position within defined enantiornithine taxa, heavily supports the identification of *C. lacustris* as an enantiornithine species.



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## APPENDIX 1

## Anatomical abbreviations used in figures 2–12

ALD	alular digit	HUM	humerus
CAR	carina	HYP	hypocleidium
CDO	dorsal cotyle of the ulna	ISC	ischium
CIR	circular depression of proximal humerus	IDO	dorsal process of ischium
CFI	fibular crest	LAG	central groove of the vertebral centrum
CME	medial condyle of the femur	LCR	lateral crests of the sternal carina
COM	costal margin of the coracoid	LGR	ligamental groove of the humerus
COR	coracoid	LPR	lateral process of the sternum
CPR	caudal projection of the lateral margin of the femur	MAC	major metacarpal
CVE	caudal vertebrae	MAD	major digit of manus
CVS	ventral cotyle of the ulna	MIC	minor metacarpal
DEP	depression of bicipital area of the humerus	MID	minor digit of manus
DVE	dorsal vertebrae	MCO	medial condyle of tibiotarsus
FAC	furcular facet of scapula	MPR	medial process of the sternum
FCO	costal fossae (parapophysis)	OPR	obturator process of ischium
FEM	femur	PEC	pectoral crest
FEH	femoral head	PUB	pubis
FOR	foramina	RAD	radius
FUR	furcula	RIB	ribs
		SCA	scapula

SNV supracoracoid nerve foramen  
 STR sternum  
 SVL groove separating the CDO and CVE  
 SYV synsacral vertebrae

TIT tibiotarsus  
 TMT tarsometatarsus  
 TUB bicipital tubercle of ulna  
 ULN ulna

## APPENDIX 2

List of characters and data matrix (0, primitive; 1, 2, derived; ?, missing or uncertain; N, not comparable) used in the parsimony analysis. The theropod dinosaurs *Dromaeosauridae* and *Archaeopteryx lithographica* are used as outgroups.

1. Fusion of premaxillae in adults: absent (0), present (1).

2. Maxillary process of premaxilla forming most of the facial margin: absent (0), present (1).

3. Frontal process of premaxilla extends caudally to the level of lacrimals: absent (0), present (1).

4. Premaxillary teeth absent: absent (0), present (1).

5. Osseous external naris considerably larger than antorbital fenestra: absent (0), present (1).

6. Loss of maxillary fenestrae: absent (0), present (1).

7. Cranial jugal border very close to the caudal margin of the osseous external naris: absent (0), present (1).

8. Ectopterygoid: present (0), absent (1).

9. Orbital process of quadrate sharp and pointed: absent (0), present (1).

10. Quadratojugal cotyle in lateral face of mandibular process of quadrate: absent (0), present (1).

11. Quadrate pneumaticity: absent (0), present (1).

12. Articular pneumaticity: absent (0), present (1).

13. Prominent ventral processes on cervicodorsal vertebrae: absent (0), present (1).

14. Dorsal vertebral count more (0) or less (1) than 13–14 elements.

15. Dorsal vertebral count more (0) or less (1) than 11 elements.

16. Wide vertebral foramen in dorsal series, with ratio between the vertical diameter of the vertebral foramen and the articular cranial facet greater than 0.40: absent (0), present (1).

17. Synsacrum with less (0) or more (1) than 8 vertebrae.

18. Heterocoelous cervical vertebrae: absent (0), present (1).

19. Pygostyle: absent (0), present (1).

20. Caudal vertebral count more (0) or less (1) than 15 elements.

21. Ossified uncinat processes: absent (0), present (1).

22. Broad, firm articulation between the coracoid and scapula: present (1), absent (0).

23. Procoracoid process: absent (0), present (1).

24. Strutlike coracoid: absent (0), present (1).

25. Scapulocoracoid articulation well below the shoulder end of coracoid: absent (0), present (1).

26. Supracoracoid nerve foramen (incision) located in the medial margin of coracoid: absent (0), present (1).

27. Coracoid forming a sharp angle with the scapula at the level of the glenoid cavity: absent (0), present (1).

28. Scapula with sharp caudal end: absent (0), present (1).

29. Sagittally curved scapular shaft: absent (0), present (1).

30. Large, rectangular ossified shaped sternum: absent (0), present (1).

31. Ossified keel of sternum: absent (0), present (1).

32. U-shaped furcula, interclavicular angle smaller than 90°: absent (0), present (1).

33. Proximal and distal ends of humerus expanded roughly in the same plane: absent (0), present (1).

34. Humerus longer (0) or shorter than or nearly equivalent (1) to ulna.

35. Craniocaudally convex, spherical head of humerus: absent (0), present (1).

36. Ventral tubercle of humerus projecting distinctly caudally, separated from the humeral head by a deep capital incision: absent (0), present (1).

37. Humerus with well-developed transverse ligamental groove: absent (0), present (1).

38. Distal condyles of humerus located mainly on cranial aspect: absent (0), present (1).

39. Dorsal condyle of ulna developed as a semilunar ridge: absent (0), present (1).

40. Shaft of radius considerably thinner than that of ulna, ratio of diameter of radius to ulna smaller than 0.70: absent (0), present (1).

41. Carpometacarpus: absent (0), present (1).

42. Extensor process on carpometacarpus: absent (0), present (1).

43. Fused pelvic elements: absent (0), present (1).

44. Acetabulum small, ratio of acetabulum to ilium less than or equal to 0.11: absent (0), present (1).
45. Ilium-ischium-pubis more-or-less parallel: absent (0), present (1).
46. Pelvis with prominent antitrochanter: absent (0), present (1).
47. Iliac brevis fossa: present (0), absent (1).
48. Iliac fossa for *M. cuppedicus* (= *M. iliofemorialis internus*): present (0), absent (1).
49. Ischiadic terminal processes not in contact: absent (0), present (1).
50. Apices of pubis not in contact: absent (0), present (1).
51. Shaft of pubis laterally compressed throughout its length: absent (0), present (1).
52. Pubic foot: present (0), absent (1).
53. Retroverted pubis, separated from the main synsacral axis by an angle smaller than 45°: absent (0), present (1).
54. Femur with distinct fossa for capital ligament: absent (0), present (1).
55. Trochanteric crest of femur: absent (0), present (1).
56. Femur with deep patellar groove: absent (0), present (1).
57. Popliteal fossa of femur bounded distally by a transverse ridge: absent (0), present (1).
58. Tibiofibular crest in the lateral condyle of femur: absent (0), poorly developed (1), prominent (2).
59. Posterior trochanter of femur: present (0), absent (1).
60. Complete fusion of calcaneum, astragalus, and tibia: absent (0), present (1).
61. Cranial cnemial crest of tibiotarsus: absent (0), present (1).
62. Extensor canal on tibiotarsus: absent (0), present (1).
63. Ilioibularis tubercle of fibula caudolaterally or caudally directed: absent (0), present (1).
64. Fibula greatly reduced in length: absent (0), present (1).
65. Free distal tarsals in adults: absent (0), present (1).

66. Distal tarsals and metatarsals fused completely to form a tarsometatarsus: absent (0), present (1).
67. Metatarsal fusion starting distally: absent (0), present (1).
68. Metatarsal V: present (0), absent (1).
69. Proximal end of metatarsal III plantarily displaced with respect to metatarsals II and IV: absent (0), present (1).
70. Intercondylar eminence of tarsometatarsus well developed: absent (0), present (1).
71. Distal vascular foramen of tarsometatarsus: absent (0), present (1).
72. Prominent bicipital crest of humerus, cranioventrally projecting: absent (0), present (1).
73. Convex external cotyle of ulna, separated from the olecranon by a groove: absent (0), present (1).
74. Convex lateral margin of coracoid: absent (0), present (1).
75. Supracoracoid nerve foramen of coracoid opening into an elongate furrow medially and separated from the medial margin by a thick bony bar: absent (0), present (1).
76. Strong lateral grooves on the bodies of dorsal vertebrae: absent (0), present (1).
77. Costal fossae (parapophyses) located in the central part of the bodies of dorsal vertebrae: absent (0), present (1).
78. Caudal projection of the lateral border of the distal end of femur: absent (0), present (1).
79. Wide and bulbous medial condyle of tibiotarsus: absent (0), present (1).
80. Metatarsal IV significantly smaller than metatarsals II and III: absent (0), present (1).
81. Trochlea metatarsal II broader than the trochlea of metatarsals III and IV: absent (0), present (1).
82. Round articular surface in the proximal end of tibiotarsus: absent (0), present (1).
83. Lateral face of the humeral bicipital crest with a small fossa for muscular attachment: absent (0), present (1).
84. Furcula laterally excavated: absent (0), present (1).

TAXA	CHARACTERS															
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	84
<i>Dromaeosauridae</i>	00000	00000	00000	00000	00000	00000	07000	00000	00000	00000	00000	00000	00000	00000	00000	0000?
<i>Archaeopteryx</i>	00000	00000	07000	?0000	00000	0000?	0000?	00000	00000	000?0	000?0	07000	00?00	00000	00?00	?0?00
<i>Iberomesornis</i>	?????	?????	??110	?0010	0??10	??10?	?1?10	?00?1	?????	070??	0???0	0???0	00?00	00?0?	00??0	010?
<i>Enantiornithes</i>	11101	??10?	?01??	1111?	01011	11101	11010	11111	1110?	110??	????1	01101	00?11	00100	01111	11111
<i>Patagopteryx</i>	?????	?????	10110	111??	01011	1111?	??100	??1?1	?1000	10111	011??	01?11	01011	?1000	10000	00000
<i>Hesperornithiformes</i>	11111	11111	01111	11111	11111	10011	0NN01	00100	??111	11111	11111	11211	11111	11111	10000	00000
<i>Ichthyornithiformes</i>	1?1??	????1	11111	11011	?1111	11111	11111	11111	11111	11111	11111	11211	11111	11211	1?111	10000
<i>Neornithes</i>	11111	11111	11111	11111	11111	11111	11111	11111	11111	11111	11111	11211	11111	11111	10000	00000
<i>Concornis</i>	?????	?????	?????	?????	01011	11?01	11010	111?1	?????	??110	07?0?	0???1	0??11	00?00	01111	11111

APPENDIX 3

List of characters and data matrix (0, primitive; 1, derived; ?, missing or uncertain) used in the cladistic analysis of tarsometatarsal characters (after Chiappe, 1993; see Varricchio and Chiappe, 1995, for *Avisaurus gloriae*). *Mononykus olecranus* (Perle et al., 1993, 1994) and *Patagopteryx deferrariisi* (Alvarenga and Bonaparte, 1992) are used as outgroups.

TAXA	CHARACTERS	
<i>Mononykus olecranus</i>	00000	00000
<i>Patagopteryx deferrariisi</i>	00100	00000
<hr/>		
<i>Yungavolucris brevipedalis</i>	1001?	?0001
<i>Lectavis bretincola</i>	1?11?	?00??
<i>Avisaurus archibaldi</i>	1111?	11111
<i>Soroavisaurus australis</i>	11111	01111
<i>Neuquenornis volans</i>	111?1	??101
<i>Avisaurus gloriae</i>	1101?	11111
<i>Concornis lacustris</i>	1???0	00101

- 1. Metatarsal IV: large (0); considerably smaller (1).
- 2. Medial rim of the trochlea of metatarsal III with a strong plantar projection: absent (0); present (1).
- 3. Plantar surface of tarsometatarsus excavated: absent (0); present (1).
- 4. Tubercle on the dorsal face of metatarsal II: absent (0); present (1).
- 5. J-shaped metatarsal I: absent (0); present (1).
- 6. Trochlea of metatarsal IV medially concave: absent (0); present (1).
- 7. Proximal articular surface dorsally inclined: absent (0); present (1).

- 8. Strong transverse convexity of the dorsal surface of the midshaft of metatarsal III: absent (0); present (1).
- 9. Distal end of metatarsal II strongly curved medially: absent (0); present (1).
- 10. Trochlea of metatarsal II broader than the trochleae of metatarsal III and IV: absent (0); present (1).

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