A New Carinate Bird from the Late Cretaceous of Patagonia (Argentina)

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ABSTRACT

A new bird from the Late Cretaceous of Patagonia (Argentina), known from associated wing elements, is described and its phylogenetic position evaluated. Fossil taxa as well as representatives of species of extant birds sampled from lineages considered to be basal within the crown clade were included in a cladistic analysis of 72 characters primarily from the thoracic limb. Based on the results of the phylogenetic analysis and identification of autapomorphies in the specimen, we name a new taxon *Limenavis patagonica.*

Limenavis patagonica is identified as closer to the crown clade than Enantiornithes by the presence of three unambiguous synapomorphies: a fossa (sometimes with two distinguishable subparts) on the dorsal, distalmost extremity of the humerus; distal fusion of metacarpals II and III; and an extensor process on metacarpal I. It is placed closer to the crown clade than *Ichthyornis,* and, thus, unambiguously as a carinate (see Methods for terminology), by two further synapomorphies: the abruptly truncate contact of the dorsal trochlear surface of the ulna with the ulnar shaft and the loss of a tubercle adjacent to the tendinal groove on the distal ulna. Finally, *Limenavis patagonica* is diagnosed by three autapomorphies: the attachment of the pars ulnaris of the trochlea humeroulnaris on the proximal ulna developed as a pit-shaped fossa; the location of the pisiform process with its proximal surface at approximately the same level as the proximal surface of metacarpal I; and a scar of the ligamentum collaterale ventrale of the ulna proximodistally elongate and extending down the caudal margin of the brachial impression.

Limenavis patagonica is placed just outside the avian crown clade. The shortest tree with the new taxon as part of the crown clade is five steps longer than the most parsimonious topology.

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RESUMEN

Se describe una nueva especie de ave del Cretácico tardío de Patagonia (Argentina), cuyo único ejemplar se encuentra representado por elementos del miembro torácico, y se evalúa su posición filogenética. Varios taxones fósiles, a la vez que representantes de linajes actuales considerados de posición basal, fueron incluídos en un análisis cladístico de 72 caracteres, principalmente caracteres del miembro torácico. Sobre la base de los resultados de este análisis filogenético y la identificación de autapomorfías en el ejemplar aqui descripto, se erige el nuevo taxón *Limenavis patagonica.*

Tres sinapormofías de optimización no ambigua indican que *Limenavis patagonica* esta más cercanamente emparentado con el ''crown clade'' (el grupo compuesto por el ancestro común de todas las aves vivientes más todos sus descendientes) de lo que lo están los Enantiornithes. Estas sinapomorfías comprenden la presencia de una fosa (a veces diferenciada en dos) en la parte dorsal de la extremidad más distal del humero, la fusión distal de los metacarpos II y III, y la presencia de un proceso extensor del metacarpo I. Otras dos sinapomorfías indican que *Limenavis patagonica* se encuentra más cercanamente emparentado al ''crown clade'' que *Ichthyornis,* y que por lo tanto puede ser reconocido de forma no ambigua como un Carinatae (ver ''Methods'' para aspectos nomenclatoriales). Estas dos sinapomorfías son el contacto abrupto entre la superficie troclear dorsal y la diáfisis de la ulna, y la pérdida de un tubérculo adyacente al surco tendinal en el extremo distal de éste último hueso. Finalmente, tres autapomorfías diagnostican a *Limenavis patagonica*: la inserción de la pars ulnaris de la troclea humeroulnaris del extremo proximal de la ulna desarrollada en forma de una pequeña fossa, la presencia de un proceso pisiforme cuya superficie proximal se encuentra a más o menos el mismo nivel que la superficie proximal del metacarpo I, y la forma proximodistalmente elongada de la inserción del ligamento colateral ventral de la ulna, que se extiende a lo largo del márgen caudal de la impresión braquial.

Los resultados del análisis cladístico indican que *Limenavis patagonica* se encuentra justo por fuera del ''crown clade.'' El árbol más corto que incluye a este nuevo taxón dentro del ''crown clade'' es cinco pasos más largo que aquél con la topología más parsimoniosa.

INTRODUCTION

Although recent discoveries have helped to fill a significant morphological and phylogenetic gap between *Archaeopteryx lithographica* and the more derived Hesperornithiformes and Ichthyornithiformes (Chiappe, 1995a; Feduccia, 1996; Padian and Chiappe, 1998), our knowledge of the early diversification of modern bird lineages and their most immediate outgroups is still limited by the paucity of relevant fossils. Thus, the discovery of a carinate bird (for terminology see Methods) from the Late Cretaceous of Patagonia (Chiappe, 1996a) provides an opportunity to increase our understanding of the origin of the avian crown clade. In fact, this fossil is 1 of only approximately 12 specimens of Mesozoic carinates, other than *Ichthyornis,* to consist of more than a single element (table 1). Chiappe (1996a) briefly reported on this specimen, PVL-4731, providing data in support of an ornithurine relationship. Here we provide a full descrip-

tion of this specimen and discuss its taxonomic status and phylogenetic position.

PVL 4731 was collected by Jaime Powell (Universidad de Tucumán, Argentina) in the mid-1980s from beds of the lower Allen Formation (Malargüe Group) exposed at the locality Salitral Moreno in the northern Patagonian Province of Río Negro (Argentina) (fig. 1). The poorly sorted yellowish to greenish-gray sandstones at Salitral Moreno have produced an array of plant remains, gastropods, fish, turtles, and a variety of dinosaurs (Powell, 1986, 1987, 1992; Salgado and Coria, 1993, 1996), including hadrosaurs, ankylosaurs, titanosaurs and theropods including the specimen herein described.

The ''Lower Member'' of the Allen Formation has been considered early Maastrichtian in age based on Ballent's (1980) conclusion that the ostracod fauna of the uppermost member of the Allen Formation was from the late Maastrichtian (Powell, 1987, 1992). A second biostratigraphic study, though cited only as a personal communi-

TABLE 1
Published Specimens Placed in Carinatae and Consisting of More than a Single Element

Taxa	Material	Provenience	Age	Reference
Ambiortus dementjevi (holotype)[a]	postcranial	Asia	Early Cretaceous	Kurochkin, 1982
Gansus yumemensis (holotype)	postcranial	Asia	Early Cretaceous	Hou & Liu, 1984
Apatornis celer (referred)	postcranial	N. America	Late Cretaceous	Marsh, 1880
Graculavidae indet.	postcranial	N. America	Late Cretaceous	Olson & Parris, 1987
Telmatornis priscus (referred)	postcranial	N. America	Late Cretaceous	Olson & Parris, 1987
Ichthyonis dispar (holotype)	cranial & postcranial	N. America	Late Cretaceous	Marsh, 1880
Ichthyornis victor (holotype)	postcranial	N. America	Late Cretaceous	Marsh, 1880
Ichthyornis spp. (multiple)	postcranial	N. America	Late Cretaceous	Marsh, 1880
Limenavis patagonica (holotype)	postcranial	S. America	Late Cretaceous	present paper
"Polarornis" [b]	cranial & postcranial	Antarctica	Late Cretaceous	Chatterjee, 1997
Presbyornithidae indet.	postcranial	Antarctica	Late Cretaceous	Noriega & Tambussi, 1995

[a]This specimen has not always been considered part of Carinatae (see Sereno and Rao, 1992).

[b]The Mesozoic age of this specimen is considered uncertain. Precise locality data for the material is unpublished and the stratigraphy of Seymour Island, with extensive Eocene outcrops as well as Cretaceous, has only been rigorously defined in the last 10 years, subsequent to the discovery of the specimen (Zinsmeister, personal commun.).

cation (Heredia and Salgado, 1999), involving pollen from the Allen Formation in the area of Lago Pellegrini (roughly 75 km northwest of Salitral Moreno), suggests an earlier, middle Campanian age (Heredia and Salgado, 1999). New paleomagnetic data (Dingus et al., 2000), consistent with both of these biostratigraphic age estimations, assign a Campanian age to the Río Colorado Formation (Neuquén Group) which directly underlies the Allen Formation.

The association at Salitral Moreno of hadrosaurs and titanosaurs may suggest a correlation of this fauna with those of the Loncoche and Los Alamitos Formations (of Mendoza and Río Negro Provinces, respectively). Currently, it is only from the faunas of these three Formations of South American localities, that both taxa are known. The presence of carinate birds, PVL 4731 among them, in these faunas contrasts with the fauna known from abundant localities of the just older Río Colorado Formation. The Río Colorado has so far produced remains of titanosaurs, and more basal avian taxa, such as *Patagopteryx deferrariisi* and the enantiornithine *Neuquenornis volans* (Chiappe, 1996a) but no hadrosaurs or carinate birds.

INSTITUTIONAL ABBREVIATIONS: **AMNH** American Museum of Natural History, New York, USA; **ET** East Texas State University, Texas, USA; **PVL** Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; **USNM** United States National Museum, Washington D.C., USA; **YPM** Yale Peabody Museum, New Haven, USA.

METHODS AND COMPARATIVE MATERIAL

Osteological and myological nomenclature follows Baumel and Witmer (1993) and Vanden Berge and Zweers (1993) when possible. When structures were not named by these authors, terminology from Howard (1929) or Stegmann (1978) was employed, or structures were named with reference to their topological relations to other named osteological features and/or relationships with muscle attachments or tendinal positions described for extant birds. English equivalents of the Latin osteological nomenclature of all authors were used. One further deviation from the terminology of Baumel and Witmer (1993) involves the names for the metacarpals and the manual digits. We accept the identification of the digits of the avian hand as digits I, II, and III of the pentadactyl limb (Meckel, 1821; George and Berger, 1966;
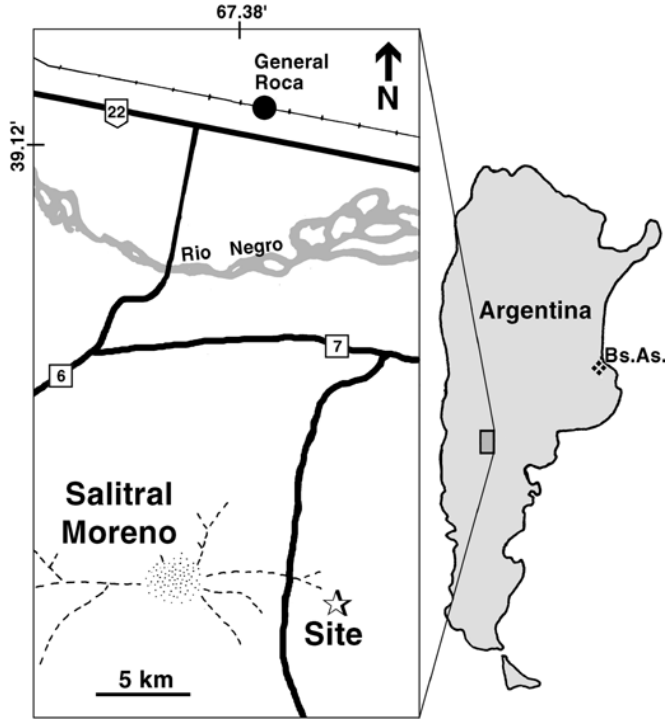
Fig. 1. Map of Argentina, indicating the locality of Salitral Moreno (Río Negro Province) where the holotype of *Limenavis patagonica* was collected.

Stegmann, 1978; Gauthier, 1986; Wagner and Gauthier, 1999).

''Crown-clade birds'' refers to the crown group (Jefferies, 1979) called Neornithes by Thulborn (1984) and the clade comprising the most recent common ancestor of the Ratitae, Tinami, and Neognathae and all of its descendants, called Aves by Gauthier (1986). ''Birds'' refers to the clade called Avialae by Gauthier (1986) or called Aves by Chiappe (1992a). ''Avian'' refers to ''birds'' as defined above. The taxon name ''Ornithurae'' is used following Chiappe (1991, 1995a, 1995b) as a node-based name (de Queiroz and Gauthier, 1992) for the most recent common ancestor of the Hesperornithiformes and modern birds plus all of its descendants. ''Carinatae'' is used for the most recent common ancestor of Ichthyornithiformes and modern birds plus all its descendants (Chiappe, 1995a). The stem-based counterpart to the node-based name for the crown clade (de Queiroz and Gauthier, 1992), including all modern birds as well as all extinct taxa more closely related to them than to *Ich-*

thyornis, is currently unnamed and will be referred to informally as the ''modern bird stem'' or ''modern avian stem''.

Several derived characters suggested that *Limenavis* is closer to the crown clade than Enantiornithes (Chiappe, 1996a). Thus, in the present cladistic analysis, *Confuciusornis sanctus* and Enantiornithes were used as outgroups. The secondarily flightless *Patagopteryx deferrariisi* and Hesperornithiformes were excluded from the phylogenetic analysis. Either the apomorphic nature or the nonpreservation of their wing elements made comparisons to *Limenavis* largely untenable. In consequence, the ingroup was assembled to sample Carinatae. Ingroup taxa included *Limenavis patagonica, Ichthyornis, Lithornis,* and 11 species of extant birds including representatives of 8 traditional ''orders''. Broader anatomical comparisons with many more extant species were undertaken. These comparisons formed the basis for references to traditional ''orders'' made in the Anatomical Description.

Representatives of two extant palaeognath

taxa (Rheidae and Tinamidae) and of four neognath taxa (Anhimidae, Anatidae, Cracidae, and Phasianidae) that have been considered to represent the earliest divergences in modern birds (e.g., Cracraft, 1988; Sibley and Ahlquist, 1990; Groth and Barrowclough, 1999) were also included. Species of some taxa (Columbidae, Gruidae, Rallidae, Burhinidae and Scolopacidae) which have been alternatively considered to be basal diverences of the crown clade (e.g., Olson 1985), or relatively basal divergences of subsequent neognath diversification (e.g., Cracraft, 1988; Sibley and Ahlquist, 1990; Ericson, 1997; Groth and Barrowclough, 1999) were also included.

The two species of Anseriformes, Galliformes and Charadriiformes included were chosen to sample basal and later divergences within these clades. These taxa were chosen following previous phylogenetic hypotheses for these clades (e.g., Sibley and Ahlquist, 1990; Chu, 1995; Livezey, 1997a, 1997b). Given the historically controversial composition of Gruiformes (e.g., Olson, 1985; Ericson, 1997; Livezey, 1998), two species of the most often included taxa (i.e., Gruidae and Rallidae) were chosen. Columbiformes was represented by one species. For extant modern birds, individual species rather than supraspecific terminals were preferred while composite terminals were used for the fossil taxa (Enantiornithes, *Ichthyornis* and *Lithornis*) in light of unavoidable issues of missing data (Wilkinson, 1995).

The data matrix consisted of 11 multistate characters (8 ordered, or additive) and 61 binary characters for a total of 72 characters. This matrix was analyzed using the phylogenetic software PAUP* 4.0b1 (ppc) (Swofford, 1998). Due to the limited number of taxa, the "branch and bound" search algorithm could be used, an algorithm guaranteeing that all shortest trees were found (Hendy and Penny, 1982). The present dataset was assembled to provide the best estimate of the phylogenetic position of *Limenavis patagonica* possible without undertaking a comprehensive analysis of basal crown-clade relationships. Thus, the option provided by PAUP* of applying topological constraints was used to require traditional "orders" of modern birds to be monophyletic. The monophyly of Anseriformes and Galliformes

(e.g., Sibley and Ahlquist, 1990), Charadriiformes (e.g., Chu, 1995), Gruiformes (here only Rallidae and Gruidae) (e.g., Sibley and Ahlquist, 1990; Livezey, 1997), and the living Palaeognathae (e.g., Lee et al., 1998) is well supported by a broad array of molecular, morphological, and ethological data. If these assumptions of monophyly are shown to be ill justified by subsequent analyses, the results of this analysis would also need to be problematized. That Galliformes and Anseriformes are most closely related to each other, and that the monophyletic clade that they are part of is sister taxon to the rest of Neognathae are well supported by extensive molecular (Groth and Barrowclough 1999; van Tuinen et al., 2000) and morphological data (Cracraft, 1988; Livezey, 1997b). Constraining for a monophyletic Galloanseres did not affect the phylogenetic placement of *Limenavis* relative to the base of the crown clade.

In the matrix (see appendix 2), states of uncertain homology were indicated with an "N", to distinguish this ambiguity from character states that were not preserved in fossil taxa, which were coded as "?". Computationally, these two entries are treated the same. Characters were not summarily rejected if a state could not be assessed in a taxon. In these few cases, these states were scored as "N". It has been suggested that the inclusion of more characters, even if with an attendant increase in missing data (though obviously not to excess), generally improves the accuracy of phylogenetic analyses (Weins, 1998).

Comparative material included in the phylogenetic analysis: *Tinamus guttatus* (AMNH 17991); *Pterocnemia pennata* (AMNH 12892); *Gallus gallus* (AMNH 18553); *Crax globulosa* (AMNH 4935); *Chauna torquata* (AMNH 3616); *Anas platyrhynchos* (AMNH 5847); *Grus grus* (AMNH 1265); *Rallus longirostris* (AMNH 5629); *Numenius phaeopus* (AMNH 3696); *Burhinus capensis* (AMNH 3595); *Columba livia* (AMNH 2002); *Ichthyornis dispar* (YPM 1450); *I. victor* (YPM 1452), and *I.* spp., material not formally referred to a species and awaiting a revision of *Ichthyornis* (YPM 1738, YPM 1775, YPM 1740, YPM 1462, YPM 1460, YPM 1453, YPM 1447, YPM 1441, YPM 1724, YPM 1726, USNM 11641); *I. antecessor* (USNM 22820); *Lithornis plebius* (USNM 336534,

AMNH 21902); *L. promiscuus* (USNM 336535, USNM 424072, AMNH 21903); *Lithornis celetius* (USNM 290554, YPM-PU 23485, YPM-PU 23484, YPM-PU 23483, YPM-PU 16961); *Enantiornis leali* (PVL 4035, PVL 4020, PVL 4023, PVL 4181) and several other isolated enantiornithine specimens [PVL 4054, PVL 4059, PVL 4023, PVL 4267, PVL 4265, PVL 4697, PVL 4025, PVL 4032–2 (see Walker, 1981, and Chiappe and Walker, in press); and a cast of *Sinornis santensis,* (see Sereno and Rao, 1992)]; and a large collection of specimens of *Confuciusornis sanctus* (see Chiappe et al., 1999).

Though the identification of certain remains referred to *Ichthyornis* has been problematized recently (Clarke, 1999), the material cited in the description, and scored for *Ichthyornis* in the analysis, is considered safely referred to that taxon. Most of the thoracic limb (humerus, ulna, radius, distal carpometacarpus) are well preserved in the holotype of the type species of *Ichthyornis, I. dispar* (YPM 1450). The proximal end of the carpometacarpus and proximal phalanx of the second manual digit were scored for *Ichthyornis* from other referred material by comparing the elements represented in YPM 1450 to corresponding elements in the other associated specimens or isolated material (in the case of the carpometacarpus). The other cranial and postcranial characters were scored from YPM 1450 with the exception of the quadrate (from YPM 1775) and the proximal coracoid (from YPM 1452). However both of these specimens have elements directly overlapping those of YPM 1450 and are considered safely referable to *Ichthyornis.* In contrast, the single tarsometatarsal character included in the analysis was not scored for *Ichthyornis* because all referred elements available are isolated and their identification as *Ichthyornis* is considered tentative.

SYSTEMATIC PALEONTOLOGY

REPTILIA
THEROPODA
AVIALAE (AVES SENSU CHIAPPE, 1995b)
CARINATAE

Limenavis patagonica (new taxon)

HOLOTYPE: *Limenavis patagonica,* including associated distal portions of a right wing given brief reference in Chiappe (1992b,

1996a). PVL 4731 consists of a portion of the shaft and distal end of the humerus; proximal and distal ends of the ulna; proximal end of the radius; proximal and distal ends of the carpometacarpus; ventral ramus (crus longus) of the ulnare; radiale; most of the proximal phalanx of digit II including the distal end; and several indeterminate fragments. The material is generally unabraded but crushed. The radius is cemented to the humerus, partially obscuring its cranial surface. The proximal carpometacarpus distal to the carpal trochlea of the incorporated semilunate carpal is covered by the attached distal end of the ulna, and the ventral surface is partially obscured by the fragment of the ulnare. The radiale is preserved roughly in articulation with the carpal trochlea.

ETYMOLOGY: *Limen,* Latin for "threshold," *avis,* Latin for bird, and *patagonica,* from the provenience of the specimen from northern Patagonia, for the window it offers into the origin of the radiation of the avian crown clade.

LOCALITY AND HORIZON: Salitral Moreno, 20 km south of General Roca, Province of Río Negro, Argentina (fig. 1); Allen Formation, Upper Cretaceous (Campanian–Maastrichtian; Powell, 1987; Heredia and Salgado, 1999).

DIAGNOSIS: Carinate bird with the attachment of the pars ulnaris of the trochlea humeroulnaris on the proximal ulna developed as a pit-shaped fossa, the location of the pisiform process with its proximal surface at approximately the same level as the proximal surface of metacarpal I, and the scar of the ligamentum collaterale ventrale of the ulna proximodistally elongate, extending down the caudal margin of the brachial impression (23:1). These autapomorphies, along with the presence of three other characters with restricted distributions: (1) a well-developed tendinal groove on the ulnare, (2) the deep infratrochlear fossa of the carpometacarpus, and (3) the presence of three fossae on the proximal surface of the dorsal supracondylar process of the humerus, provide a unique suite of characters diagnosing *Limenavis patagonica.*

ANATOMICAL DESCRIPTION

The humerus is crushed craniocaudally. However, most of its morphology is still

readily discernible (fig. 2A). The dorsal and ventral condyles are clearly developed on the cranial surface. The dorsal condyle is oriented primarily in the long axis of the humerus and angling toward the ventral surface. The ovoid ventral condyle is oriented dorsoventrally at the distal edge of the humerus. In *Confuciusornis sanctus, Enantiornithes, Patagopteryx deferrariisi, Ichthyornis dispar,* and modern birds the condyles are similarly developed cranially (Chiappe, 1996b) and a ventrally angled, elongate dorsal condyle is present. In enantiornithines, however, the ventral condyle developed as a straplike ridge as opposed to the hemispherical form it has in the other listed taxa.

The measure of the long axis of the dorsal condyle is more than the same measure of the ventral condyle as in *Confusiusornis sanctus, Ichthyornis dispar, Ichthyornis* spp. (YPM 1738, YPM 1447), and neognaths. The angle (declination) between the dorsal humeral margin and the long axis of the dorsal condyle is relatively high compared to most taxa of the crown clade. It is roughly 45° in *Limenavis,* whereas within the crown clade, as well as in *Confuciusornis sanctus and Ichthyornis dispar,* it more closely approximates 30°. In enantiornithines, it approaches 75° to 80°.

The area where the brachial fossa (when present) is developed is largely destroyed by crushing and obscured by the location of the attached fragment of the radius. No distinct fossa is discernible. However, close to the proximal end of the radial fragment and slightly dorsal to it, there is a small area of differently textured bone. The brachial fossa in *Ichthyornis dispar* and *Ichthyornis* spp. (YPM 1738, YPM 1447), as well as in some crown-clade taxa, is also often not developed as a fossa, but as a scar.

The dorsal supracondylar tubercle of the humerus is well developed, though not as the pointed process seen in Charadriiformes and Passeriformes (Baumel and Witmer, 1993). Further, although the process is of similar proportion to that of other crown-clade birds (e.g., Tinamidae), it is more cranially rather than dorsally projected. A shallow circular fossa is located on the dorsal supracondylar tubercle and opens proximally (fig. 2A). Two smaller fossae lie adjacent and just proximal

to this larger fossa on the craniodorsal edge of the humeral shaft. The more ventral of these forms a short groove. A similar grouping of three fossae occurs in *Lithornis celetius* (YPM-PU 23485), *Ichthyornis dispar, Ichthyornis* spp. (e.g., YPM 1738, YPM 1447), and *Ichthyornis antecessor* (fig. 3). These fossae are especially prominently developed in the latter taxon and one specimen of *Ichthyornis* sp. (YPM 1447) although they are present in all *Ichthyornis* humeri. Brodkorb (1963) described comparable pits on the dorsal supracondylar tubercle of the Late Cretaceous bird, *Torotix clemensi,* and considered them peculiarities of the specimen. The two proximal fossae were not observed in any crown-clade taxa examined, though the single large fossa is present in some extant taxa (e.g., Tinamidae) (fig. 3F).

The distal end of the dorsal surface of the humerus of *Limenavis patagonica* bears two faint fossae (fig. 2A, C). These fossae are observed in varying degrees of development in all crown-clade birds considered as well as in *Ichthyornis dispar* and *Ichthyornis antecessor.* They are have been identified as the origins of the m. extensor digitorum communis and the m. extensor carpi ulnaris (Brodkorb, 1963; McKitrick, 1991).

Proximal to the ventral condyle, on the cranioventral surface of the humerus, there is a well-developed, pit-shaped fossa. A small and incompletely preserved facet, or flat, angling bone surface, lies dorsally adjacent and slightly distal to this fossa. These two features are identified respectively as the attachment of the m. pronator superficialis and lig. collaterale ventrale (m. pronator brevis and anterior articular ligament, respectively, sensu Howard, 1929). The attachment of the m. pronator superficialis is developed as a small pit-shaped fossa in enantiornithines, *Ichthyornis dispar* and *Ichthyornis* spp. (YPM 1738, YPM 1447), as well as within the avian crown-clade. While located on the ventral humeral surface in enantiornithines and some crown-clade taxa, it is developed obliquely cranioventrally in *I. dispar* and other taxa of the crown.

The flexor process of the humerus is short, extending less distally than either of the condyles. The ventral epicondylar surface may bear two faint tendinal impressions. How-
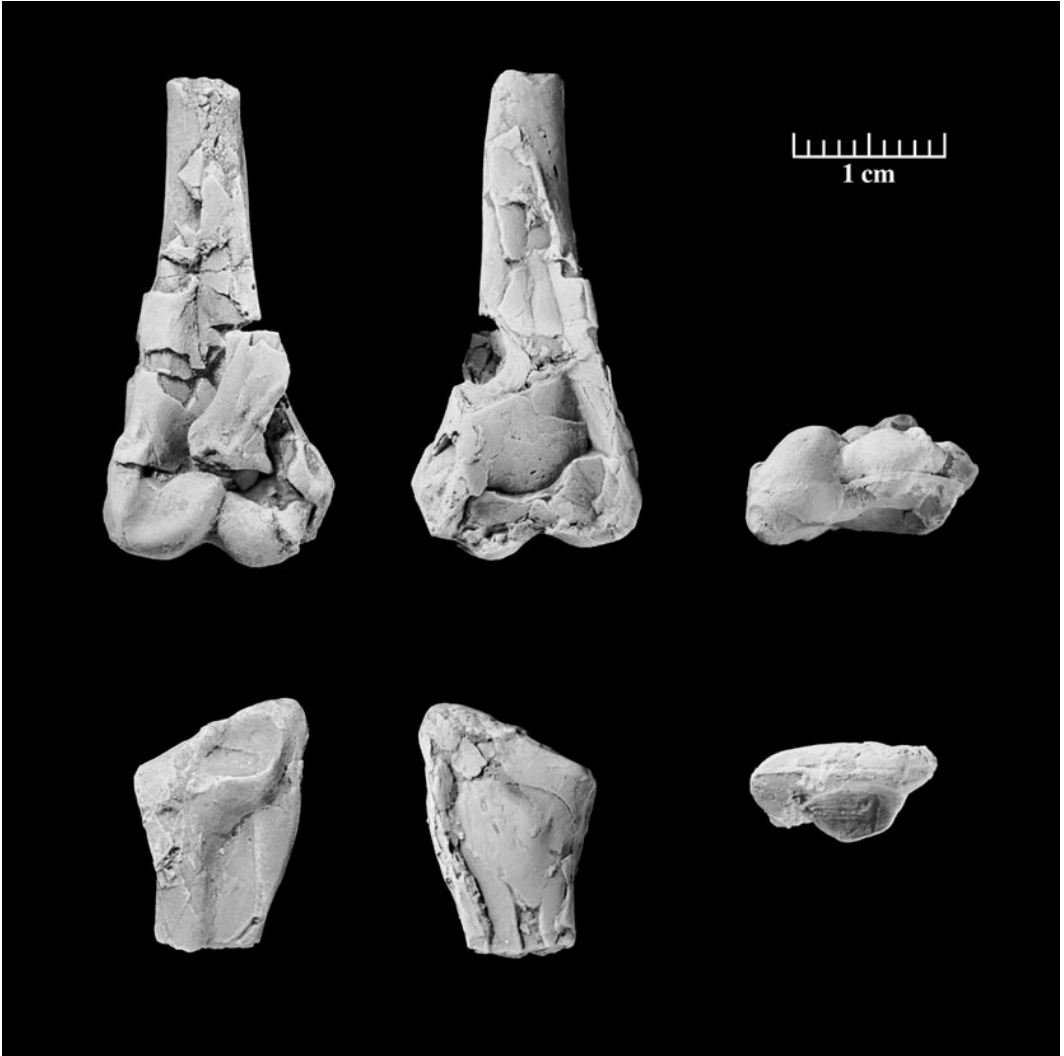
Fig. 2. *Limenavis patagonica,* holotype (PVL 4731). Right distal humerus attached proximal end of the radius in **A,** cranial; **B,** caudal; **C,** distal views. Right ulna **D,** ventral; **E,** dorsal; and **F,** proximal views. (Casts were used in photographs). **bim** bicipital impression; **bit** bicipital tubercle; **bri** brachial impression; **dca** dorsal cotyla; **dco** dorsal condyle; **ddf** dorsal distal fossae; **dst** dorsal supracondylar tubercle; **hut** attachment humeroulnar trochlea; **imb** impression of m. brachialis; **lev** attachment lig. collaterale ventrale; **ole** olecranon; **psa** m. pronator superficialis attachment; **rad** radius; **vca** ventral cotyla; **vco** ventral condyle; **vdf** ventral distal fossae.

ever, this area is incompletely preserved. The flexor process is short (as defined above) in *Confuciusornis sanctus, I. dispar,* and *Ichthyornis* spp. (YPM 1447, YPM 1738), as well as in some taxa of the crown clade. In enantiornithines, the whole ventrodistal humeral margin angles farther distally than either of the condyles. The two distal fossae described above are present in both enantiornthines and *Confuciusornis sanctus* as well as within the avian crown. In enantiornithines, however, these fossae are positioned more ventrally and are aligned proximodistally rather than craniocaudally.

The morphology of the olecranon fossa could not be determined as the caudal surface
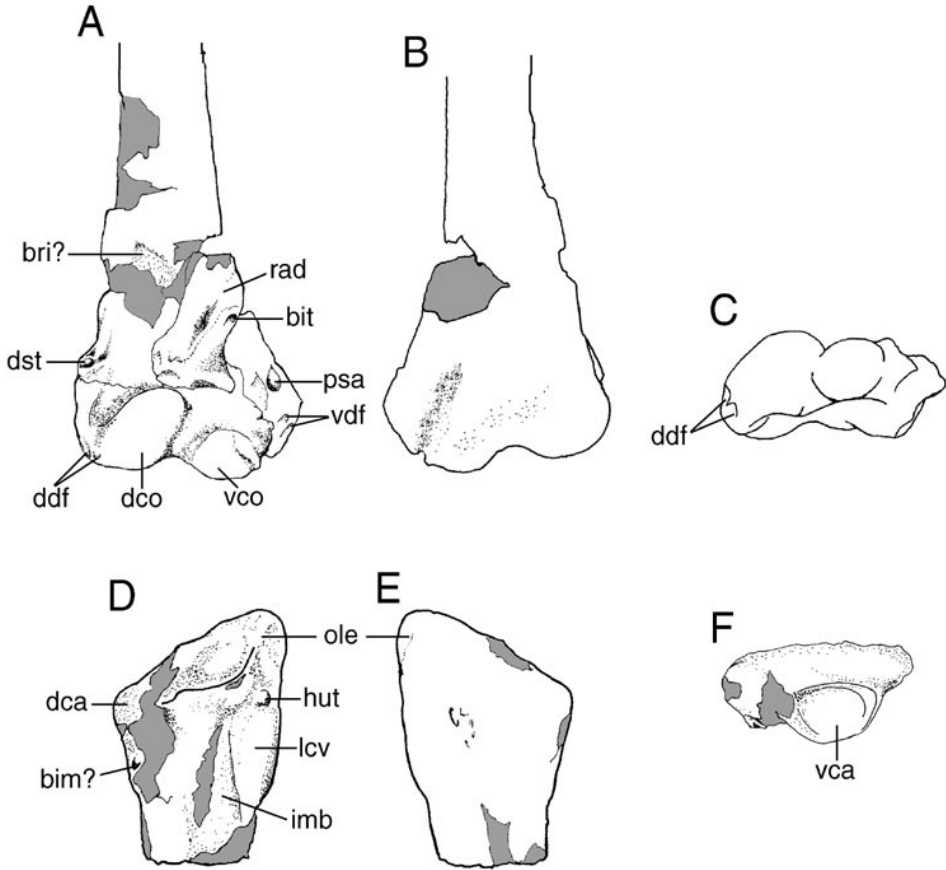
Fig. 2. Continued.

of the humerus is severely crushed (fig. 2B). It is, however, not strongly developed. There is no evidence of grooves for the m. scapulotriceps or the m. scapulohumeralis. In *I. dispar,* the groove for the m. scapulotriceps is absent or extremely faintly developed, as appears the condition in *Confuciusornis santus,* enantiornithines as well as the living palaeognath birds. It is clearly indicated in most extant neognath birds.

The dorsal surface of the ulna is crushed, while the ventral surface is relatively undistorted (figs. 2D–F). The olecranon and the cotylae are well developed. The impression of the m. brachialis is also present with an excavated lip bounding it caudally. The cranial margin of this impression is difficult to

determine and its excavation is exaggerated by breakage.

Just caudal and proximal to the area of the ulnar brachial impression lies a well-preserved, flat, triangular area of textured bone that in extant birds marks the insertion of the lig. collaterale ventrale (fig. 2A). In *Limenavis patagonica,* this attachment surface extends along the caudal edge of the brachial impression and up the caudoventral surface toward the olecranon. It terminates approximately at the level of the lip of the ventral cotyla where there is a distinctive circular pit in the approximate location of the insertion of the pars ulnaris of the trochlea humeroulnaris in extant birds, a ligament that positions the m. flexor carpi ulnaris (Benz and Zusi,
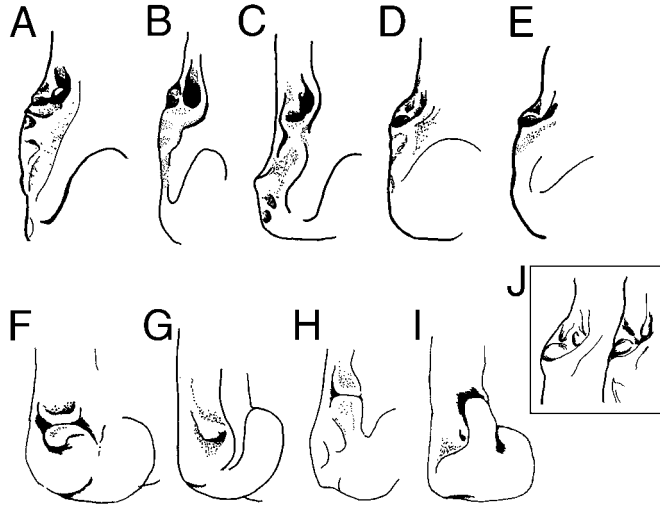
Fig. 3. Fossae associated with the dorsal supracondylar tubercle in **A,** *Ichthyornis antecessor;* **B,** *Ichthyornis* sp. (YPM 1447); **C,** *Ichthyornis dispar;* **D,** *Lithornis celetius,* YPM-PU 23485; **E***, Limenavis patagonica;* **F,** *Tinamus guttatus;* **G,** *Crax globulosa;* **H,** *Rallus longirostris;* **I,** *Burhinus capensis.* **J,** Inset with details of fossae in *Lithornis celetius* **(right)** and *Limenavis patagonica* **(left).**

1982; Baumel and Raikow, 1993). The development of this attachment as a circular pit in *Limenavis patagonica* is distinct from the poorly defined depression observed in crown-clade taxa.

The olecranon arises directly from the dorsal edge of the ventral cotyla, with the excavation of this cotyla extending three-quarters of the way up the ventral surface of the process (fig. 2D). The caudal contact between the ventral cotyla and the olecranon appears concave in proximal view (fig. 2F). The ventral cotyla is slightly concave and larger than the flat to slightly convex dorsal cotyla.

In *Limenavis,* as in *Ichthyornis dispar,* the dorsal cotyla of the ulna does not appear to project cranially (fig. 2E). In contrast, a well-developed process of the dorsal cotyla is present in *Patagopteryx deferrariisi* (Chiappe, 1996b) and within the crown clade, where it forms a rounded flange. A weak ridge extends distally from the cranial edge of the dorsal cotyla and borders the radial depression. It terminates close to a small fossa, possibly marking the insertion of the m. biceps brachii. This fossa lies in the same position as the bicipital tubercle, the insertion of this muscle in extant birds. The morphology of the radial depression could not be determined.

Distally, the dorsal condyle of the ulna is developed as a semilunate ridge (fig. 4A). Its dorsal surface bears a tendinal pit and groove (sensu Howard, 1929) close to the cranial margin, a condition very similar to that of *Ichthyornis dispar, Ichthyornis* sp. (YPM 1740, YPM 1462, YPM 1460) and seen in crown-clade birds. The tendinal groove lies distal to the pit and roughly parallel with the edge of the shaft. The pit is somewhat oblong and angles caudally toward the proximal end of the ulna. In enantiornithines, at least one tendinal impression is present.

On the caudal surface of the ulna, the semilunate ridge of the dorsal condyle appears truncated distally (fig. 4A). In *Ichthyornis dispar, Ichthyornis* spp. (e.g., YPM 1740, YPM 1462), enantiornithines, and some taxa of the crown clade this ridge slopes smoothly into the ulnar shaft. The morphology of the ventral condyle is obscured by the carpometacarpus and a fragment of the ulnare (fig. 4B). The distal trochlear ridge of the dorsal condyle appears longer transversely across the width of the ulnar shaft than it is in its extent down the caudal margin. In at least some enantiornithines (e.g., PVL 4020, PVL 4032–2) the reverse is true, while in *Ichthyornis dispar* and *Ichthyornis* spp. (YPM 1453, YPM 1740, YPM 1462) these dimen-

sions are subequal. This proportion is variable across the crown clade.

The radius is preserved in articulation with the distal humerus (fig. 2A) and a well-projected bicipital tubercle is visible on its ventral surface. A bicipital tubercle is present in Enantiornithes, *Patagopteryx deferrariisi, Ichthyornis* spp. (e.g., USNM 11641, YPM 1775), *Lithornis plebius,* and some crown-clade taxa. Adjacent to this process is a slight groove, possibly representing the ligamental papilla (Howard, 1929), which is developed as a depression in some crown-clade birds and *Ichthyornis* spp. (YPM 1741, USNM 11641).

A fragment of the ventral arm (crus longus; Baumel and Witmer, 1993) of the ulnare is preserved crushed against the carpometacarpus (fig. 4B). A strongly developed longitudinal groove is conspicuous on its convex and probably ventral (external) surface. The development of such a groove varies across modern birds from a barely visible impression to the deep incision present in the fossil. Enantiornithines have this groove although it is but weakly developed. A well-developed groove is present in *Lithornis plebius* (AMNH 21902).

The radiale (fig. 4C) is somewhat abraded but both the articular surfaces (carpal and radial) seen in crown-clade birds are well-developed. A radiale is not preserved in any of the *Ichthyornis* material and although it is known in some specimens of *Confuciusornis sanctus* and Enantiornithes, little of its morphology could be discerned beyond the apparent presence of both of the major articular facets.

Pisiform and extensor processes are present on the carpometacarpus of *Limenavis* (fig. 4B). A pisiform process, while not present in *Confuciusornis sanctus,* is present in enantiornithines as well as in carinates. An extensor process is known only for carinate birds. Although Chiappe (1996b) described a subcircular extensor process for Enantiornithes, it is the overall shape of the enantiornithine metacarpal I that is best described as subcircular. A distinct process projecting from the proximocranial margin of this metacarpal is absent in enantiornithines but present in *Ichthyornis* sp. (YPM 1724) and crown-clade birds. The pisiform process is slightly ovate at its base and angles slightly craniocaudally. The ventral tip may be bro-

ken. Its proximal surface is approximately even with the proximal surface of metacarpal I. This condition contrasts with that of enantiornithines, *Ichthyornis* spp. (YPM 1775, YPM 1724), and crown-clade birds surveyed in which the proximal surface of the pisiform process is located conspicuously distal to the proximal surface of metacarpal I in ventral view. The pisiform process is often in a distinctly more distal position in these taxa; it lies at the approximate midpoint of metacarpal I, or distal to it.

Proximocranial to the pisiform process, there is a slight ridge that borders a deeply excavated infratrochlear fossa. A shallow muscle scar is located proximal and cranial to the ridge. A comparable ridge and prominent infratrochlear fossa are present in *Ichthyornis* sp. (YPM 1724) and *Lithornis* sp. (AMNH 21903), but are uncommon within the crown clade.

On the dorsal aspect of the carpometacarpus (fig. 4A), the supratrochlear fossa is a faint, ellipsoidal depression oriented craniocaudally and angling slightly proximally as in enantiornithines, *Ichthyornis* spp. (YPM 1775, YPM 1724), *Lithornis* sp. (AMNH 21903), and crown-clade birds. A distinct notch or fossa just proximal and slightly cranial to the supratrochlear fossa is present. This feature is clearly seen in *Ichthyornis* sp. (YPM 1724) and in crown-clade taxa. It does not appear to be present in enantiornithines.

In cranial view, metacarpal I has an elongate hourglass shape (i.e., a slightly dorsoventrally expanded extensor process and articular surface for digit I). Metacarpal I is also dorsoventrally thin (fig. 4C) compared to the width of the carpal trochlea in proximal view. In enantiornithines this metacarpal is almost as wide as the carpal trochlea, while in *Ichthyornis* spp. (YPM 1775, YPM 1724), it is, like *Limenavis patagonica,* significantly narrower. This width varies across modern birds. The distal articular surface of this metacarpal (for the first phalanx) is shelf-like and angles slightly ventrally, as opposed to opening directly distally.

Metacarpals II and III are fused distally (figs. 4D–F). In this region, they are subparallel, indicating that the intermetacarpal space was probably narrow. The distal shaft of metacarpal III is oval in cross section at the level
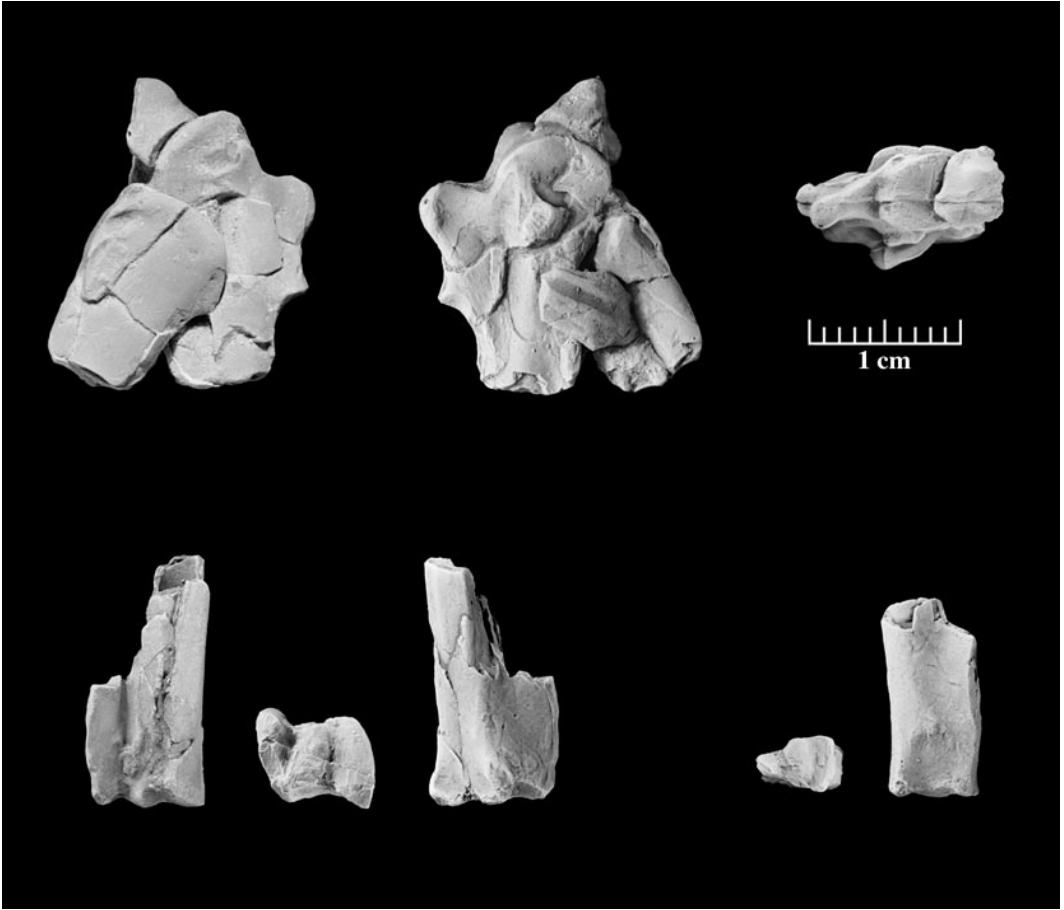
Fig. 4. *Limenavis patagonica,* holotype (PVL 4731). Right proximal carpometacarpus, distal ulna, radiale and ulnare (**A–C**), right distal carpometacarpus (**D–F**), and phalanx 1 of right digit II (**G–H**). **A,** dorsal view of carpometacarpus, with caudal surface of distal ulna; **B,** ventral view of carpometacarpus with ventral ramus of ulnare; **C,** proximal view of carpometacarpus with attached radiale; **D, H,** dorsal; **E, G,** distal; and **F,** ventral views. **acf** anterior carpal fovea, **exp** extensor process; **fdI** articular facet for first phalanx, digit I; **fdII** articular facet for first phalanx, digit II; **fdIII** articular facet for first phalanx, digit III; **inf** infratrochlear fossa; **pip** pisiform process; **rae** radiale; **ras** radial articular surfac; **sdc** sulcus m. digitorum communis; **sid** sulcus m. interosseus dorsalis; **siv** sulcus m. interosseus ventralis; **spf** supratrochlear fossa; **tpg** tendinal pit and groove; **ule** ulnare; **uln** ulna; **vdp** ventral distal process; **vtg** ventral tendinal groove.

of the proximal end of the synostosis. The facets for the proximal phalanges of these metacarpals are equal in distal projection (fig. 4D) as in *Ichthyornis dispar.* In *Confuciusornis sanctus,* metacarpal III is conspicuously shorter than metacarpal II (Chiappe et al., 1999), while in enantiornithines metacarpal III extends farther distally than metacarpal II (Zhou, 1995). Both conditions are widely distributed in the crown-clade taxa.

There are three visible grooves on the dorsal aspect of the distal metacarpal synostosis (fig. 4D). The most cranial of the three is identified as the tendinal groove for the m. extensor digitorum communis and is located on the dorsal surface of metacarpal II. A more caudal groove is probably for the m. interosseus dorsalis (Stegmann, 1978), and a third, in the deep interosseal groove, probably represents that for the m. interosseus pal-
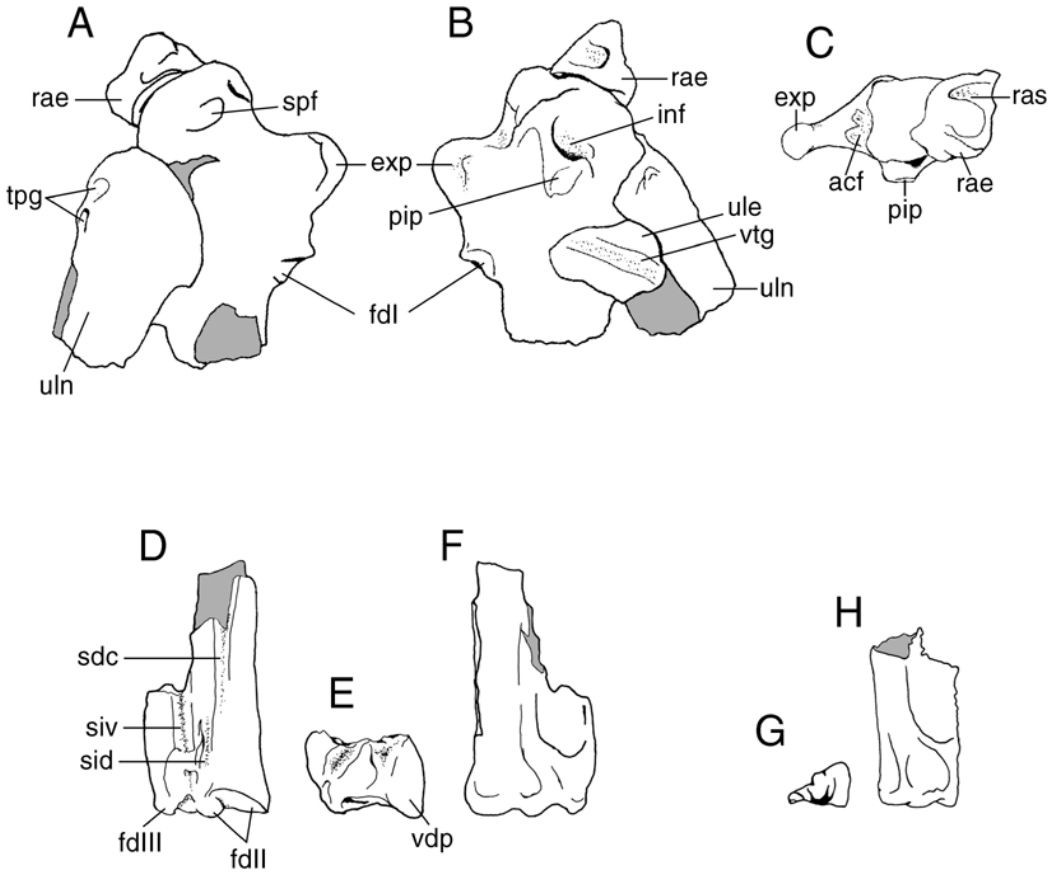
Fig. 4. Continued.

maris (Stegmann, 1978). These three grooves appear in similar topological relations to one another in *Ichthyornis dispar* and *Limenavis.* Their development and position relative to one another varies across the crown clade.

Best seen in distal view (fig. 4E), metacarpal II bears a ventrally directed distal process (Stegmann, 1978; tuberosity of metacarpal II sensu Howard, 1929). Another protuberance of comparable development defines the ventrocaudal edge of metacarpal II. These two ventral projections border a concave surface. These ridges also define a similar concave area in *Ichthyornis dispar, Ichthyornis* sp. (YPM 1724), and some crownclade birds. The distal process in *Limenavis* is not, however, the extremely well-developed process seen in *Ichthyornis dispar* or in some crown-clade taxa.

The proximal phalanx of digit II is expanded caudally (figs. 4G, H). In dorsal and ventral views, its cranial and caudal edges are parallel for the distalmost 3.3 mm; the rest of the caudal edge is broken. The cranial edge is dorsoventrally convex, flattening somewhat distally. There is no distal projection of the caudal edge past the articular surface. A conspicuous projection of this part of the phalanx, the internal index process (Stegmann, 1978), as well as a concave cranial surface, is present in some crown-clade taxa as well as in *Ichthyornis* sp. (YPM 1726).

PHYLOGENETIC RESULTS

The dataset initially was composed of only the 54 characters from the thoracic limb (appendix 1). The resultant 30 most parsimoni-

ous trees (Length: 143 steps, CI: 0.44, RI: 0.52, RC: 0.23), from this preliminary analysis, could be divided into two basic classes of topologies. In one these classes, *Limenavis, Ichthyornis,* and *Lithornis* were outgroups of the crown clade, although varying in their placement relative to one another. In the other class of topologies, *Limenavis, Ichthyornis,* and *Lithornis* formed a clade with the extant palaeognaths (sometimes clustered with galliforms), that fell as the sister taxon of all neognaths or the nongalliform neognaths, respectively. The strict consensus tree of these fundamental cladograms was completely unresolved. Not surprisingly, a limited set of characters from the thoracic limb does not include synapomophies specifying all well-corroborated relationships (e.g., the monophyly of modern birds and of some traditional ''orders''). Eighteen additional characters considered by previous authors germane to further resolution of basalmost carinate relationships were added to the analysis (e.g., Houde, 1988; Cracraft, 1988).

The analysis of this expanded dataset resulted in a single most parsimonious tree (Length: 172 steps, CI: 0.47, RI: 0.57, RC: 0.27). In this tree, *Limenavis patagonica* is the sister taxon of a clade formed by *Lithornis* and the crown clade (fig. 5), and *Ichthyornis* is the sister taxon of the clade formed by these carinate taxa. Because the interrelationships of extant avian clades are beyond the scope of this study, the topology of the resultant cladogram, although fully resolved, should not be taken as an explicit hypothesis of their phylogenetic relationships.

In this single tree, state changes in five characters are unambiguously optimized as synapomorphies of Carinatae relative to Enantiornithes (fig. 5). These synapomorphies are as follows: brachial fossa of the humerus (9); one or two fossae on the distal, dorsal surface of the humerus (14); complete proximal and distal fusion of the distal carpals and metacarpals (36); extensor process on metacarpal I (41); and extensor groove on the distal tibiotarsus (64). Although two of these synapomorphies (i.e., 9, 64) are not preserved in the only known specimen and holotype of *Limenavis patagonica*, the presence of the three remaining synapomorphies place *Limenavis* closer to Aves than to Enantiornithes.

Two unambiguous synapomorphies indicate that *Limenavis* is phylogenetically closer to the crown clade than *Ichthyornis* and thus place it within Carinatae. These synapomorphies are the abruptly truncate contact of the dorsal trochlear surface of the ulna with the ulnar shaft (25), and the loss of a tubercle adjacent to the tendinal groove on the distal ulna (28).

The sister-taxon relationship between *Lithornis* and the crown clade is supported by only one unambiguous synapomorphy (for which *Limenavis* preserves the primitive state): metacarpal III extends further distally than does metacarpal II (48).

State changes in six characters are unambiguously optimized as synapomorphies of the crown clade. These synapomorphies include the following: loss of two small fossae on the dorsal supracondylar tubercle of the distal humerus (13); loss of a deeply excavated infratrochlear fossa of the carpometacarpus (37); intermetacarpal process developed as a small tuberculum (45); distalmost caudal margin of phalanx 1, digit II, bowed caudally (54); and loss of a foramen through the coracoid marking the passage of m. supracoracoideus nerve (66). *Limenavis* has the primitive state for four of these characters (13, 37, 52, 54); the states for the remaining two characters are not preserved in the holotype.

DISCUSSION

The presence of two autapomorphies, morphologies seen in no other taxa, (i.e., a pit-shaped fossa marking the attachment of the trochlea humeroulnaris on the ulna and the location of the pisiform process with its proximal surface at approximately the same level as the proximal surface of metacarpal I), along with the one local autapomorphy required by the analysis (i.e., the scar of the ligamentum collaterale ventrale of the ulna proximodistally elongate, extending down the caudal margin of brachial impression) (see Diagnosis), establish PVL 4731 as part of a new taxon, *Limenavis patagonica.*

Limenavis patagonica is placed outside of the crown clade in the phylogenetic analysis. An increase in tree length of a minimum of five additional steps is required for it to be part of the crown clade. Only additional ma-
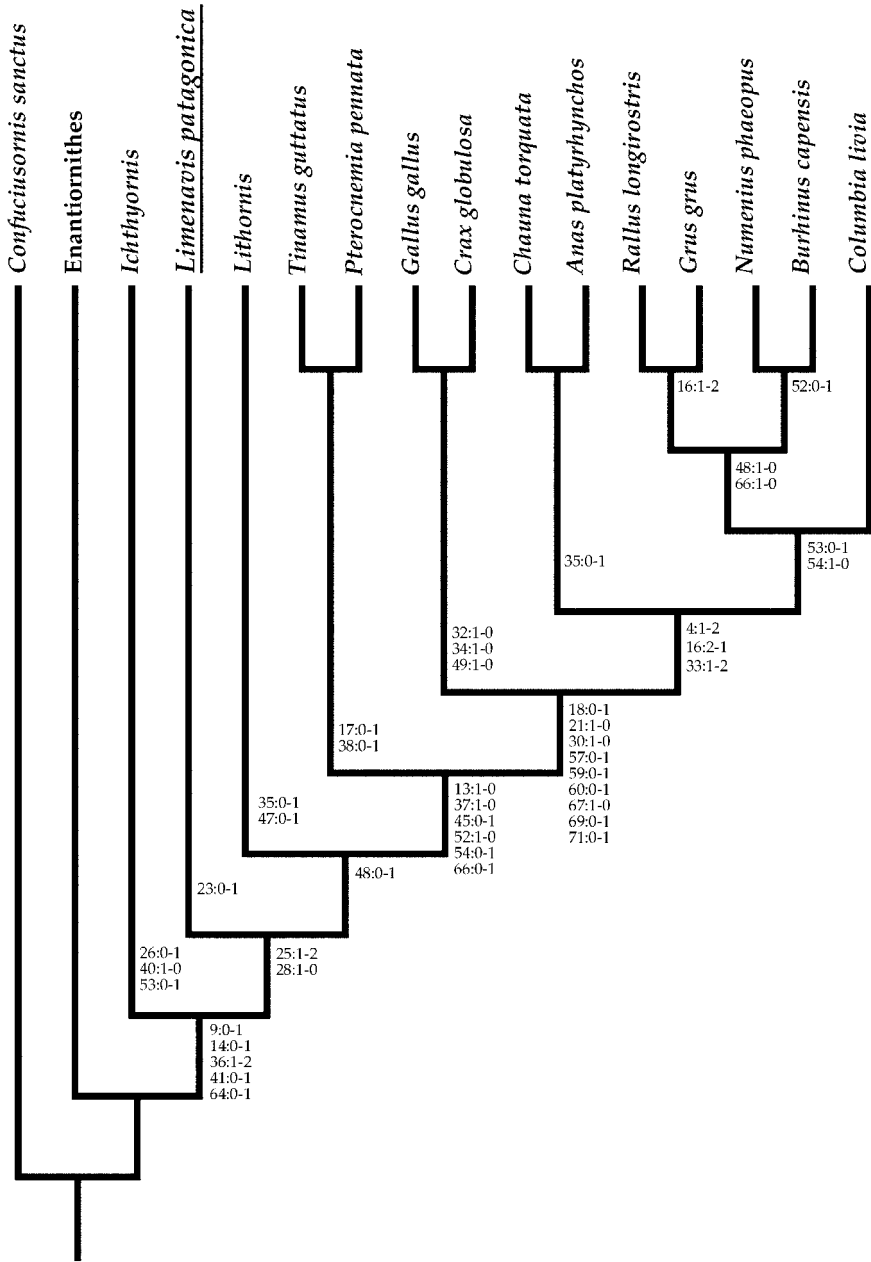
Fig. 5. Cladogram depicting the single most parsimonious arrangement of 14 ingroup taxa with *Confuciusornis sanctus* and Enantiornithes as outgroups (Length: 172, CI: 0.48, RI: 0.57, RC: 0.27). Only autapomorphies for fossil carinates and unambiguous synapomorphies are indicated. Character states optimized as autapomorphies of extant species are not shown.

terial of *Limenavis* will potentially yield stronger support of its position outside the crown and its specific relationship to *Lithornis*. Although *Lithornis* is found to be closer

to the crown clade by one derived character for which *Limenavis* exhibits the primitive state, the single local autapomorphy of *Limenavis* (23) is missing data for *Lithornis*.

And similarly, the two autapomorphies of *Lithornis* (35, 47) are missing data in *Limenavis patagonica.* An increase in tree length of one additional step is necessary for *Limenavis* to be placed alternatively as the sister taxon of *Lithornis,* or closer to the crown clade than this latter taxon.

Virtually all specimens of Mesozoic carinates consist of single postcranial elements, and it has been common practice to assign these isolated and often fragmentary bones to modern "orders" (e.g., Brodkorb, 1963; Cracraft, 1972; Olson and Parris, 1987). Of the several Mesozoic carinates known by more than isolated bones (table 1), only *Ichthyornis, Ambiortus,* and now *Limenavis* have been included in phylogenetic analyses. Interestingly, all of these taxa have been found to be outside the crown clade. The presence of at least five lineages of the crown clade in the Cretaceous has been suggested (see literature in Chiappe, 1995a; Padian and Chiappe, 1998). However, the timing of the diversification of modern avian lineages remains the topic of much debate (Chiappe, 1995a; Feduccia, 1995; Hedges et al., 1996; Cooper and Penny, 1997; Bleiweiss, 1998; Stidham, 1998; Dyke and Mayr, 1999; Marshall, 1999).

Given that *Ichthyornis* is known from the Upper Cretaceous (Marsh, 1880; Lucas and Sullivan, 1982; Fox, 1984; Parris and Echols, 1992), that the lineage leading to modern birds must be present from this time onward is apparent when ghost lineages (Norell, 1992) are projected for these taxa. However, such inference constrains only the minimum age of divergence for the modern avian stem lineage and does not speak to the question of the timing of divergences within crown-clade birds (Dingus and Rowe, 1998). That *Limenavis* is placed outside the crown clade does not provide evidence either for or against the question of a Cretaceous divergence time for modern birds.

However, the results of the current analysis fit a concordant pattern, of admittedly negative evidence, seen in the Mesozoic fossil record of mammals (Novacek et al., 1998). In the case of mammals, there is no evidence for any part of modern placentals or marsupials in the Cretaceous, either from fossils or from estimating ghost lineages (Novacek et al., 1998). As more complete specimens have been described, Cretaceous taxa considered previously to be part of mammalian crown clades have been found to occupy more basal "stem" positions outside of these clades (Rougier et al., 1998). In the case of birds, *Limenavis,* known from relatively complete material for Mesozoic carinates, is just one more example of this apparent pattern, namely, that the more complete the specimen and the more comprehensive the analysis, the more these taxa are found to fall outside the respective crown clades. This suggests that given the amount of homoplasy expected for individual characters across an ingroup as large as that of crown-clade birds plus near sister taxa, the small numbers of characters preserved in fragmentary material (and often the only ones used in discussions of their phylogenetic affinities in noncladistic analyses) may often fail to represent the signal from the whole skeleton.

Strong evidence for the presence of lineages of extant birds in the Cretaceous should come from identifying synapomophies for all hierarchical levels such as that attempted in this analysis (e.g., Carinatae, Neognathae, Galliformes). Only more complete specimens of Mesozoic carinates, further phylogenetic analyses of the interrelationships of the major clades of modern birds, and further diagnoses of these clades, will allow better assessment of the presence of crown-clade lineages in the Cretaceous.

ACKNOWLEDGMENTS

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APPENDIX 1

List of 72 morphological characters used in this analysis. All characters are unordered except the eight otherwise specified.

1. Humerus, proximal end, caudal surface, dorsal margin, ''crista m. supracoracoidei'' (Baumel and Witmer, 1993), a proximodistally oriented, elongate scar distally to dorsal tubercle: (0) absent; (1) present.

2. Humerus, proximal end, capital incisure: (0) developed as a groove, open distally; (1) developed as a pit, closed distally.

3. Humerus, proximal end, proximal view, deltopectoral crest: (0) projected dorsally; (1) projected cranially.

4. Humerus, proximal end, dorsal tubercle: (0) absent; (1) present as a raised area of insertion; (2) present as a well-developed tubercle. (ORDERED)

5. Humerus, proximal end, ventral tubercle: (0) absent; (1) present.

6. Humerus, proximal end, ''transverse groove'': (0) absent; (1) present, developed as discreet depressed scar on proximal surface of bicipital crest; (2) present, developed as a transverse groove. (ORDERED)

7. Humerus, proximal end, one or more pneumatic foramina: (0) absent; (1) present.

8. Humerus, proximal end, pneumatic foramina: (0) minute perforation; (1) developed as a broad foramen or a cluster of multiple smaller foramina (i.e., extensive pneumatization).

9. Humerus, distal end, brachial fossa: (0) absent; (1) present, developed as a flat scar or as a fossa.

10. Humerus, distal end, dorsal supracondylar tubercle: (0) present; (1) developed as a distinct, proximally directed pointed process.

11. Humerus, distal end, dorsal supracondylar tubercle: (0) located approximately at the same level proximodistally as the attachment of the m. pronator superficialis on the ventral margin; (1) located far proximal to this attachment.

12. Humerus, distal end, dorsal supracondylar tubercle, pit-shaped fossa opening proximally: (0) absent; (1) present.

13. Humerus, distal end, dorsal supracondylar tubercle, two smaller fossae proximal and adjacent to larger fossa (see previous character): (0) absent; (1) present.

14. Humerus, distal end, dorsal surface, distalmost extremity, fossa, sometimes with two distinguishable subparts, or two fossae: (0) absent; (1) present.

15. Humerus, distal end, cranioventral surface, fossa m. pronator superficialis: (0) opening ventrally; (1) opening obliquely cranioventrally.

16. Humerus, distal end, distalmost ventral surface, fossae: (0) two fossae aligned proximodistally; (1) two fossae aligned craniocaudally; (2) one fossa developed cranially, and the other as a distally facing facet.

17. Humerus, distal end, cranial surface, ventral condyle: (0) length of long axis of condyle less than the same measure of the dorsal condyle; (1) equal to or greater than this measure.

18. Humerus, distal end, caudal surface, groove for passage of m. scapulotriceps: (0) absent; (1) present.

19. Ulna, proximal end, impression of m. brachialis: (0) a flat scar sometimes with a slightly raised proximocaudal edge; (1) a shallow fossa with a distinct, raised proximocaudal lip.

20. Ulna, proximal end, intercotylar crest: (0) nearly absent, depressions of two cotylae continuous; (1) present, so that outline of ventral cotyla is a bordered circle; (2) absent, cotyla separated by a groove.

21. Ulna, proximal end, process of the dorsal cotyla with a ridge extending caudodistally and forming the dorsal margin of the radial incisure: (0) absent; (1) present.

22. Ulna, proximal end, ventral surface, proximal view, caudal contact between ventral cotyla and olecranon: (0) concave; (1) flat to convex.

23. Ulna, proximal end, scar of the ligamentum collaterale ventrale (Baumel and Witmer, 1993): (0) impression of subequal length and width, mostly proximal to impression of m. brachialis; (1) impression proximodistally elongate, triangular, extending down caudal margin of brachial impression.

24. Ulna, distal end, ventral condyle, distal view, distinct ventral projection past angle of intercondylar surface: (0) absent; (1) present.

25. Ulna, distal end, dorsal condyle, dorsal trochlear surface, contact with body of ulna proximodorsally: (0) no dorsal extension of trochlear surface; (1) surface of dorsal condyle sloping smoothly into ulnar shaft; (2) present, surface abruptly truncate. (ORDERED)

26. Ulna, distal end, dorsal condyle, dorsal trochlear surface, extent along caudal margin:(0) less than transverse measure of dorsal trochlear surface; (1) equal to this measure; (2) greater than this measure.

27. Ulna, distal end, tendinal pit and groove: (0) absent; (1) present.

28. Ulna, distal end, tubercle adjacent to tendinal groove: (0) absent; (1) present.

29. Ulna, distal end, caudal surface, transverse muscle impression: (0) absent; (1) present.

30. Radius, proximal end, bicipital tubercle: (0) absent; (1) present.

31. Radius, proximal end, dorsal view, prominent tubercle on edge of humeral cotyla: (0) absent; (1) present.

32. Radius, distal end, dorsal surface, tendinal groove(s), occupying most of dorsal surface: (0) absent, dorsal surface convex; (1) present.

33. Ulnare, ventral ramus (new term, equivalent to ''crus longum''; Baumel and Witmer, 1993): (0) shorter than dorsal ramus (new term equivalent to ''crus breve''; Baumel and Witmer, 1993); (1) same length as dorsal ramus; (2) longer than dorsal ramus. (ORDERED)

34. Ulnare, ventral ramus, proximoventral surface, tendinal groove: (0) absent or very faint impression; (1) present, developed as prominent longitudinal groove.

35. Ulnare, dorsal ramus, tubercle where this ramus joins the ventral ramus: (0) absent; (1) present.

36. Distal carpals and metacarpals: (0) incomplete proximal fusion; (1) complete proximal fusion; (2) complete proximal and distal fusion. (ORDERED)

37. Carpometacarpus, proximal end, ventral surface, infratrochlear fossa, deeply excavated proximal surface of pisiform process: (0) absent; (1) present.

38. Carpometacarpus, proximal end, ulnocarpal articular facet: (0) absent; (1) present; (2) well projected (i.e., distal extent approaching craniocaudal width of carpal trochlea). (ORDERED)

39. Carpometacarpus, proximal end, caudal view, metacarpal III: (0) joined to metacarpal II conspicuously ventrocaudally, appearing to contact only the distal extension of the ventral carpal trochlea; (1) joined to metacarpal II dorsally as far as the middle of shaft; (2) joined to metacarpal II conspicuously dorsocaudally as well as ventrocaudally.

40. Carpometacarpus, proximal end, ventral surface, ridge between metacarpal III and pisiform process: (0) absent; (1) present.

41. Carpometacarpus, proximal end, extensor process: (0) absent; (1) present.

42. Carpometacarpus, proximal end, caudal carpal fovea: (0) absent; (1) present.

43. Carpometacarpus, proximal end, supratrochlear fossa: (0) absent; (1) present.

44. Carpometacarpus, proximal end, fossa directly proximal and cranial to the supratrochlear fossa: (0) absent; (1) present.

45. Carpometacarpus, proximal end, intermetacarpal process: (0) absent; (1) present, developed as a small tubercle (i.e., ''tuberculum muscularis''; Stegmann, 1978); (2) present, developed as a conspicuous flange. (ORDERED)

46. Carpometacarpus, proximal end, metacarpal I, articulation with first phalanx: (0) produced as a gynglimus with a distal lip; (1) produced as a shelf.

47. Carpometacarpus, proximal end, ventral surface, conspicuous fossa caudodistal to pisiform process: (0) absent; (1) present.

48. Carpometacarpus, distal end, metacarpals II and III, articular surfaces for digits: (0) metacarpal III subequal to or surpassed by metacarpal II in distal extent; (1) metacarpal III surpassing metacarpal II in distal extent.

49. Carpometacarpus, distal end, ventral surface, cranioventrally projected distal process: (0) absent; (1) present.

50. Carpometacarpus, distal end, ventral surface, caudoventrally projected tubercle such that ventral surface appears concave in distal view: (0) absent; (1) present.

51. Carpometacarpus, distal end, tendinal groove of m. interosseus dorsalis (Stegmann, 1978): (0) absent; (1) ossified ridge present associated with the passage of the m. interosseus dorsalis in some living birds.

52. Carpometacarpus, distal end, interosseal groove, impression of m. interosseus palmaris or ventralis (Stegmann, 1978): (0) absent; (1) present, distinct impression for, or ossified bridge associated with, the passage of the tendon of this muscle in some living birds.

53. Phalanx I, digit II, distal extremity, projection of caudal margin farther than the distal artic-

ular surface (''internal index process''; Stegmann, 1978): (0) absent; (1) present.

54. Phalanx I, digit II, distal-most caudal margin: (0) sub-parallel to cranial margin; (1) bowed caudally.

55. Maxilla and dentary, teeth: (0) absent; (1) present.

56. Mandibular symphysis: (0) unossified; (1) ossified.

57. Palatine and pterygoid: (0) broadly overlapping contact; (1) reduced primarily dorsoventral contact.

58. Vomer and pterygoid: (0) broadly contacting; (1) noncontacting or trace contact.

59. Eustacian tubes: (0) opening laterally; (1) opening on, or close to cranial midline.

60. Quadrate, prootic and squamosal cotylae: (0) contiguous; (1) separated by an intercotylar incisure.

61. Dorsal vertebral series, articulations: (0) completely amphycoelous; (1) at least some of series heterocoelous.

62. Anyclosed sacral vertebrae number: (0) 10 or less; (1) 11 or more.

63. Scapula, acromium process: (0) blunt; (1) punctiform.

64. Tibiotarsus, distal end, extensor groove: (0) absent; (1) present (2) present and bridged by an osseous supratendinal bridge. (ORDERED)

65. Sternum, cranial edge, coracoidal sulci: (0) mediolaterally adjacent; (1) crossed on midline.

66. Coracoid, foramen marking the passage of the m. supracoracoideus nerve: (0) present; (1) absent.

67. Osseous continuation of the interorbital septum (mesethemoid) rostral to the posterior limit of external nares: (0) present; (1) absent.

68. Flange of proximal ischium contacting or closely approaching pubis: (0) absent; (1) present.

69. Ilium and ischium: (0) unfused caudally; (1) fused caudally (''ilioischiadic foramen'' closed).

70. Dorsal vertebrae, pnuematicity, central pleurocoels: (0) present; (1) absent.

71. Squamosal, ventral or ''zygomatic'' process: (0) long, closely following the angle of the quadrate ventrally; (1) short, close only to proximal head of the quadrate.

72. Tarsometatarsus, hypotarsus with distinct intertendinal grooves and ridges: (0) absent; (1) present.

APPENDIX 2

Data matrix: "?", condition not preserved; "N", noncomparable. The eight ordered characters, as indicated in the text of appendix 1 are 4, 6, 25, 33, 38, 45, 64.

Characters

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Confuciusornis sanctus	?	0	0	?	0	?	0	?	0	0	0	1	?	0	?	1	0	0	N	1	?	?	?	?	?	0	0	0	?	?	1	?	?	?	?
Enantiornithes	0	0	0	1	1	1	0	?	0	0	0	?	?	0	0	0	1	0	1	2	0	0	0	0	1	2	1	1	1	0	0	0	0	2	0
Ichthyornis	0	0	0	1	1	1	0	?	1	0	0	1	1	1	1	2	0	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	?	?	?
Limenavis patagonica	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	1	?	0	0	1	?	1	0	1	?	2	0	1	0	0	1	?	?	?	1
Tinamus guttatus	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	2	1	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	1	0
Pterocnemia pennata	1	N	1	N	N	N	0	N	N	0	0	0	N	1	0	2	1	0	0	0	1	N	N	0	0	0	N	N	0	N	0	N	N	N	N
Gallus gallus	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	2	0	1	0	0	0	1	0	1	2	0	1	0	1	0	0	0	1	0	0
Crax globulosa	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	2	0	1	0	1	0	0	0	0	2	0	1	1	1	0	1	0	1	0	0
Chauna torquata	0	0	1	2	1	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	2	0	1	0	0	0	1	1	2	0	1
Anas platyrhynchos	N	0	1	2	1	1	1	1	1	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1	2	1	1	1	0	0	1	1	2	1	1
Rallus longirostris	0	0	1	2	1	1	1	0	1	0	0	0	0	1	0	2	0	1	0	1	1	0	0	1	2	0	1	0	1	0	1	1	1	1	0
Grus grus	0	0	1	2	1	1	1	1	1	0	0	0	0	1	0	2	0	1	1	1	0	0	1	1	2	0	1	0	0	1	1	1	2	1	0
Numenius phaeopus	0	0	1	2	1	2	1	0	1	1	1	0	0	1	0	1	0	1	1	1	0	1	1	2	0	1	1	0	1	1	1	1	2	1	0
Burhinus capensis	0	0	1	2	1	1	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Columbia livia	0	0	1	2	1	2	1	1	1	0	1	0	0	1	1	1	0	1	0	1	0	1	0	1	2	0	1	1	1	0	1	1	2	1	0
Lithornis	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	2	0	0	1	0	1	0	?	0	2	0	1	0	0	1	1	1	1	1	1

Taxa	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
Confuciusornis sanctus	0	?	?	?	?	0	?	0	?	0	0	0	0	?	?	?	?	0	0	1	?	0	?	?	1	0	0	0	0	?	?	?	0	0	0	0	0
Enantiornithes	1	0	0	2	1	0	0	1	0	0	?	?	1	?	?	?	?	0	0	0	0	0	1	?	?	0	0	0	0	0	0	?	0	0	0	?	0
Ichthyornis	2	1	0	?	0	1	1	1	1	0	1	0	0	1	1	1	1	0	0	0	?	?	?	0	0	0	1	1	1	0	?	?	?	0	?	?	?
Limenavis patagonica	2	1	?	?	?	1	?	1	1	?	1	?	0	1	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tinamus guttatus	2	0	2	0	1	1	1	1	1	1	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1	1	1	0	1	0	1
Pterocnemia pennata	2	0	1	1	N	0	1	1	1	1	0	0	0	N	N	0	0	0	1	1	1	0	0	0	0	1	1	0	1	0	1	1	1	0	1	0	1
Gallus gallus	2	0	1	0	0	1	1	1	2	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	0	2	0	1	0	1	1	1	1	1
Crax globulosa	2	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	2	0	1	0	1	1	1	1	1
Chauna torquata	2	0	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	2	0	1	0	1	1	1	1	1
Anas platyrhynchos	2	0	0	2	0	1	1	1	1	0	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	2	0	1	0	1	1	1	1	1
Rallus longirostris	2	1	0	2	1	1	1	1	1	0	1	0	0	0	1	0	1	0	0	N	1	1	1	1	1	1	1	1	0	2	0	0	0	1	1	1	1
Grus grus	2	0	0	2	0	1	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	2	0	0	0	1	1	1	1	1
Numenius phaeopus	2	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	2	0	0	0	1	1	0	1	1
Burhinus capensis	2	0	0	1	0	1	1	1	1	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	2	1	0	0	1	1	N	1	1
Columbia livia	2	0	0	2	0	1	1	1	1	1	0	1	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	0	2	0	1	0	1	1	1	1	1
Lithornis	2	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	1	1	1	1	0	1	1	?	1	0	1