

A NEW BIRD FROM THE EARLY CRETACEOUS OF LAS HOYAS, SPAIN, AND THE EARLY RADIATION OF BIRDS

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ABSTRACT. *Concornis lacustris* gen. et sp. nov. is a new fossil bird from the Early Cretaceous (Barremian) of Las Hoyas, Cuenca, Spain. *Concornis* is roughly twice the size of *Iberomesornis*, the first bird described from Las Hoyas, but it is not the adult of the latter. *Concornis* is more derived than *Iberomesornis*, with a true tibiotarsus and a fan-like distal metatarsal zone with distinct trochlear structures. Only the proximal metatarsal region is fused. The sternum has a slight but conspicuous posterior median keel. The phalangeal structure of the manus is like that of extant birds. The metacarpus is not distally fused. *Concornis* is one of the closer known sister taxa of the Ornithurae. This sister group plus *Iberomesornis* form the clade Euornithes, diagnosed by a strut-like coracoid, a derived avian furcula and a pygostyle. The more probable topological structure within the Euornithes is (*Iberomesornis* + (*Concornis* + (*Ambiortus* + (Enantiornithes + Ornithurae)))). There is increasing evidence for an adaptative radiation of birds during the Early Cretaceous. After feathers appeared, the first stage of the radiation was the rapid evolution of active flight structures. Later transformations probably involved refinement of the flight apparatus (tail reduction, development of the sternum) that altered the centres of gravity and balance. The synsacrum evolved as the maximum tail reduction was reached, and can be envisaged as a new flight functional unit. Based on a 'legginess index' in extant birds, we suggest an aquatic habitat for Las Hoyas birds.

THE Early Cretaceous (Barremian) outcrop of Las Hoyas (Cuenca Province, Spain) has yielded a diversified flora and fauna (Sanz *et al.* 1988) including a new bird (Sanz, Bonaparte and Lacasa-Ruiz 1988) that has been designated as the genus *Iberomesornis* (Sanz and Bonaparte, 1992). A second avian specimen has been found in Las Hoyas, which could become one of the most significant Early Cretaceous outcrops for primitive birds.

The record of Early Cretaceous birds is poor. Isolated feathers are known from several localities in Eurasia and Australia (Ferrer-Condal 1954; Molnar 1980; Lacasa-Ruiz 1985), but many Early Cretaceous osteological avian fossils are fragmentary and difficult to interpret, such as the material from Cornet, Romania (Kessler and Jurcsak 1984). *Enaliornis* (Seeley 1876) from the English Albian is considered to be a hesperornithiform (Martin and Tate 1976; Feduccia 1980). *Ambiortus* (Kurochkin 1985a, 1985b) is a Mongolian bird, very similar in age to *Iberomesornis* and the new Las Hoyas bird, but very derived, and Kurochkin considers it a member of the Carinatae (see also Olson 1985; Cracraft 1986). *Gansus* Hou and Liu, 1984, from the Chinese Lower Cretaceous is poorly represented, although a new Lower Cretaceous avian skeleton has been recently reported from China (Rao and Sereno 1990).

The Upper Cretaceous bird record from Argentina can provide significant information about the early radiation of birds. A new articulated enantiornithine bird specimen has been recently reported (Chiappe and Calvo 1989; Chiappe 1991).

The most complete Early Cretaceous birds to date have come from Las Hoyas. The main goal of the present paper is to assess the phylogenetic relationships of both Spanish avian forms, and to evaluate the new information that fills the structural and functional gaps between Late Jurassic and Upper Cretaceous birds.

SYSTEMATIC PALAEOLOGY

Class AVES

Subclass ARCHAORNITHES

Content. *Archaeopteryx lithographica* Meyer, 1861 from the Tithonian of Germany

Diagnosis. Derived characters with respect to non-avian theropods: Feathers present. Quadratojugal-squamosal articulation absent. Postorbital greatly reduced. Calcaneo-astragular fusion. No scapulo-coracoidal fusion. Combination of the following primitive characters: Teeth present. Squamosal without long zygomatic processes. Nasal process of the premaxilla extending posteriorly to level of lacrimals. Free caudal vertebrae: pygostyle absent. Coracoid not strut-like. Furcula with broad clavicular angle (90°) and without hypocleidium. No calcified sternum. Gastralia present. Unfused pelvic elements. Humeral pneumatic fossa absent. Humeral head not well defined. Humeral brachial depression absent. External cnemial crest absent. Metatarsals not completely fused.

Subclass EUORNITHES nov.

Content. Group that comprises the most recent common ancestor of *Iberomesornis* and Ornithurae (*sensu* Gauthier 1986 and Cracraft 1986) and all of its descendants. All other taxa proposed as avian subclasses (Neornithes, Enantiornithes, etc.) are included within Euornithes at a lower taxonomic level.

Diagnosis. The following derived characters with respect to Archaeornithes: Reduced cervical neuropophyses. Fused cervical ribs. Eleven or fewer dorsal vertebrae. Free caudal vertebrae, and pygostyle. Gastralia absent. Strut-like coracoid. Furcula with a developed hypocleidium and a lower clavicular angle (60°). Ulnar length exceeding humeral length.

Family indet.

Genus CONCORNIS gen. nov.

Type species. *C. lacustris* sp. nov.

Diagnosis. As for the species.

Distribution. Upper Neocomian, Barremian; Province of Cuenca, Spain.

Derivation of name. After the Latin term for Cuenca province (*Conca*) + 'ornis' (Gr.), bird.

Concornis lacustris sp. nov.

Text-figs 1-8

Holotype. Specimen LH2814, housed in the Unidad de Paleontología, Universidad Autónoma de Madrid, Spain. The specimen comprises most of the postcranial skeleton, including wing, hind limbs, and coracoids, furcula, and sternum.

Type locality. Las Hoyas, La Cierva township, Province of Cuenca, Spain.

Diagnosis. *Concornis lacustris* is characterized by two autapomorphic traits: metacarpals II and III closely joined distally but not yet fused, and sternal keel extending just in the posterior region. Also by the following combination of characters: Ulnar shaft with large diameter, arched, without scars for feather attachment. Metacarpus elongated, with reduced slitlike intermetacarpal space. Phalangeal structure of hand reduced, with formula ?/2/1/-/-. No manual unguals. Manual



TEXT-FIG. 1. *Concornis lacustris* gen. et sp. nov. LH2814. Las Hoyas; Early Cretaceous. A, hand acropodial skeleton. F, femur; MC, metacarpus; MT, metatarsus; T, tibiotarsus; U, ulna. Scale in mm.

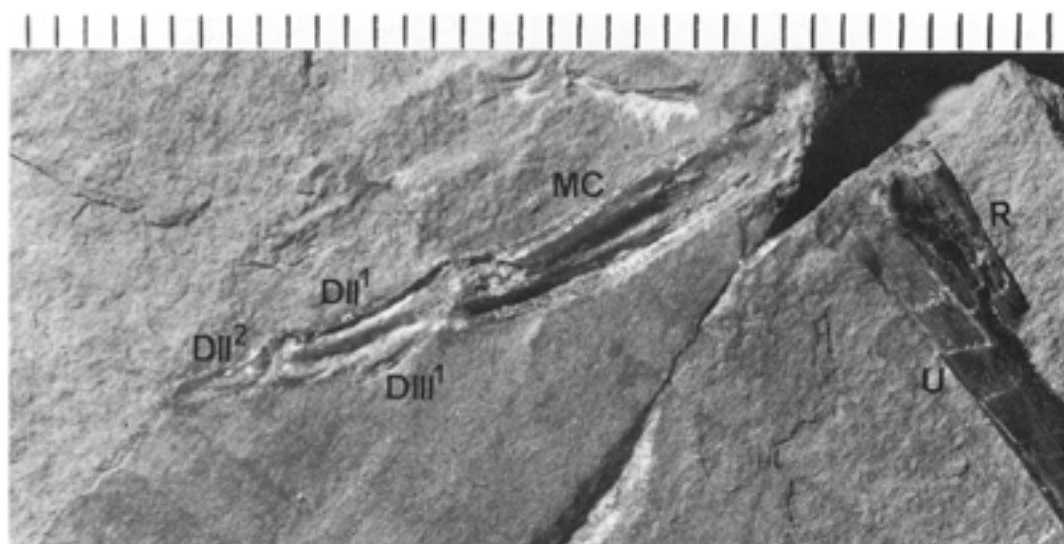
phalanges similar to those of extant birds. Tibiotarsus present. No true tarsometatarsus: metatarsals being fused proximally only. Fan-like metatarsal region, with trochlear structures. Pedal unguals with reduced flexor tubercle. Pedal phalangeal formula 2/3/?/5/-. Strut-like coracoid. Furcula with a styloid hypocleidium and clavicular angle of about 60°. Thoracic sternal process developed, with an anterior projection. Abdominal sternal process with smaller diameter

than those of the thoracic or xiphial ones. Lateral and medial sternal notches similarly developed in their anterior region.

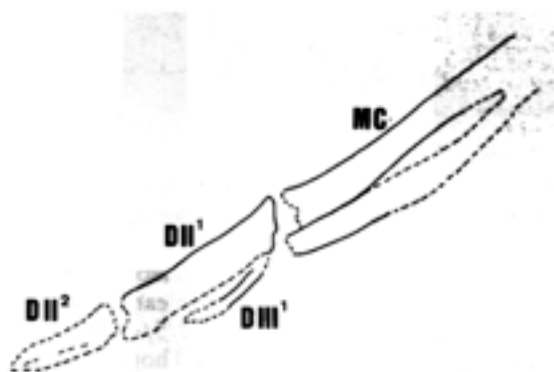
Derivation of name. 'lacustris', Latin, referring to its possible lacustrine habitat.

Description. Fewer skeletal elements are preserved in *Concornis* than in *Iberomesornis*, but there is osteological evidence of the hand (Text-figs 1-3), and in ultraviolet light, feathers can be seen connected to the wing skeleton (Text-fig. 4). The specimen is preserved in limestone and consists of a main slab with an associated small piece that contains the furcula, both coracoids, and the sternum (Text-figs 7-8). Both pieces, the main slab and the associated piece, belong to the same limestone block, which is about 160 mm long. The original (as preserved) distance between the proximal part of the ulna and the thoracic sternal process is about 20 mm. So both remains belong to the same individual.

Several appendicular bones are present in the main slab (Text-figs 1-6). There is no evidence of the humerus. The ulna has a broad arched shaft, with proximal and distal ends damaged. There is no evidence of ulnar scars



TEXT-FIG. 2. *Concornis lacustris* gen. et sp. nov. LH2814. Las Hoyas; Early Cretaceous. D II¹, first phalanx of the hand, second digit. D II², second phalanx of the hand, second digit. D III¹, single phalanx of the hand, third digit. MC, metacarpus; R, radius fragment; U, ulna. Scale in mm.



TEXT-FIG. 3. *Concornis lacustris* gen. et sp. nov., LH2814. Las Hoyas; Early Cretaceous. Schematic interpretation of the skeleton of the hand. Abbreviation as in Text-fig. 2. Scale bar = 5 mm.



TEXT-FIG. 4. *Concornis lacustris* gen. et sp. nov. LH2814. Las Hoyas; Early Cretaceous. Ultraviolet fluorescence induced photograph. $\times 1.9$.

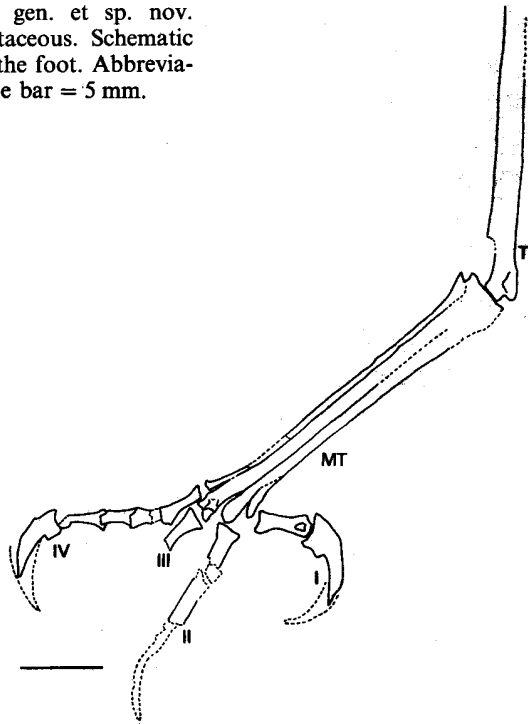
for feather attachment. A small fragment of the radius allows an estimate of its shaft diameter as half that of the ulna.

The skeletal structure of the hand is visible except for the carpus and proximal region of the metacarpus. The metacarpus is elongated, with a narrow space between both metacarpals. It is not clear whether the metacarpals are fused proximally. Metacarpal III seems to be as long as Mc II, because their distal ends are situated at the same level. The metacarpals are closely joined, but not distally fused, indicating that there is no true carpometacarpus. The phalangeal elements are reduced in number, with no trace of the innermost digit (I). The middle finger (II) seems to have two phalanges. The proximal one is relatively flat and roughly rectangular in



TEXT-FIG. 5. *Concornis lacustris* gen. et sp. nov. LH2814. Las Hoyas; Early Cretaceous. Mt, metatarsus; T, tibiotarsus. I-IV, foot digits. Scale in mm.

TEXT-FIG. 6. *Concornis lacustris* gen. et sp. nov. LH2814. Las Hoyas; Early Cretaceous. Schematic interpretation of the skeleton of the foot. Abbreviation as in Text-figure 5. Scale bar = 5 mm.



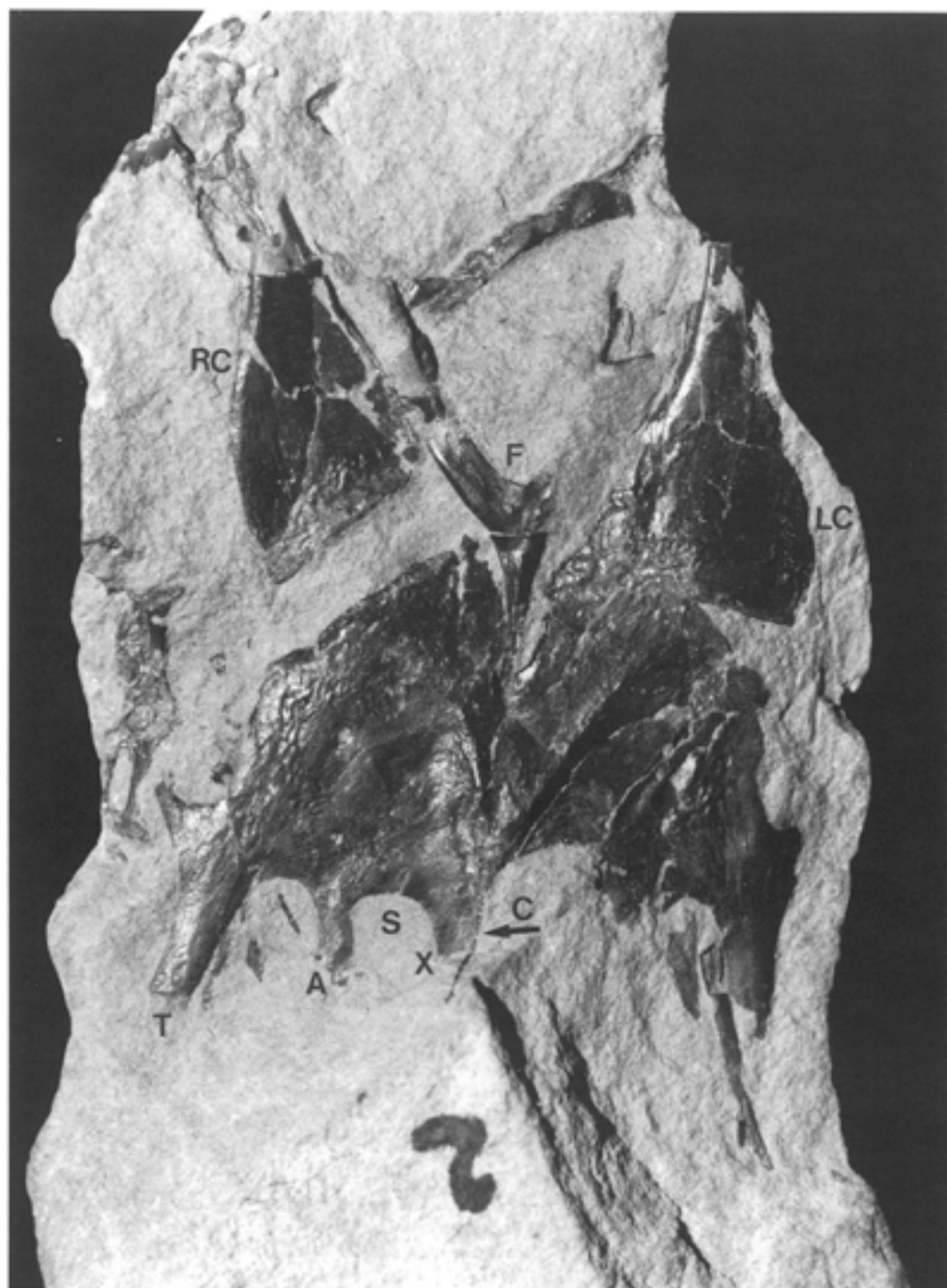
shape, with a longitudinal ridge. The distal phalanx is visible in outline from a mould in the limestone matrix, and is triangular in shape. Another small mould in the matrix, in front of the corresponding metacarpal, seems to indicate the presence of a splint-like phalanx, the only one of the outer digit (III). Therefore the phalangeal formula for the hand of *Concornis* is derived (?/2/1/-/-), as in extant birds. Neither distal phalanx is an unguis.

The femur is damaged. Its shaft is pneumatic, like the rest of the preserved bones. The ulna is clearly more robust than the femur. The tibia has a longitudinal ridge in its proximal region that could be interpreted as the *crista fibularis*. If so, the tibia is the right element, seen in anteromedial view.

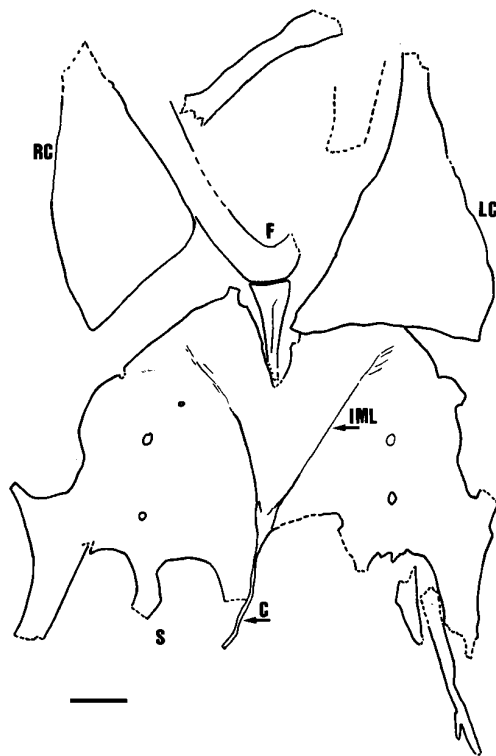
One of the most significant traits of *Concornis* is the presence of a tibiotarsus. The distal articular surface of the tibia has two condyles that lie on the proximal articular surface of the metatarsus. There is no evidence of the distal tarsals, and there is no true tarsometatarsus. The metatarsus is fused only proximally, for about 10 per cent of the length of the metatarsal structure. Along their remaining lengths the metatarsal elements are closely joined along their shafts, but they are not fused. Like the tibia, the metatarsus is seen in anteromedial view. The first metatarsal (Mt I) is reduced and its distal region is reversed. Mt II and Mt III have broader shafts; the latter is the longer. Distally, Mt II and Mt IV separate from Mt III, forming a fan-like structure like that of extant birds. This trait occurs in other Early Cretaceous birds like *Gansus* (Hou and Liu 1984), but this Chinese genus has a true tarsometatarsus. The distal articular area of Mt III in *Concornis* is a trochlear surface.

The phalangeal structure of the foot is well preserved except for the third digit. Digit I has two phalanges, of which the unguis is clearly larger. Digit II has three phalanges, of which the second is the longest. Digit IV has five elements, of which the unguis is the longest. The phalangeal formula of the foot is therefore 2/3/?/5/-. All the pedal unguis are only slightly recurved, like those of *Archaeopteryx*, with the flexor tubercle reduced (Text-figs 5-6).

Both coracoids appear broken, with a fracture below their heads (Text-figs 7-8). The right coracoid is separated from the sternal outline, but the left remains in contact with the sternum. The coracoidal morphology of *Concornis* is derived and strut-like, like that of *Iberomesornis* but more robust. However it is probably not significantly more robust taking into account the deformation generated by the sediment compression, and the fact that *Concornis* is about twice the linear dimensions of *Iberomesornis*. The coracoidal scapulo-glenoidal region is very damaged and it is not possible to check some of the most characteristic enantiornithine traits.



TEXT-FIG. 7. *Concornis lacustris* gen. et sp. nov. LH2814, Las Hoyas; Early Cretaceous. A, abdominal process. C, sternal carina; F, furcula; LC, left coracoid; RC, right coracoid; S, sternum; T, thoracic process; X, xiphial process. $\times 5$.



TEXT-FIG. 8. *Concornis lacustris* gen. et sp. nov. LH2814. Las Hoyas; Early Cretaceous. Schematic interpretation of the pectoral region. Abbreviations as in Text-figure 7 and IML, intermuscular line. Scale bar = 2 mm.

TABLE 1. Measurements (mm) and indices of the appendicular skeleton of the two bird genera from Las Hoyas.

	<i>Iberomesornis</i> (LH022R)	<i>Concornis</i> (LH2814)
Femur length	15.0	c. 25.0
Tibia length	20.0	c. 31.0
Metatarsus length	12.0	22.0
Length ratio tibia/femur	1.3	1.2
Length ratio tibia/metatarsus	1.6	1.4
Length ratio femur/metatarsus	1.2	1.1

Nevertheless, the lack of a prominent sterno-coracoidal process (Walker 1981) and a convex lateral outline of the coracoid (Chiappe and Calvo 1989) seem to be traits similar to those of enantiornithes.

The furcula of *Concornis* is also similar to that of *Iberomesornis*. The interclavicular angle is about 60°. The hypocleidium is styloid, with a conspicuous sagittal crest in *Concornis*. The hypocleidium lies on the sternal surface, and seems to reach its midregion.

The most striking trait of the sternum is its small surface area compared with those of extant birds. Its anteroposterior development is about the same length as the coracoid (see Table 2). Both coracoidal margins are large, with an arched outline. The costal margin should appear caudal to the coracoidal margin, but there is no evidence of ribs or costal structures. This region is reduced to a small notch delimited posteriorly by an acute anterior projection of the thoracic lateral process. The latter has a large caudal process, but the abdominal process is more slender. The lateral and medial sternal notches are about equally developed anteriorly. The xiphial area is more robust than the abdominal process. The sternal surface is flat and clearly

TABLE 2. Additional measurements (mm) of *Concornis* (LH2814).

	Ulna
Length c. 32.0, diameter 2.5.	
	Metacarpus
Length c. 15.0.	
	Coracoids
Length c. 16.0. Width of the sternal margin: right coracoid c. 6.0, left coracoid c. 7.0.	
	Sternum
Maximum width 18.0, maximum visible anteroposterior length 12.0.	

distorted by preservation. On the sternal surface, two oblique ridges meet at the basal region of the xiphisternal process. From this meeting point, a slender keel (carina) extends beyond the exposed zone of the xiphial area. A section of this thin carina can be seen in the adjacent limestone matrix (Text-fig. 7). A similar structural condition to that of *Concornis* can be seen in the ventral posterior sternal region of the extant Old World common quail (*Coturnix*). Since the sternum is flattened by compression it is difficult to evaluate the actual extension of the keel, but this structure apparently extended only in the posterior area of the sternum. A series of three foramina perforate the sternal surface at the level of the abdominal process. The central one is largest, and it occurs in a sternal zone similar to that of some oviraptorosaur dinosaurs (Barsbold 1983). It is difficult to compare the sterna of the two Las Hoyas birds because they are exposed differently, but it does seem that the costal margin is much larger in *Iberomesornis*. The sternum of *Concornis* generally resembles those of some extant birds, such as Galliformes (Ghetie *et al.* 1981).

The most striking difference between *Iberomesornis* and *Concornis* is size (Table 1): *Concornis* is almost twice as large, and discrete characters suggest that we are dealing with separate taxa rather than ontogenetic stages (see below).

One of the unexpected surprises in the study of *Concornis* was the discovery of traces of feathers under ultraviolet light (Text-fig. 4). There is little possibility of a precise description, but the feathers seem to have asymmetric vanes and belong to the hand. They may therefore be primary remiges.

CHARACTER ANALYSIS

Like Ostrom (1976), Padian (1985), Gauthier (1986), and Cracraft (1986), we have chosen the theropod dinosaurs as the closest avian outgroup (see Table 3). In all cases the primitive condition is coded with a zero (0).

1. Diameter of the ulnar shaft equal to or slightly larger than that of the radius (0); much greater (1).
2. Shape of ulnar shaft proximally straight (0); proximally arched (1).
3. Metacarpal structure. Mt II and Mt III with parallel shafts and a split-like intermetacarpal space (0); Mt II and Mt III closely joined distally but not yet fused (1). This is the postulated intermediate character state for *Concornis*. The hand is unknown in Hesperornithiformes, but a similar condition could be present in

TABLE 3. Data matrix. See text for character definition. ? indicates missing data. The primitive state of character 11 in *Ambiortus* is uncertain.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Non-avian Theropods	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Archaeopteryx</i>	0	1	0	0	0	0	0	0	1	0	0	?	0	0
<i>Iberomesornis</i>	1	1	?	?	1	0	0	0	1	1	1	?	0	1
<i>Concornis</i>	1	1	1	1	1	1	1	0	1	1	1	1	0	?
Hesperornithiformes	0	0	?	?	0	1	1	1	1	1	1	0	1	1
Carinatae	1	1	2	1	1	1	1	1	1	1	1	2	1	1
<i>Ambiortus</i>	?	?	2	0	?	?	?	?	?	1	?	2	?	?
Enantiornithes	1	1	2	?	1	1	1	0	1	1	?	2	?	1

Baptornis (Martin and Tate 1976). Ostrom (1976) predicted a similar intermediate metacarpal character state between those of *Archaeopteryx* and Ornithurae. Finally, we consider a second state of derivation (2) in which the shaft of Mt III is separate from that of Mt II to form a broad intermetacarpal space, but both metacarpals fuse distally into a true carpometacarpus.

4. Phalangeal structure of the hand. Phalangeal formula of the hand is 2/3/4/-/-, with elongated phalanges and presence of unguals (0). Digit II with two phalanges, digit III with one phalanx; phalanges characteristically rectangular or triangular in shape, without unguals (1).

5. Diameter of the femoral shaft greater than that of the ulnar shaft (0); ulnar shaft equal to or greater than femur in diameter (1).

6. Tibiotarsus. Astragalus and calcaneum not fused to the distal region of the tibia, with no condylar structures (0); true tibiotarsus with distinct condylar structures (1).

7. Distal metatarsal region. Not expanded distally, without trochlear structures (0); fan-like structure at the distal end, presence of trochlear structure (1).

8. Metatarsal fusion. Theropods generally lack fused metatarsals. *Elmisaurus* (Osmólska 1981) has a proximally fused metatarsus. The family Avisauridae originally considered non-avian theropods (Brett-Surman and Paul 1985), have been reinterpreted as true birds of the Order Enantiornithes (Chiappe and Calvo 1989). In some cases, as in *Ceratosaurus* (Gilmore 1920), the fusion seems to be teratological. In *Archaeopteryx*, the smaller specimens seem to have no metatarsal fusion, the largest one has partly fused metatarsals (Ostrom 1976; Wellnhofer 1988a, 1988b), so the character changes ontogenetically. We thus define character polarity as follows: no metatarsal fusion, or only proximal fusion (0); fused (true tarsometatarsus) (1).

9. Reversal of the first digit of foot. Metatarsal I placed nearly at the midpoint of Mt III (Tarsitano 1985) (0); Mt I placed distally (1).

10. Coracoids. Not strut-like (0); avian strut-like coracoid (1).

11. Furcula. Most theropods lack an ossified furcula. Some oviraptorosaurs have a furcular structure like that of *Archaeopteryx* (Barsbold 1983); we suggest the following polarity of character states: clavicular angle broad, about 90°, without a hypocleidium (0); clavicular angle of 60°, with a distinct hypocleidium (1).

12. Sternum. Several groups of dinosaurs (including Saurischia and Ornithischia) have pairs of sternals without a keel. The sterna of some oviraptorosaurs are sometimes fused with each other (Barsbold, Maryanska and Osmólska 1990), forming a sternal plate even with grooves for the coracoids, but no traces of a keel. The sternum is unknown in *Archaeopteryx* and was probably not ossified. *Iberomesornis* has an ossified sternum, but it is difficult to identify a keel in it (lateral or medial exposure). We think that the thin posterior keel of the sternum of *Concornis* is homologous to that of carinate birds. The two oblique ridges that meet at the beginning of the keel (see description and Text-figs 7–8) could be homologous to the intermuscular lines (*sensu* Howard 1980). If this interpretation is correct, it could mean that the structural relationships between the sternal muscles in *Concornis* would be different from those of extant birds. The small posterior sternal keel in *Concornis* seems to suggest that the evolutionary development of the keel in carinate birds operated posterocranially. In sum we thus define character polarity as follows: sternum without sternal keel (0); sternal keel present only in the posterior area (1); sternal keel present both in anterior and posterior areas (2).

13. Sternal development. Anteroposterior sternal length similar to coracoidal length (0); much greater than coracoidal length (1).

14. Pygostyle absent (0); present (1).

Characters not included in the analysis

Some characters are not obviously homologous, or seem very variable within Ornithurae, so it is difficult to establish their levels of generality.

1. Ulnar scars for feather attachment. These structures seem to be absent in *Archaeopteryx* and in the birds from Las Hoyas. The absence of the trait could be interpreted as primitive, although *Concornis* has developed remiges like those in the more derived ornithurine birds. If this proposal is correct, then the ulnar scars may have evolved later to reinforce the attachment between feathers and wing skeleton, and the trait could be apomorphic at some hierarchical level within Ornithurae. Kurzanov (1987) suggested that *Avimimus* has an ulnar ridge for feather attachment. If he is correct, then the absence of this character in primitive birds could be considered derived, with a reversal in extant birds. Nevertheless, a homology between the ulnar crest of *Avimimus* and the ulnar scars for feather attachment seems very problematic.

2. Size of the unguis on the first pedal digit. In *Archaeopteryx* and in theropods the unguis of digit I is relatively small in comparison to those of the other digits, especially digit III (Ostrom 1974; see measurements of *Archaeopteryx* in Wellnhofer 1974). In *Concornis* the unguis of digit I is the larger of the preserved unguis,

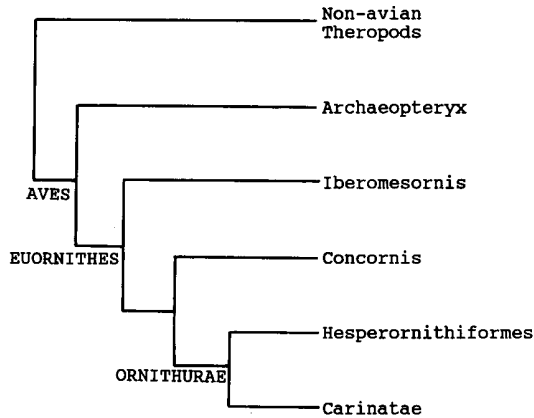
though the ungual of digit III is missing. So, both Las Hoyas specimens are derived with respect to *Archaeopteryx*. Nevertheless the polarity of this character within the Ornithurae is unclear. It seems plesiomorphic both in groups such as Galliformes or Piciformes. It seems derived in Passeriformes (Cracraft 1988).

3. Size and morphology of the first phalanx of the first pedal digit. This is one of the most striking differences between the two Las Hoyas specimens. In *Iberomesornis*, both phalanges of the first digit are similar in length. The first one is very slender, with a large fovea. In *Concornis* (Text-figs 5–6) the ungual is larger than the first phalanx, which is very robust compared to that of *Iberomesornis*. The difference is substantial enough to show that the two Las Hoyas specimens are not ontogenetic stages of the same species. The primitive character state seems to be a slender first phalanx that is as long as, or longer than, the ungual. In small theropods such as *Compsognathus*, *Procompsognathus* and *Coelophysis* the first phalanx is longer than the ungual (Ostrom 1978). The phalanges are similar in length in mid- to large-sized theropods such as *Deinonychus* (Ostrom 1969), *Allosaurus* (Gilmore 1920) and *Gorgosaurus* (Lambe 1917). One could postulate, therefore, that *Iberomesornis* has the primitive condition for this character, and *Concornis* has the derived condition, but the distribution of the trait seems very variable within the Ornithurae.

4. Flexor tubercle of the pedal unguals. The flexor tubercle is small in theropods and in *Archaeopteryx*. This is also true for the Las Hoyas specimens and for some ornithurine taxa such as Galliformes. This primitive character state has been cited by Ostrom (1974) as support for his 'from-the-ground-up' hypothesis for the origin of flight. Other authors, such as Yalden (1985), agree with this functional interpretation, but suggest arboreal habits for *Archaeopteryx* based on the interpretation of the claws of the hand. The flexor tubercle of the pedal unguals seems to be well developed in many extant birds, and could be synapomorphic above the Neognathae (*sensu* Cracraft 1988).

Phylogenetic analysis of the clade Euornithes

The program HENNIG (Version 1.5; Farris 1988) was applied to the first 5 taxa of the matrix of Table 3: *Archaeopteryx*, *Iberomesornis*, *Concornis*, Hesperornithiformes, and Carinatae (*sensu* Cracraft 1986, 1988). The consensus tree is shown in Text-figure 9. In our analysis, the clade Aves

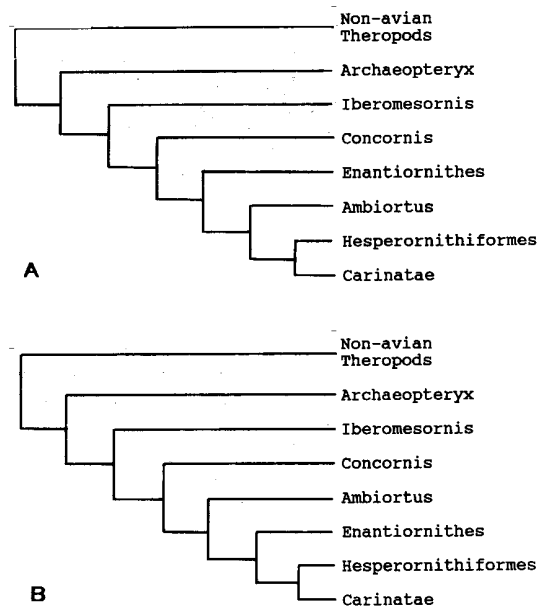


TEXT-FIG. 9. Proposed cladogram for the phylogenetic relationships of some of the best-known early birds. See data matrix in Table 3.

is diagnosed by an arched ulna and the reversal of the first digit of the foot. The sister group for *Archaeopteryx* is a postulated clade for which we propose the name Euornithes. It is mainly characterized by the presence of a strut-like coracoid, a furcula with a well-developed hypocleidium and low clavicular angle, and a pygostyle. Such a combination of evolutionary novelties suggests that euornithine birds had well-developed powers of flight. The new genus *Concornis* is, in this selected ingroup, the closest sister group of Ornithurae. This clade (Ornithurae + *Concornis*) is characterized by a true tibiotarsus and a fan-like metatarsal region with trochlear structures. The presence of a calcified, keeled sternum is synapomorphic at higher hierarchical level above the Carinatae.

In order to compare the two specimens from Las Hoyas within a broader ingroup, two more taxa have been included in a second phylogenetic analysis: *Ambiortus* and the Enantiornithes. The results of an analysis of maximum parsimony are 36 trees with a length of 23 and a consistency index of 0.69. From the 36 trees, 21 placed the Hesperornithiformes as the sister group of all the remaining ingroup except *Archaeopteryx*. Many of the remaining 15 trees placed *Ambiortus* or the Enantiornithes in an unlikely branching. All these resulting trees are very dependent on the great number of missing data for the two taxa mentioned above. From the remaining trees, two are figured in Text-figure 10. The position of *Ambiortus* and Enantiornithes is problematical, but we think that the more probable tree is that which considers Enantiornithes as the sister group of Ornithurae.

TEXT-FIG. 10. Phylogenetic hypotheses of early birds including all the taxa in the cladogram of Text-figure 9, and *Ambiortus* and Enantiornithes. B is the preferred one.



CONCLUSIONS

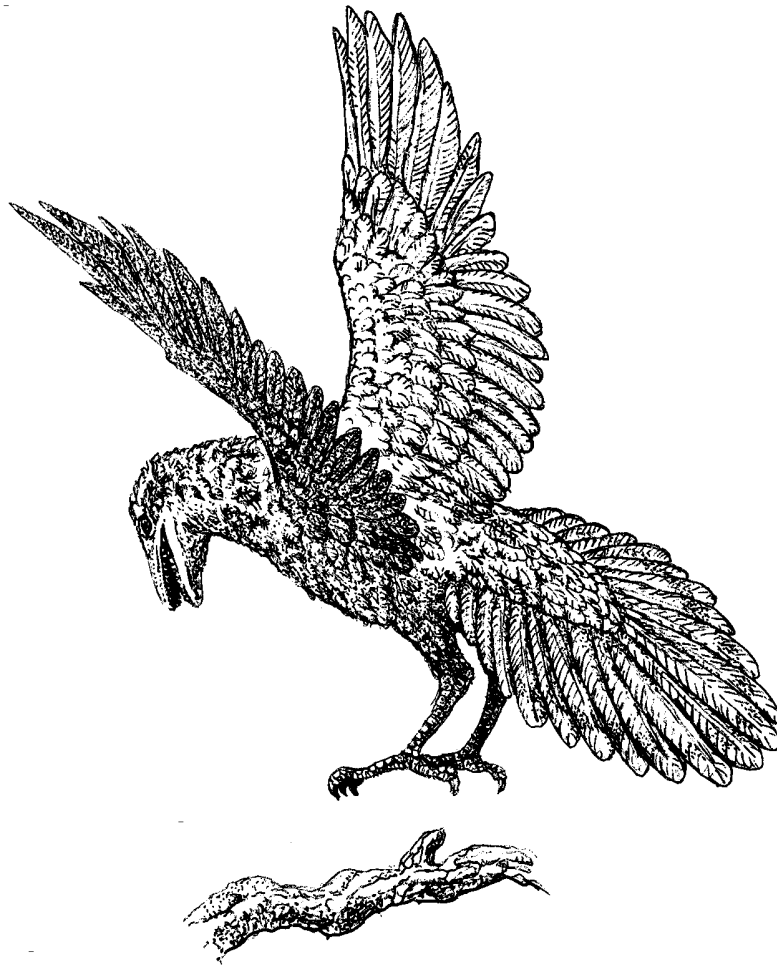
Two bird specimens are now known from Las Hoyas: the partly complete skeleton LH022R, *Iberomesornis romerali* (Sanz *et al.* 1988a; Sanz and Bonaparte 1992), and LH2814, *Concornis lacustris*, gen. et sp. nov. The specimens represent different taxa and are not ontogenetic stages of the same species. Both the degree of slenderness of the coracoids, and of fusion of the metatarsals, could be interpreted as ontogenetic differences. However, there are distinct differences in sternal morphology, in the distal metatarsal region, and in the first phalanx of the first digit of the foot, that do not seem to be ontogenetic. The difference in size between the specimens seems to be significant: *Concornis* is almost twice the size of *Iberomesornis*.

Concornis is more derived than *Iberomesornis*. It has a tibiotarsus and a fan-like metatarsal distal region with trochlear structures, like those of extant birds. In the phylogenetic hypothesis of Text-figure 9, *Concornis* is considered the closest sister-group of the Ornithurae. It is not an ornithurine bird because it lacks a true tarsometatarsus. The phylogenetic hypothesis predicts character states in the metacarpal and manual phalangeal structures in Hesperornithiformes. This group of toothed birds has some trait that could be interpreted as reversals, probably generated by their aquatic habits. Those traits include the diameter and shape of the ulnar shaft, and a sternum without a keel.

The evidence of Early Cretaceous birds seem to corroborate the suggestion of Sanz and Bonaparte (1992) that selective pressure favoured a decrease in size in early birds after *Archaeopteryx*. The avian footprint record of the Early Cretaceous (Kim 1969; Currie 1981) seems to confirm this proposal, as well as the new sparrow-sized bird skeleton from China (Rao and Sereno 1990), probably a very primitive euornithine bird close to *Iberomesornis*. After *Archaeopteryx*, the achievement of full-powered flight as possible by means of some evolutionary novelties of the flight apparatus: strut-like coracoid, derived furcula and pygostyle. This process between *Archaeopteryx* and the first euornithine birds was favoured by a decrease in size. Active flight is biomechanically easier for a smaller tetrapod (Alexander 1989). In short, we suggest that in the evolutionary succession – ‘non-avian theropods – *Archaeopteryx* – early birds – later birds’ – size was constrained by flight. From non-avian theropods to *Archaeopteryx* there is a size decrease. This decrease is greatest from *Archaeopteryx* to the first Euornithes, when most of the structures of the extant bird flight apparatus appeared. Later birds could increase their size (when the flight apparatus was sufficiently refined), both in flightless birds (terrestrial or aquatic) or active fliers. The weights of the Las Hoyas birds have been estimated from empirical allometric functions relating limb bone dimensions and weight in extant birds (Olmos 1988). The mass of *Iberomesornis* is estimated as 16.5 g based on its femoral length, and 26.6 g based on its humeral length: it probably weighed about as much as a sparrow (*Passer domesticus*). Based on femoral length, *Concornis* weighed about 76.5 g. *Concornis*, with a possible weight three or four times that of *Iberomesornis*, is clearly more derived.

According to the criteria of recognition of macroevolutionary patterns from Eldredge and Cracraft (1980), the Early Cretaceous avian record suggests a bird adaptative radiation during this time as postulated by Simpson (1980) and Olson (1985). This record shows a great structural diversity: *Iberomesornis*, *Concornis*, Hesperornithiformes (*Enaliornis*), *Ambiortus*. The concept of ‘key innovation’ or ‘key adaptation’ seems vague (Eldredge and Cracraft 1980), but could be interesting just as speculative narrative explanations (Raikow 1986). We postulate a key adaptation – the evolution of a strut-like coracoid and derived furcula, associated with a pygostyle. It is unlikely that an adaptative radiation is defined by a single trait (Kemp 1985) but rather by a combination of evolutionary novelties (Benton 1987). If a combination of synapomorphies is functionally novel, a key adaptation may appear. This complex of synapomorphies could be considered a series of structural stages (expressed as nodes on a cladogram) in which each combination of character-states is correlated to perform a function. The combination of a strut-like coracoid, a derived furcula, and a pygostyle in the Euornithes suggests that even the earliest members of the group had well-developed powered flight.

So from *Archaeopteryx* to Ornithurae there seems to be a series of avian forms that reflect a noticeable transformation of the flight apparatus. The currently known temporal sequence of transformations indicates that, of the major components of the avian flight apparatus, the strut-like coracoid and pygostyle are the first to appear. Then the true tibiotarsus and a keeled sternum are acquired. The last structures to appear seem to be the fused metatarsus and synsacrum. Although the tail may have contributed to steering in *Archaeopteryx* (Rietschel 1985), the evolution of a pygostyle suggests a further improvement in steering and other functions of the tail. The functional differences between the tails of *Archaeopteryx* and *Iberomesornis* may reflect greater movability of the tail feathers, made possible by the evolution of a fleshy terminal structure supported by the free caudal vertebrae and pygostyle (Text-fig. 11). The reduction of the tail produced significant changes in the position of the centre of gravity of early birds (Wellnhofer 1985). These were accentuated by the evolution of a sternum and were balanced by the evolution of the synsacrum. According to Pennycuik (1986) the synsacrum acts as part of a lever: its posterior region is attached by powerful muscles to the femur, allowing the anterior part of the bird to be raised. Nevertheless, the caudal reduction in *Iberomesornis* does not involve dramatic changes in the sacropelvic region, which remains structurally primitive and consequently it seems very likely that the evolution of the pygostyle and synsacrum were not correlated events. The evolution of the synsacrum may be correlated with further reduction of the tail (decrease of the size of the pygostyle). So the functional



TEXT-FIG. 1 Life reconstruction of a flying *Iberomesornis*. Note the great fleshy caudal structure.

interpretation of the synsacrum is not clear, but its biomechanical interpretation as a lever seems unlikely. It seems more probable that the synsacrum can be envisaged as a flight functional unit related to the fine-tuning of the flight apparatus.

The first habitat of aquatic birds may have been freshwater environments (Elzanowski 1983). Kirkwood *et al.* (1989) have proposed a relationship between a 'legginess index' (metatarsal length/body weight³) of birds and their general habitat. If we have estimated the body weights of *Iberomesornis* and *Concornis* correctly, they had legginess indices of 44 and 59 respectively, within the range of extant aquatic birds (57 ± 3.4). The value for *Iberomesornis* is close to the lower values for aerial habitats (52 ± 2), but many anatids show a range of 41.7–46.6. An aquatic habitat for Las Hoyas birds is consistent with the relative abundance of avian remains from this site.

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