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Authors: CLARKE, JULIA A., and NORELL, MARK A.

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The Morphology and Phylogenetic Position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia

JULIA A. CLARKE¹ AND MARK A. NORELL²

ABSTRACT

The avialan taxon *Apsaravis ukhaana* from the Late Cretaceous of southern Mongolia is completely described and its phylogenetic position is evaluated. *Apsaravis ukhaana* is from continental sandstones exposed at the locality of Ukhaa Tolgod, Omnogov Aimag, Mongolia. The holotype specimen consists of the nearly complete, articulated skeleton of a small volant avialan.

Apsaravis ukhaana is unambiguously differentiated from other avialans based on the presence of several unique morphologies: a strong tubercle on the proximal humerus, a hypertrophied trochanteric crest on the femur, and extremely well-projected posterior wings of a surface of the distal tibiotarsus that in Aves articulates with the tibial cartilage. Ten other homoplastic characters optimize as autapomorphies of *Apsaravis ukhaana* in the phylogenetic analysis. They are as follows: ossified mandibular symphysis; dentary strongly forked posteriorly; hooked acromion process on scapula; highly angled dorsal condyle of humerus; humeral condyles weakly defined; distal edge of humerus angling strongly ventrally; humerus flared dorsoventrally at its distal terminus; lateral condyle of tibiotarsus wider than medial one; neither condyle of tibiotarsus tapering toward the midline; and metatarsal II trochlea rounded rather than ginglymoid.

Phylogenetic placement of *Apsaravis ukhaana* as the sister taxon of Hesperornithes + Aves resulted from analysis of 202 characters scored for 17 avialan ingroup taxa. The implications of *Apsaravis ukhaana*, and the results of the phylogenetic analysis, for the evolution of flight after its origin and character support for enantiornithine monophyly are extensively discussed.

¹ Frick Postdoctoral Fellow, Division of Paleontology, American Museum of Natural History. e-mail: jclarke@amnh.org

² Curator and Chair, Division of Paleontology, American Museum of Natural History. e-mail: norell@amnh.org

INTRODUCTION

The holotype specimen of *Apsaravis ukhaana* (figs. 1–3) was discovered during the 1998 field season of the Mongolian Academy of Sciences/American Museum of Natural History Paleontological Expeditions. It was recovered from the Camel's Humps sublocality of Ukhaa Tolgod, a locality in the Nemegt Basin of southern Mongolia known for abundant, exquisitely preserved vertebrate fossils (Dashzeveg et al., 1995; fig. 4). Fossils from Ukhaa Tolgod, including the holotype specimen of *Apsaravis ukhaana*, are from a structureless red sandstone facies attributed to the Djadokhta Formation (Loope et al., 1998). The continental Djadokhta Formation is considered late Campanian to early Maastrichtian in age (Loope et al., 1998). The sandstone facies were originally considered to have an aeolian origin (Jerzykiewicz et al., 1993), but recently have been reinterpreted (Loope et al., 1998) as representing dune-sourced alluvial fan deposits. These deposits are inferred as derived from alternatively active and stabilized dune fields that developed under fluctuating conditions ranging from xeric to mesic (Loope et al., 1998).

In an earlier paper (Norell and Clarke, 2001), we gave a brief description of *Apsaravis ukhaana* and its phylogenetic position. We discussed its importance as one of only a handful of specimens placed phylogenetically as near outgroups of Aves and represented by more than a single bone (Norell and Clarke, 2001; Clarke and Norell, 2001). Implications of *Apsaravis ukhaana* for the evolution of the flight stroke in theropod dinosaurs, for support of enantiornithine monophyly and for previously proposed patterns of avialan ecological diversification outlined in Norell and Clarke (2001) and Clarke and Norell (2001) are further explored in this paper.

INSTITUTIONAL ABBREVIATIONS: **AMNH** American Museum of Natural History; **BMNH** British Museum of Natural History, London; **IGM** Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar; **IVPP** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **GMV** National Geological Museum of China, Beijing; **MACN** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Ai-

res; **SMM** Sternberg Memorial Museum, Hays; **USNM** United States National Museum, Washington DC; **YPM** Yale Peabody Museum, New Haven.

MATERIALS AND METHODS

Osteological, arthrological, and myological nomenclature follows Baumel and Witmer (1993), Baumel and Raikow (1993), and Van den Berge and Zweers (1993), where possible. When these authors did not name osteological structures, or discuss muscles, terms from other sources were used and cited. English equivalents of the Latin osteological nomenclature of all authors were used. The terms of orientation for the anatomical position of a bird, as specified by Clark (1993), were followed with one exception. The "time-honored" terms (Clark, 1993) of zoological nomenclature "anterior" and "posterior" were used, rather than "cranial" (and "rostral") and "caudal" as proposed by Clark (1993) in the *Handbook of Avian Anatomy: Nomina Anatomica Avium* (Baumel et al., 1993). Clark (1993) suggested that "cranial" and "caudal" should be preferred because "anterior" and "posterior" in other vertebrates correspond to "dorsal" and "ventral" as used in human anatomy. However, it seems to us that Clark's (1993) solution is an imperfect one, resulting in the superfluous creation of a special terminology for Aves (or operationally Avialae); although Clark (1993) advocated the use of "cranial" and "caudal" for all vertebrates, the influence of the *Handbook* (Baumel et al., 1993) remains largely limited to those interested in avialan anatomy. Such special terminologies can hinder comparison between avialan morphologies and those of all other vertebrates.

The phylogenetic definitions of taxon names used herein are as follows: "Avialae" is used sensu Gauthier (1986) as a node-based name for the most recent common ancestor of *Archaeopteryx* + Aves and all of its descendants. "Ornithurae" (Haeckel, 1866) is used as an apomorphy-based name (de Queiroz and Gauthier, 1992) sensu Gauthier and de Queiroz (2001: 27) for the "clade stemming from the first panavian with a 'bird tail,' namely, a tail that is shorter than the femur (subequal to or shorter than the

tibiotarsus) with a pygostyle of avian aspect . . . that is homologous (synapomorphic) with that of Aves (*Vultur gryphus*; Linnaeus, 1758)". This usage differs from that of previous authors who have applied this name to a variety of more or less inclusive clades (see discussion in Gauthier and de Queiroz, 2001). The currently known contents of this Ornithurae are approximately the clade comprised of the last common ancestor of *Apsaravis ukhaana* and Aves and all of its descendants. However, as noted above, "Ornithurae" is an apomorphy-based name and is not defined with reference to *Apsaravis ukhaana*. "Aves" (Linnaeus, 1758) is used for the last common ancestor of extant birds and all of its descendants as defined in Gauthier (1986) using the internal referents *Ratitae*, *Neognathae*, and *Tinami*. This usage is consistent with that of Gauthier and de Queiroz (2001), although the specifiers used by those authors to bracket the avian crown clade are species taxa. "Neoaves" (Sibley et al., 1988) is used following Gauthier and de Queiroz (2001) as a node-based name for the last common ancestor of all extant neognaths more closely related to *Passer domesticus* than to *Galloanserae*. The definitions of the names "Aves" and "Avialae" preferred here have been used by an array of workers (e.g., Gatesy and Dial, 1996; Holtz, 1996, 2001; Brochu and Norell, 2000; Norell and Makovicky, 1997, 1999; Norell et al., 2001; Rayner, 2001); however, their usage remains contentious (see Gauthier and Gall, 2001).

The clade notation in the text, "taxon + taxon", refers to the last common ancestor of the two given taxa and all of its descendants. It does not imply that these taxa share a sister taxon relationship. Numbers in parentheses used throughout the text (e.g., 81:0) refer to characters and their correspondent states as listed in appendix 2.

SYSTEMATIC PALEONTOLOGY

THEROPODA MARSH, 1881
(sensu GAUTHIER, 1986)

AVIALAE GAUTHIER, 1986

ORNITHURAE HAECKEL, 1866
(sensu GAUTHIER AND DE QUEIROZ, 2001)

Apsaravis ukhaana Norell and Clarke, 2001

HOLOTYPE: IGM 100/1017. The holotype is a nearly complete skeleton in partial artic-

ulation (figs. 1, 2, 3, 5–23). It is comprised of the following elements: a crushed skull with a ring of scleral ossicles in the left(?) orbit; incomplete left quadrate, partial left jugal, partial mandible; 12 cervical vertebrae, 7 thoracic vertebrae; 10 ankylosed sacral vertebrae; 5 free caudal vertebrae; a pygostyle, fragmentary thoracic ribs; fragment of the anterior sternum, both scapulae; both coracoids, both humeri, ulnae, radii, radiale, right ulnare, partial right and left carpometacarpus, right phalanx one of manual digit II; ilia, ischia (right missing distal end); pubes (right, fragmentary); both proximal femora, both distal tibiotarsi; both tarsometatarsi (co-ossified metatarsals II–IV); incomplete series of pedal phalanges of digits II–IV from both feet. Several of these phalanges including three unguals were prepared apart from the main block and are preserved together in a separate, unfigured block. The distal end of the right humerus was removed from the block and prepared separately. Also, a small, midshaft section from the right radius was removed for study (compare figs. 1 and 12).

DIAGNOSIS: *Apsaravis ukhaana* can be differentiated from other avialans based on the unique presence of a tubercle on the proximoposterior humerus (see below), a hypertrophied trochanteric crest on the femur, and well-projected wings of the posterior trochlear surface of the tibiotarsus (Norell and Clarke, 2001; trochlea cartilaginosa tibialis; Baumel and Witmer, 1993). Ten other characters optimize as autapomorphies of *Apsaravis ukhaana* in the phylogenetic analysis. They are as follows: (6:1) ossified mandibular symphysis; (42:1) dentary strongly forked posteriorly; (104:1) hooked acromion process on scapula; (120:1) highly angled dorsal condyle of humerus; (121:1) humeral condyles weakly defined; (122:1) distal edge of humerus angling strongly ventrally; (123:1) humerus flared dorsoventrally at its distal terminus; (182:2) lateral condyle of tibiotarsus wider than medial; (183:1) neither condyle of tibiotarsus tapering toward the midline; and (197:1) trochlea metatarsal II rounded rather than ginglymoid. All of these autapomorphies are the same as in Norell and Clarke (2001), with the exception of character 102. This character was eliminated because based on observation of additional



Fig. 1. *Apsaravis ukhaana*, holotype (IGM 100/1017). See appendix 1 for anatomical abbreviations.

specimens, we could not define discrete, non-arbitrary, states describing scapular blade width. A narrow intercondylar groove on the tibiotarsus (184:1 in Norell and Clarke [2001] and the current analysis) is now ambiguously optimized with the inclusion of *Vorona berivotrensis*, which also has the derived state for this character (Forster et al., 1996).

DESCRIPTION

Skull

The skull is crushed against the right forelimb (fig. 1). The left(?) orbit contains a poorly preserved ring formed by an uncertain number of sclerotic ossicles (fragments of approximately 12 are visible; fig. 1). Close to the left orbit, and near phalanx 1 of right manual digit

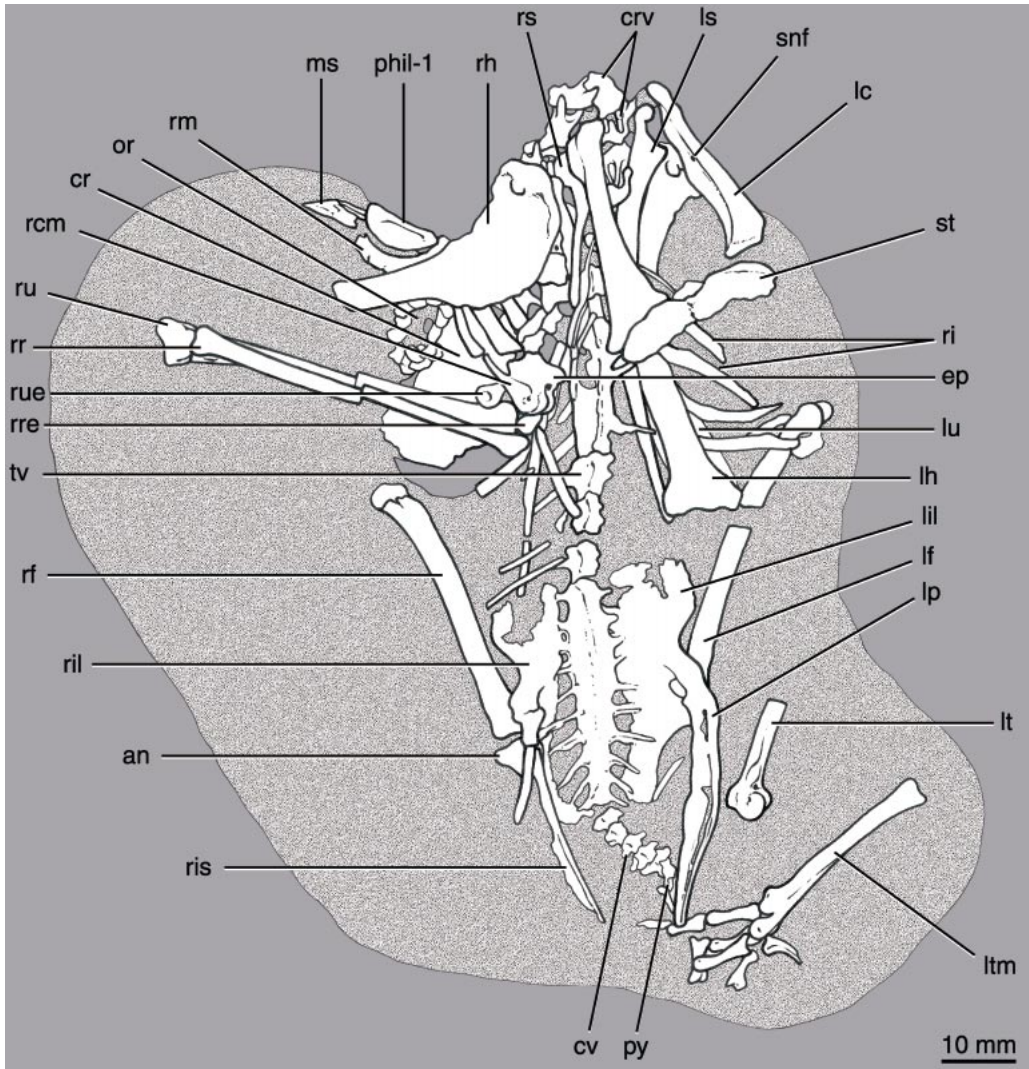


Fig. 1. Continued.

II, the partial right mandible is preserved as a crushed arch of bone (fig. 1). Part of the mid-section of the left jaw is visible on the underside of the holotype block (figs. 2, 3, 5–7). A splint of bone lying parallel to the left jaw may be part of the left jugal (figs. 5, 6). If so, it would lack an ascending process separating the orbit from the subtemporal fenestra. Conservatively, *Apsaravis ukhaana* was scored as missing data for jugal characters (e.g., 50) in our analysis, because the element preserves no morphologies to unambiguously identify it as the jugal. The dentaries are edentulous and

fused into an osseous symphysis (figs. 1, 7); posteriorly they are strongly forked (figs. 5, 6). The ossified symphysis is short, in contrast to some other basal avialans (e.g., *Confuciusornis sanctus*). On the lateroproximal surface of the right dentary, a row of small foramina parallels its dorsal edge; however, due to abrasion, they are now preserved as a shallow groove (fig. 7).

A fragment of the left quadrate identified as the otic process is pressed against the posterior cranium (fig. 5). Norell and Clarke (2001) tentatively made this identification, which is considered supported on further



Fig 2. Underside of the *Apsaravis ukhaana* (IGM 100/1017) holotype block.

study of the specimen. Two additional characters were then scored for *Apsaravis ukhaana* (i.e., 35 and 36) to reflect this new information. The capitulae are not widely separated by a deep intercapitular incisure (fig. 5); however, as these articular surfaces are abraded, it is not possible to discern their degree of individuation (see character 36). The

expanded posterodorsal tip of the otic process of the quadrate is slightly hooked. The morphology of the ventral portion of the quadrate is not discernable.

Vertebral Column

Twelve cervical vertebrae are preserved. However, the anteriormost cervicals are

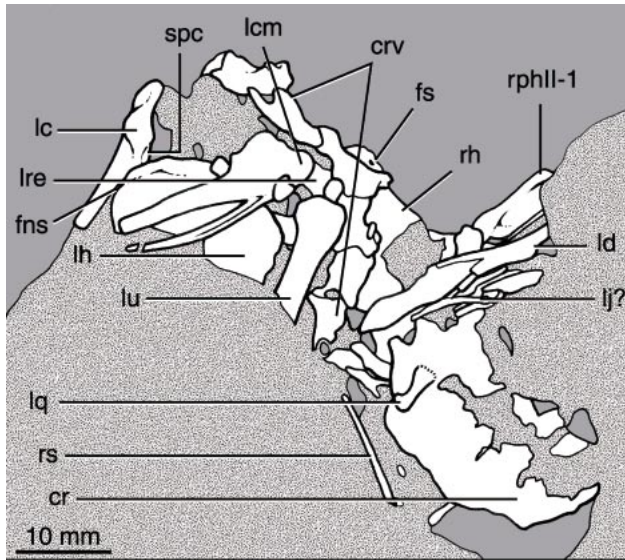


Fig. 3. Detail of morphologies exposed on the underside of the *Apsaravis ukhaana* holotype block. See appendix 1 for anatomical abbreviations.

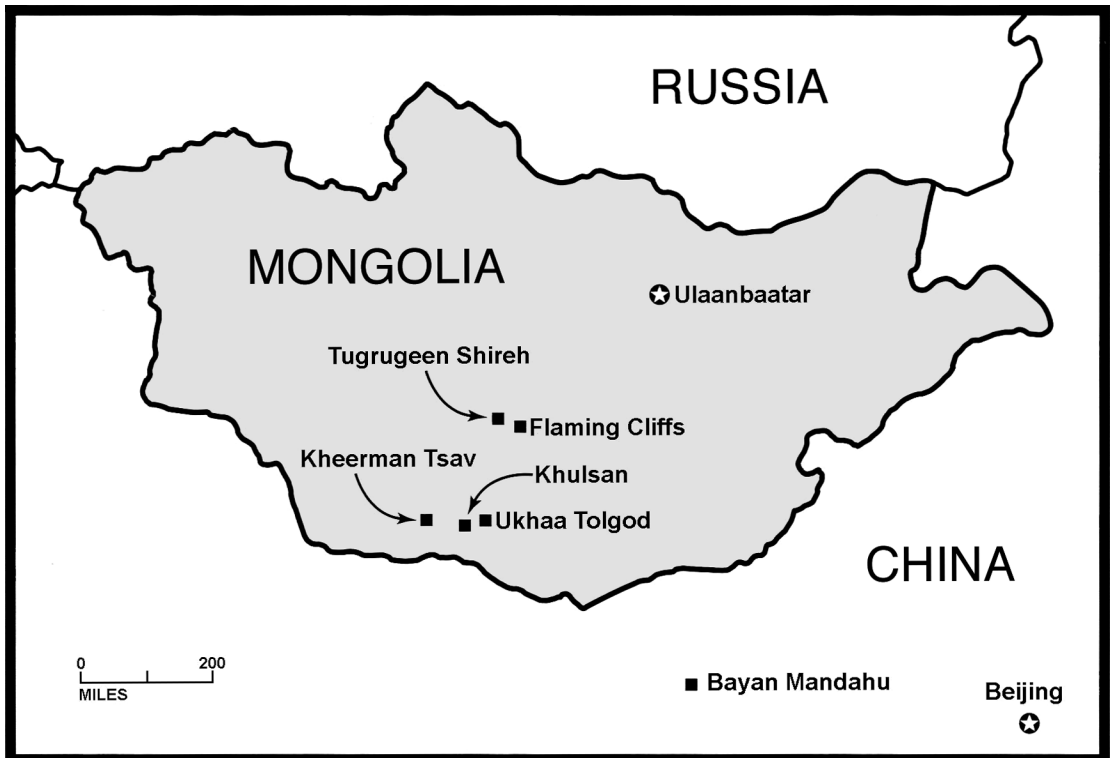


Fig. 4. Map of Mongolia indicating the locality of Ukhaa Tolgod, where the holotype specimen of *Apsaravis ukhaana* was collected.



Fig. 5. Detail of the cranium, the anterior cervical vertebrae, and the left jaw of the *Apsaravis ukhaana* holotype specimen. See appendix 1 for anatomical abbreviations.

poorly preserved, and the atlas–axis complex is not distinguishable, making the total number of presacral vertebrae unknown in *Apsaravis ukhaana*. The midseries cervicals are comparatively well preserved and clearly heterocoelous (fig. 8). These vertebrae have conspicuously elongate pre- and postzygapophyses and arched postzygapophyses. Cervical ribs are fused and completely enclose transverse foramina (fig. 8).

Six opisthocoelous thoracic vertebrae with very shallow lateral depressions are exposed (fig. 9). An additional rib indicates the pres-

ence of a seventh vertebra. Aves possess 5–10 thoracics, while more primitive avialans have 12 or more (Chiappe, 1996). Well-developed ventral processes are not preserved on either the posterior cervicals or anterior thoracics. Two of the anteriormost thoracics are extremely poorly preserved and may have been fused to each other (fig. 9). Because fusion only in this anteriormost part of the thoracic series is not known in Aves, it is considered more likely that the edges of these vertebrae are simply not preserved. Martin (1983) considered two fused anterior

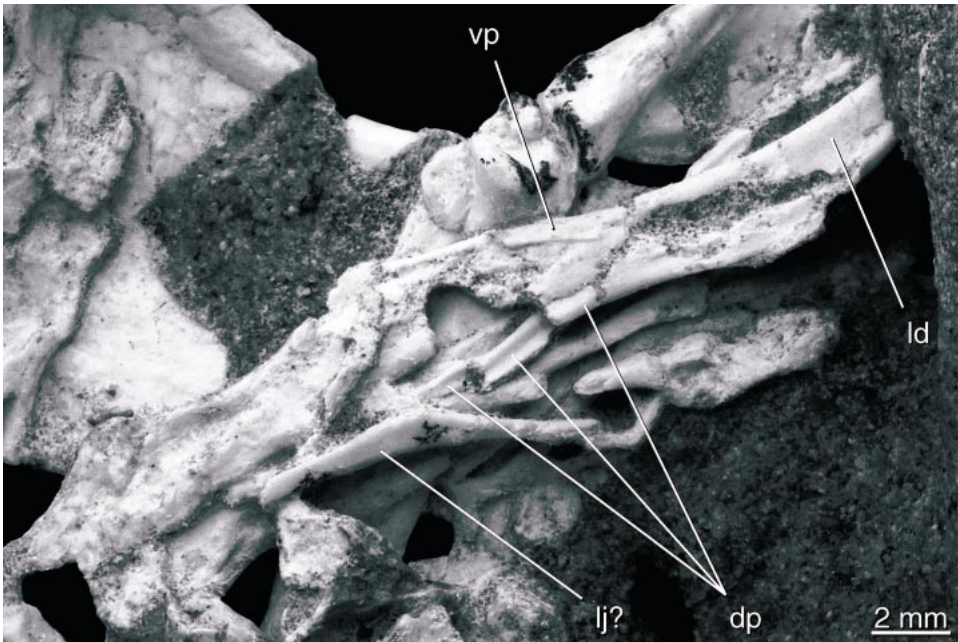


Fig. 6. The left jaw and jugal of *Apsaravis ukhaana*. Note the dorsal and ventral processes of the posterior left dentary. See appendix 1 for anatomical abbreviations.

thoracics to be present in *Archaeopteryx lithographica* and to comprise an avian “notarium”. Gauthier (1986) considered the presence of a notarium to be a synapomorphy of the crown clade. However, the presence of a notarium does not optimize as primitive to the crown clade (Clarke, 2002; this analysis). The *Archaeopteryx lithographica* condition would not optimize as homologous with either the condition in *Apsaravis ukhaana* or that derived within Aves, even if fusion was established to be present in both of these fossil taxa.

The sacrum is formed of 10 completely ankylosed vertebrae (figs. 1, 10). Ten or more sacral vertebrae are only known for Hesperornithes, *Ichthyornis dispar*, and Aves, while nine or fewer are present in more basal avialans (e.g., Chiappe, 1996). All sacral vertebrae in *Apsaravis ukhaana* have conspicuous transverse processes in ventral view (fig. 10), and spinal nerve openings along the entire sacral series are equally spaced (fig. 10), indicating that midseries sacral vertebral centra are equal in length. In contrast, in *Ichthyornis dispar* (and optimized as primitive to Aves) three or more midseries sacral verte-

brae have short centra with diminutive, dorsally directed transverse processes (not visible in ventral view; Clarke, 2002).

Apsaravis ukhaana has five free caudal vertebrae and a completely ankylosed and strongly mediolaterally compressed pygostyle. The pygostyle is broken at its base and is missing its distal tip. However, it appears to have been short (figs. 10, 11). Because we cannot be certain of its exact length, we have scored this character (68) as missing data for *Apsaravis ukhaana*. No chevrons are preserved. The length of the transverse processes of the caudals approximates the width of their centra (fig. 11).

Pectoral Girdle and Ribs

Only the anterior margin of the sternum is preserved. The coracoid grooves are dorsoventrally broad (fig. 12) and adjacent to each other on this anterior edge of the sternum (fig. 13). Unlike the condition in *Ichthyornis dispar*, *Ambiortus dementjevi*, and *Lithornis*, they did not cross each other on the midline. In Hesperornithes, these grooves are widely separated. Coracoidal processes of the ster-

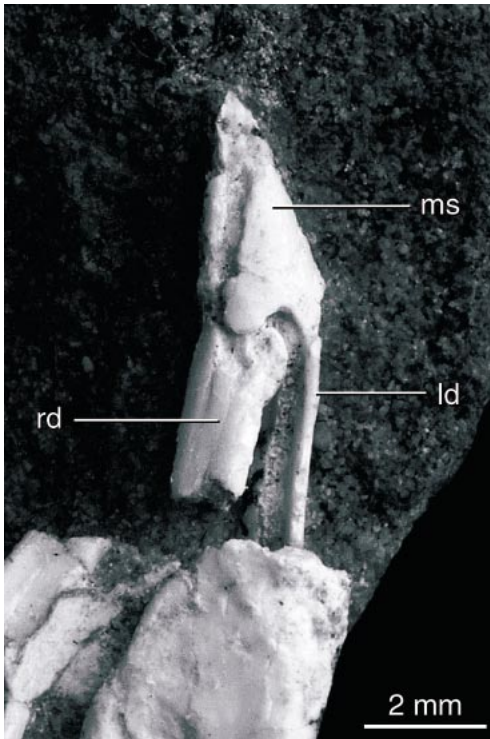


Fig. 7. Mandibular symphysis in ventral view. See appendix 1 for anatomical abbreviations.

num and facets for articulation of the sternal ribs are not preserved. A ventral median ridge extends posteriorly from the anterior edge of the sternum (fig. 12). This ridge is interpreted as indicative of the presence of an anterior sternal carina. An anterior ridge has so far been associated with an anteriorly developed keel in all known Avialae with this region preserved (Norell and Clarke, 2001; Clarke, 2002). An exclusively posterior medial ridge or keel is present in some enantiornithines and in *Confuciusornis sanctus* (Chiappe et al., 1999), but it is not associated with the presence of an anterior midline ridge. On the anterior surface of the sternal rostrum, there is a midline fossa bordered in part by a slight anterior projection of the dorsal lip of the sternum (figs. 13, 14A). No uncinata processes, gastralria, or a furcula are preserved.

The scapula is slightly less than twice the length of the coracoid; its narrow blade is curved and tapers distally (fig. 1). The acromion is long and has a strongly hooked an-

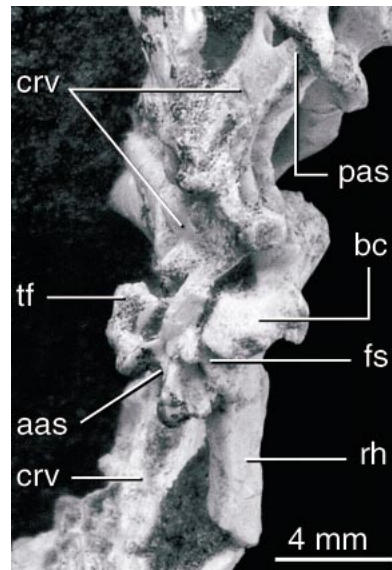


Fig. 8. Detail of the fifth and sixth preserved cervical vertebrae illustrating heterocoelous anterior and posterior articular surfaces. Also note the fossa on the anterior surface of the bicipital crest of the right humerus. See appendix 1 for anatomical abbreviations.

terior tip (fig. 12, 14), which does not narrow to a point as it does in the hooked acromion of lithornithids (Houde, 1988). The scapular articular surface for the coracoid is not developed as a robust hemispherical tubercle like in *Ichthyornis dispar* (Marsh, 1880). Instead, it is virtually unprojected and is developed as a slight boss (fig. 14). In *Hesperornis regalis*, the entire anterior end of the scapula is rounded and fits into the concave end of the coracoid while fusion of the coracoid and scapula is primitive for Avialae (e.g., Chiappe, 1996).

A concave scapular cotyla on the coracoid is developed in *Apsaravis ukhaana*, *Hesperornis regalis*, and *Ichthyornis dispar* (Clarke, 2002). However, the scapular cotyla in *Apsaravis ukhaana* is much shallower than in *Ichthyornis dispar*, corresponding to the more weakly developed coracoid articular surface of the scapula. The acrocoracoid process lies dorsal to a prominent, laterally projected, glenoid facet, and it does not hook medially (fig. 12). A procoracoid process is not present. Where this process is developed in other avialans, there is only a very slight

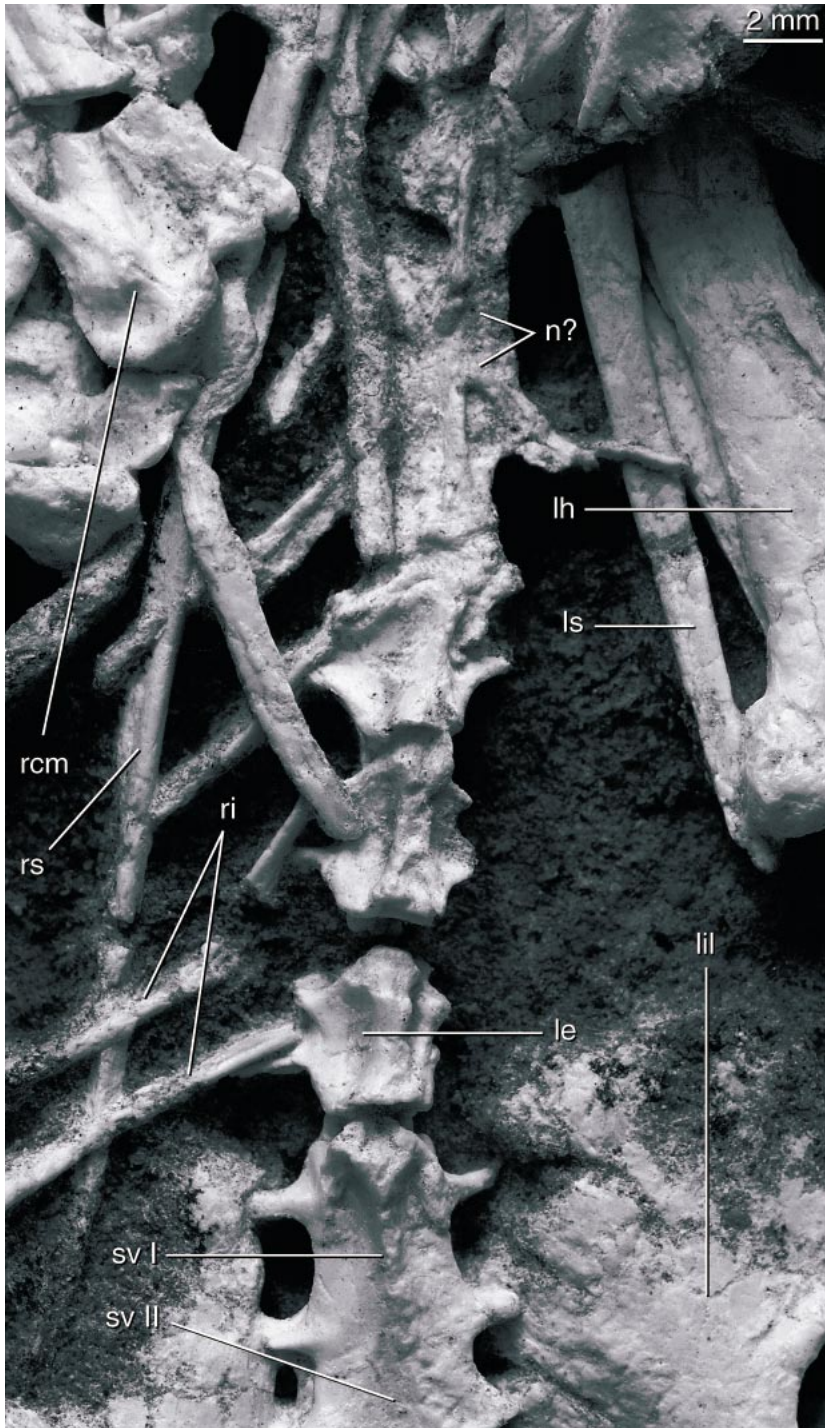


Fig. 9. Thoracic region of *Apsaravis ukhaana* showing its possible notarium and opisthocoelous thoracic vertebrae. See appendix 1 for anatomical abbreviations.

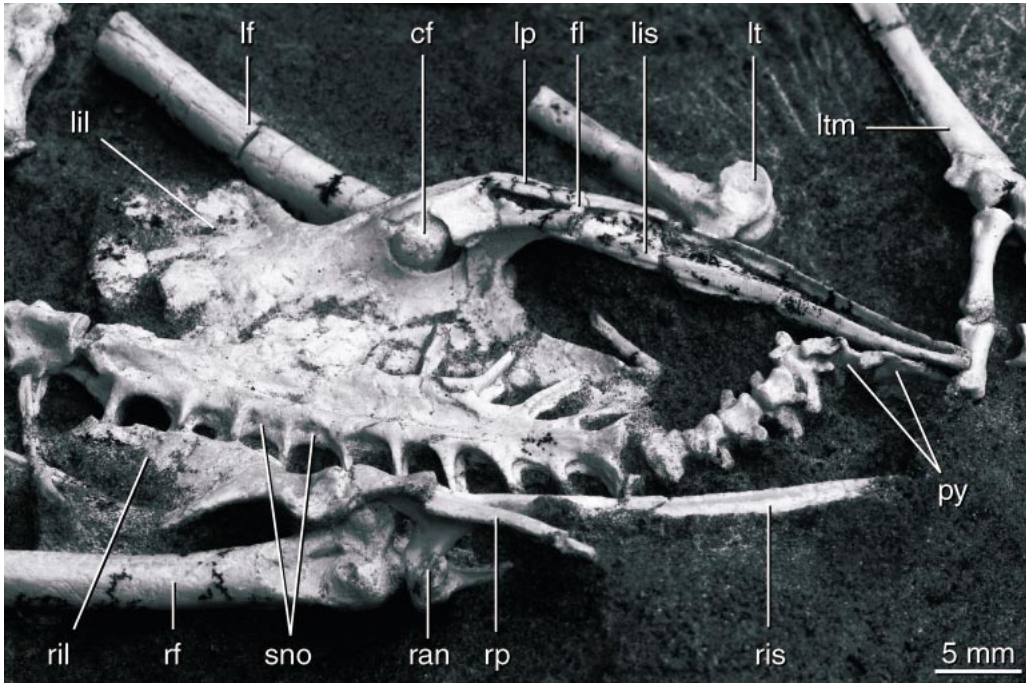


Fig. 10. Oblique ventral view of the *Apsaravis ukhaana* sacrum with ten fused sacral vertebrae. See appendix 1 for anatomical abbreviations.

bulging of the medial surface of the coracoid (fig. 14). Penetrating the medial surface of the coracoid, near its midpoint, is the supracoracoideus nerve foramen (fig. 14). A groove extends just proximal and distal to this foramen (fig. 14). The supracoracoideus nerve foramen exits into a deeply concave

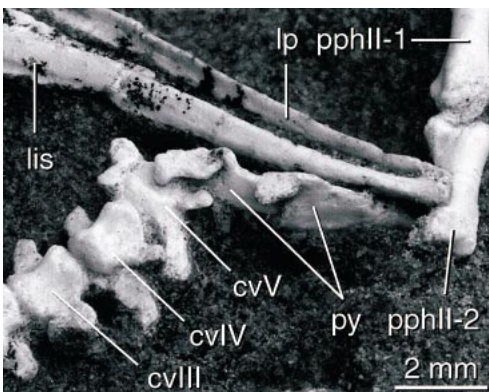


Fig. 11. Detail of posterior free caudal vertebrae and incomplete pygostyle. See appendix 1 for anatomical abbreviations.

dorsal surface just distal to the scapular cotyla (fig. 15). The concave dorsal coracoidal surface, location of the foramen, and development of a groove at its medial opening are morphologies developed in enantiornithine taxa (e.g., Chiappe, 1991; Chiappe and Calvo, 1994) as well as in *Apsaravis ukhaana*.

The coracoid's lateral margin is straight to slightly concave (fig. 12), unlike the convex margin of Enantiornithes (Chiappe, 1996). At the sternal articulation, the lateral margin flares into a diminutive lateral flange (fig. 12) of uncertain homology with the lateral process developed in some Aves and other avialans. This process bears a conspicuous muscle impression that extends proximally along the lateral margin of the coracoid (fig. 13). Elliptical foramina with irregular edges on the ventral surfaces (fig. 13) of the coracoids are probably artifacts.

Pectoral Limb

Both humeri were preserved in articulation with the radii and ulnae. However, the distal end of the right humerus was removed and

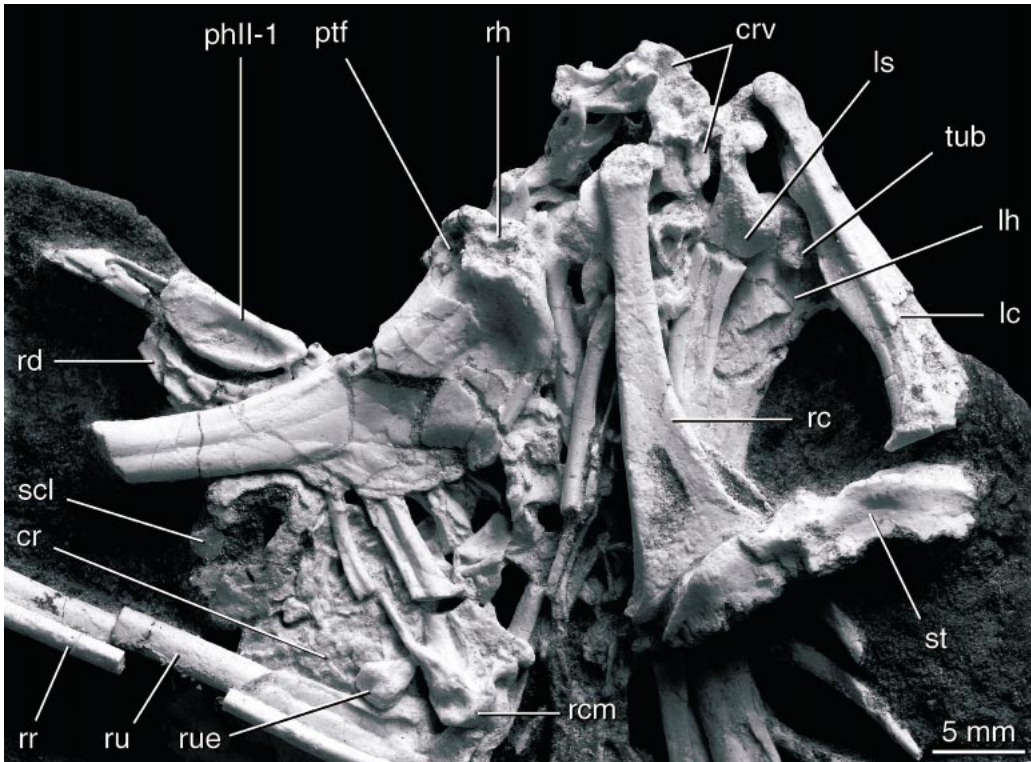


Fig. 12. Pectoral girdle of *Apsaravis ukhaana*. The coracoids and sternum are in ventral view. See appendix 1 for anatomical abbreviations.

prepared to expose its anterior surface (fig. 16). The humeral head is globose and projects more proximally than does the deltopectoral crest (fig. 12), a condition known for

Ichthyornis dispar and Aves, but not present in *Patagopteryx deferrariisi* or Enantiornithes (Chiappe, 1996). The deltopectoral crest in *Apsaravis ukhaana* is dorsally directed, as

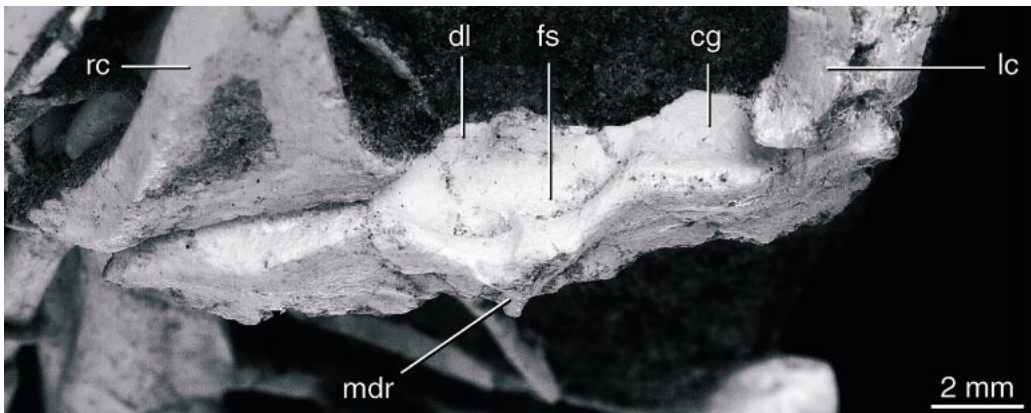


Fig. 13. Anterior view of sternum indicating the unusual midline fossa and coracoidal grooves. The midline ridge on the sternum's ventral surface is also visible. See appendix 1 for anatomical abbreviations.

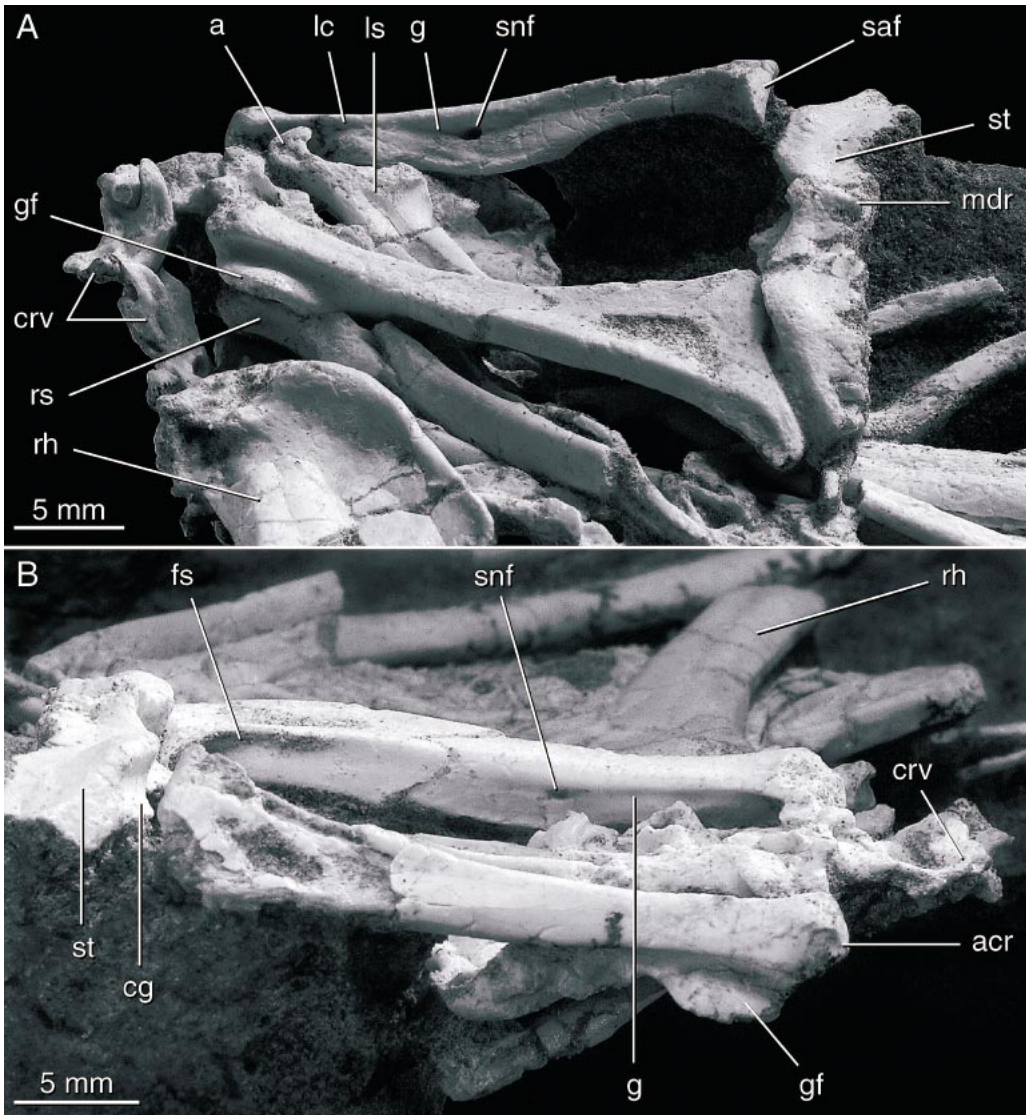


Fig. 14. Pectoral girdle in (A) oblique right-ventral view and (B) oblique left-ventral view. See appendix 1 for anatomical abbreviations.

opposed to the condition in Aves where it is anteriorly projected (fig. 12). The deltopectoral crest is relatively large and projects dorsally approximately the width of the humeral shaft (fig. 12).

The posterior surface of the deltopectoral crest is concave proximally (fig. 12). A shallow pneumotricipital fossa is present but does not contain a pneumatic foramen (fig. 12). The ventral tubercle lies adjacent to the pneumotricipital fossa (fig. 12). A marked

capital incisure is not developed. An unusual, second, equally developed tubercle (“tub” in fig. 12) protrudes from the posterior surface distal to the humeral head and dorsal to the pneumotricipital fossa. It lies in the position of a muscle insertion that within Aves (e.g., in Galliformes and Tinamidae) sometimes distally “closes” the capital incisure. However, this insertion where developed in Aves is not projected as extensively as it is in *Ap-saravis ukhaana*. On the anterior surface of

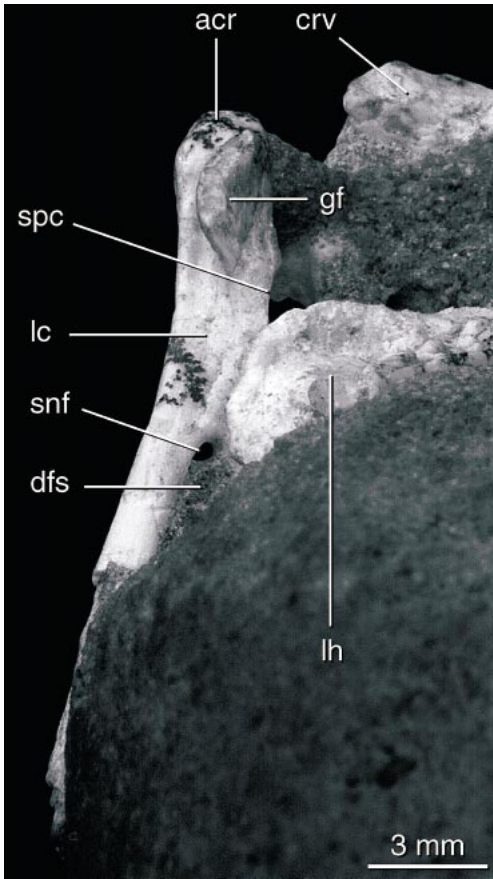


Fig. 15. Dorsolateral view of left coracoid. Note supracoracoideus nerve foramen opening into the top of the dorsal fossa. See appendix 1 for anatomical abbreviations.

the bicipital crest of the right humerus lies a pit-shaped fossa (figs. 2, 8). This area of the left humerus is covered by matrix. A fossa in the position observed in *Apsaravis ukhaana* has been considered a synapomorphy of Enantiornithes (Sanz et al., 1995; Chiappe, 1996). The entire anterior surface of the bicipital crest is projected and slightly bulbous (fig. 8). On the anteroventral edge of the left humerus, the impression of the lig. acrocoracohumerale (“transverse groove”) is developed as a fossa rather than as a groove (fig. 8).

The anterior surface of the distal humerus is somewhat crushed, but the condyles are clearly visible developed on this surface as in other basal avialans (Chiappe, 1996; fig.

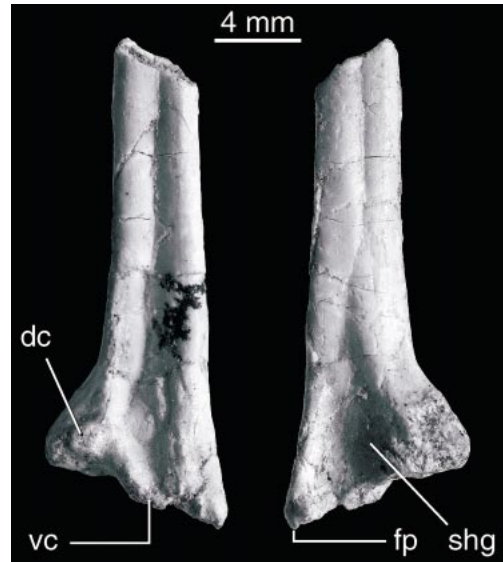


Fig. 16. Right distal humerus in anterior (left) and posterior (right) views. See appendix 1 for anatomical abbreviations.

16). The distal humerus is anteroposteriorly compressed and expanded dorsoventrally, giving the entire distal end a “spatulate” appearance (fig. 16). The dorsal condyle angles ventrally at a relatively high angle (more than 45°) to the axis of the humeral shaft. The ventral condyle is developed as a weak, “straplike” ridge at the distal edge of the anterior surface (fig. 16). These last three conditions have been considered characteristic of enantiornithines (Chiappe, 1996). A brachial fossa or scar is not visible.

The posterior humeral surface is depressed ventrally by a poorly defined olecranon fossa and by the impression of the m. humerotriceps (fig. 16). The m. scapulo-triceps groove is not developed. The entire distal margin of the humerus angles ventrally as in Enantiornithes (Chiappe, 1996; fig. 16). This morphology has also been referred to as the presence of a well-developed flexor process in Enantiornithes (e.g., Chiappe, 1996).

The ulna and humerus are approximately the same length (fig. 1). Proximally, the ulna has a well-developed olecranon process and a large bicipital tubercle (fig. 17). The dorsal and ventral cotylae were not separated by a groove as in some enantiornithines (Chiappe, 1991; fig. 17). The distal end of the ulna is

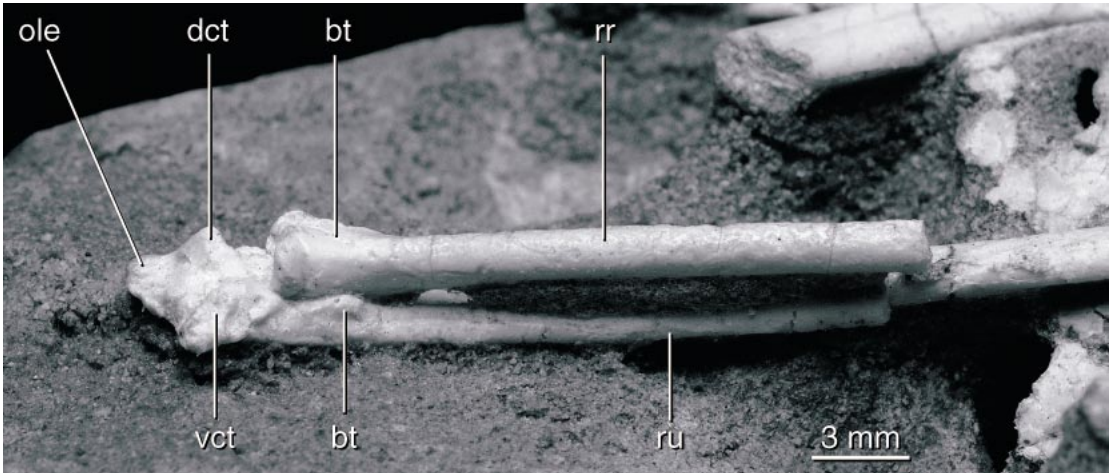


Fig. 17. Right ulna and radius in dorsal view. See appendix 1 for anatomical abbreviations.

semilunate, and the carpal tubercle is well developed (fig. 2).

The nearly straight radius is approximately half the width of the ulna (fig. 17). Proximally, it has a conspicuous bicipital tubercle (fig. 17), which is also present in *Ichthyornis dispar*. It lacks the deep longitudinal groove seen in Enantiornithes (Chiappe and Calvo, 1994) and bears a flat muscle scar in this area as in Aves. Radiale are preserved in rough articulation with the carpal trochlea in both wrists (figs. 3, 18). The ventral ramus (“long arm”) and part of the body of the ulnare are visible in close association with the posterior carpometacarpus (fig. 18).

The semilunate carpal and metacarpals I, II, and III are firmly ankylosed proximally (fig. 18). Whether metacarpals II and III were also fused distally is unknown because the distal extreme of the left carpometacarpus is not preserved and that of the right is almost completely obscured by the right humerus (figs. 5, 6). A pisiform process is connected by a low ridge to metacarpal III (fig. 18). A shallow infratrochlear fossa is developed just proximal to the pisiform process (fig. 18). The carpal trochlea is incised with a strong midline groove (fig. 18), unlike the condition in *Ichthyornis dispar*. Metacarpal III is flat, bowed caudally, and much less than half the width of metacarpal II (fig. 18). Its anterior surface bears a muscular depression. Such a depression in Aves is associated with the attachment of the mm. interossei (Baumel and

Witmer, 1993) and is notably present in Enantiornithes, *Ichthyornis dispar*, and Aves. In Aves, these muscles are responsible for flexion, extension, and elevation of the phalanges of the second digit (Raikow, 1985).

A projected extensor process is developed on the proximal end of metacarpal I (fig. 18). The anterior margin of metacarpal I is concave between the process and the slightly flared phalanx 1 articulation (fig. 2) and unlike the broadly convex condition found in *Confuciusornis sanctus* and enantiornithines (Norell and Clarke, 2001). The proximal surface of metacarpal I is excavated by a deep anterior carpal fovea (fig. 18). Distally, the articulation for the first phalanx is developed as a weak ridge, rather than primitively as a ginglymus (fig. 2). A small fragment of the first phalanx of digit I of the left hand is preserved against this surface (fig. 2).

The right proximal phalanx of digit II is preserved in articulation with metacarpal II (figs. 1, 5). The posterior surface is strongly compressed dorsoventrally, and its edge is bowed posteriorly (fig. 1). The posterior margin of this phalanx is not bowed in *Ichthyornis dispar* or in more basal avialans with this digit preserved (e.g., *Confuciusornis sanctus*, Enantiornithes, or *Ambiortus dementjevi*).

Pelvic Girdle

The pre- and postacetabular blades of the ilium are approximately equal in length (fig.

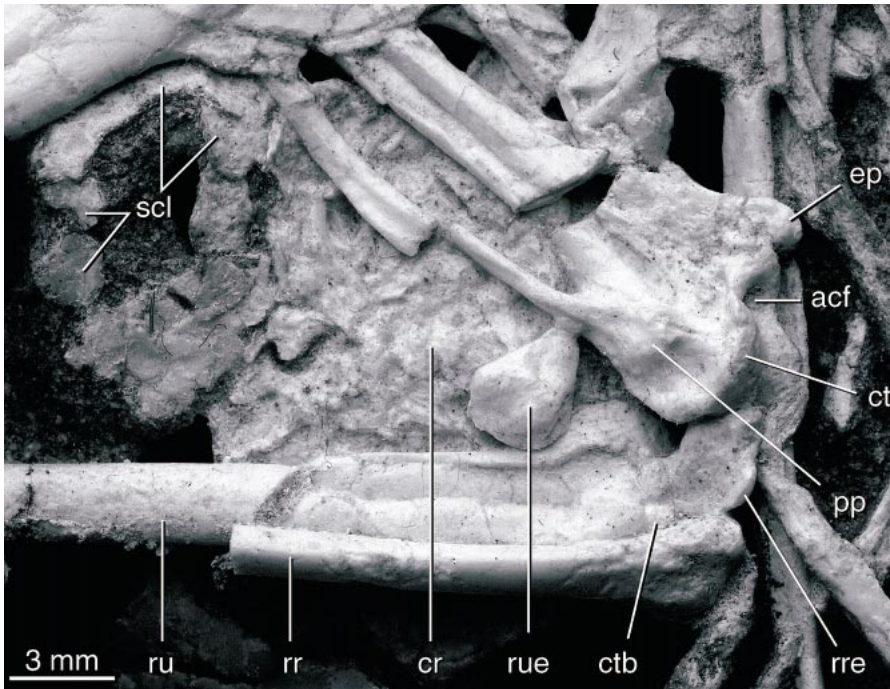


Fig. 18. Distal right forelimb with proximal carpals and carpometacarpus in ventral view. See appendix 1 for anatomical abbreviations.

1). The ischium and pubis are approximately equal in length, and lie parallel to the ilium (fig. 10). The ischium and pubis are not ankylosed distally although they are extremely closely appressed. All three pelvic bones are firmly ankylosed proximally. Unlike the primitive avialan condition seen in *Confuciusornis sanctus* and *Enantiornithes* (Chiappe, 1996), the pubes do not contact each other distally and the pubic apices are widely separated. The pubes are very narrow and mediolaterally compressed throughout their length. By contrast, the pubes in *enantiornithines* and *Patagopteryx deferrariisi* and other more basal avialans are rodlike, robust, and uncompressed (Chiappe, 1996). The mediolaterally compressed pubic shaft in *Apsaravis ukhaana* (fig. 10) is otherwise only known with certainty from *Hesperornis regalis* and Aves (Chiappe, 1996). The pubes in *Apsaravis ukhaana* are notably more delicate than those in *Ichthyornis dispar* (Clarke, 2002). The obturator foramen is slightly demarcated distally by a flange of the ischium (fig. 10). A well-developed antitro-

chanter lies on the posterodorsal corner of the acetabulum (figs. 10, 19). No pectineal process is present.

Pelvic Limb

The femur is moderately bowed and longer than the tarsometatarsus (fig. 1). The capital ligament fossa is visible on the head of the left femur, which is exposed through the left acetabular opening (fig. 10). The lateral surfaces of the femora are not well exposed. A hypertrophied projection of the posterolateral edge of the femur forms a large trochanteric crest, an autapomorphy of *Apsaravis ukhaana* (fig. 19). The morphology of the proximal portion of this crest is not well preserved. A patellar groove extends onto the anterior surface of the distal femur, a condition known only for *Hesperornithes*, *Ichthyornis dispar*, and Aves (Chiappe, 1996). The posterodistal surface is poorly preserved, and the presence of a popliteal fossa cannot be determined. An intermuscular line, visible on the right femur, follows the medial edge of



Fig. 19. Right femur in ventrolateral view. See appendix 1 for anatomical abbreviations.

the posterior surface proximally for about one-half the length of the bone.

Only the distal ends of the tibiotarsi are preserved (figs. 1, 20, 21). The right is preserved in articulation with the tarsometatarsus (fig. 21). The astragalus and calcaneus are completely fused to the tibia; no sutures are visible. Although neither fibula is preserved, they are inferred not to have reached the tarsal joint; no associated indentation or groove is present on the lateral edges of the either tibiotarsus.

Paired ridges are developed on the anterodistal surface of both tibiotarsi (fig. 21). These ridges are identified, based on their position and morphology, as topologically correspondent to the tubercles for attachment of the extensor retinaculum in Aves (tuberositas retinaculi extensoris; Baumel and Wit-

mer, 1993; fig. 21). An extensor groove and a supratendinal bridge are not developed in *Apsaravis ukhaana*.

A slight depression on the distal end of the tibia in *Patagopteryx deferrariisi* was previously identified as a possible homolog with an avian extensor groove (Alvarenga and Bonaparte, 1992; Chiappe, 1996). Here it is reinterpreted as morphologically correspondent to the area demarked by the attachments of the retinaculum (Clarke, 2002) because it is shallower and more proximally developed than an extensor groove in other avialans.

The extensor retinaculum in Aves directs the passage of the m. tibialis cranialis as well as the m. extensor digitorum longus (Baumel and Raikow, 1993), two primary avian foot extensors (Baumel and Raikow, 1993). Evidence for the retinaculum tubercles (associ-

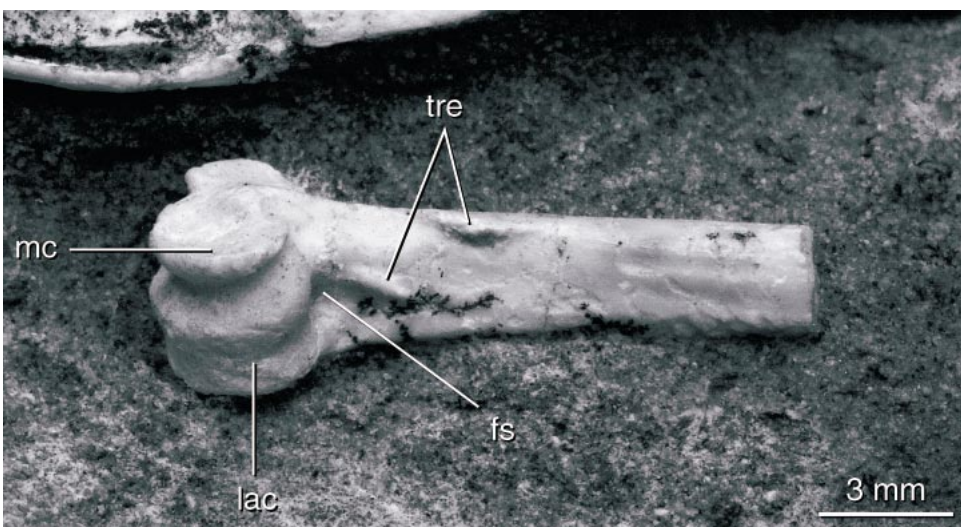


Fig. 20. Distal left tibiotarsus in anterior view. See appendix 1 for anatomical abbreviations.

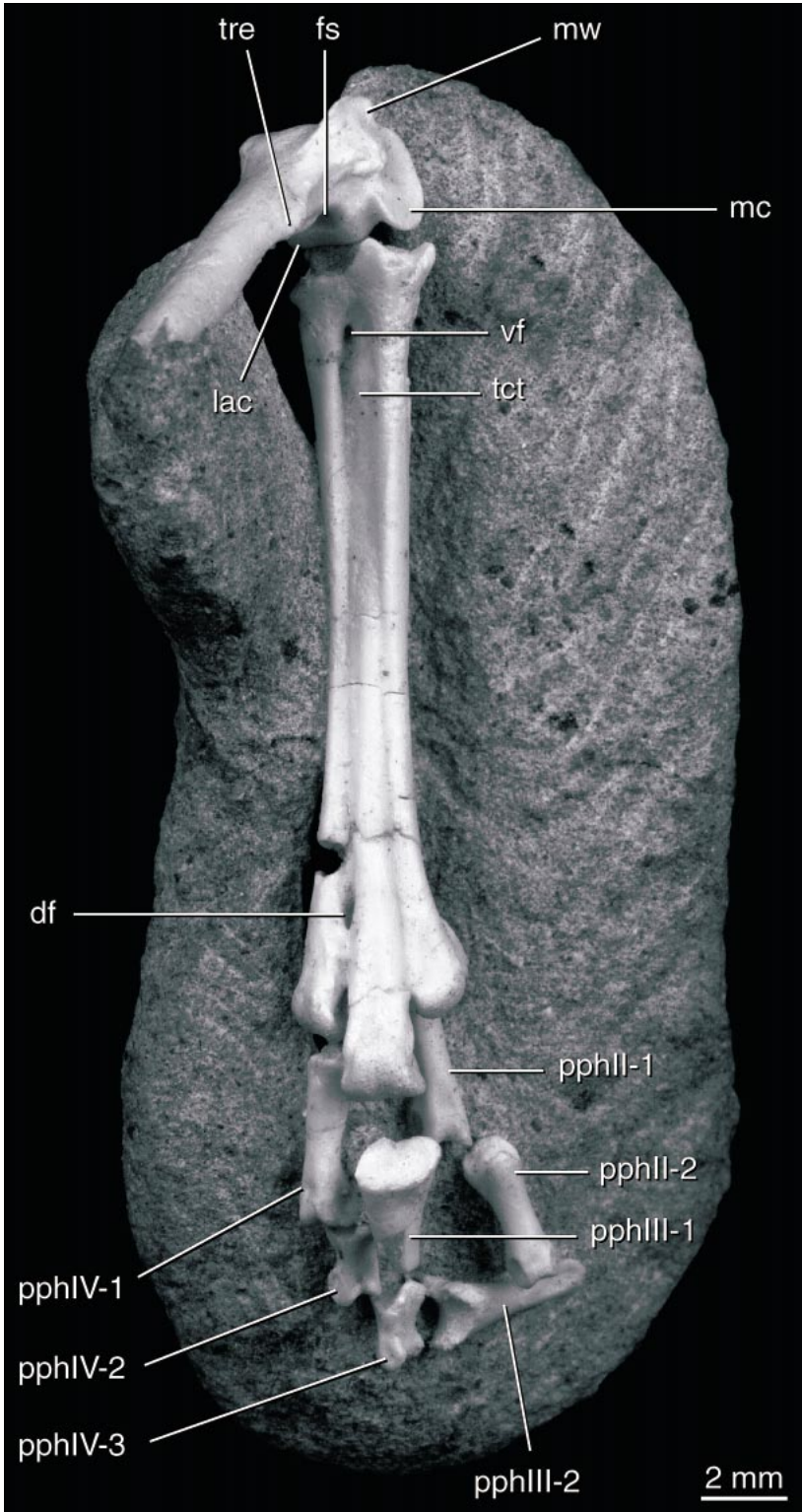


Fig. 21. Distal right tibiotarsus and tarsometatarsus in anterodorsal view. See appendix 1 for anatomical abbreviations.

ated with both the m. tibialis cranialis and m. extensor digitorum longus) occurs phylogenetically earlier (synapomorphy of *Confuciusornis sanctus* + Aves; Clarke, 2002 and this analysis) than evidence for the extensor groove, an additional constraint on the passage of the m. extensor digitorum longus (a synapomorphy of Hesperornithes + Aves; Clarke, 2002 and this analysis).

Shifts in the function and/or relative importance of the m. tibialis cranialis and m. extensor digitorum longus may explain the variation in position and development of metatarsal tubercles in basal avialans (Chiappe, 1996) vs. in Aves and near outgroups (Clarke, 2002). A large tubercle on the anterior surface of metatarsal II in some basal avialans (e.g., *Confuciusornis sanctus* [Chiappe et al., 1999], *Vorona berivotrensis* [Forster et al., 1996], and Enantiornithes [Chiappe, 1996]) appears topologically correspondent to the m. tibialis cranialis tubercles in Aves (Chiappe, 1996). In *Apsaravis ukhaana*, and optimized as primitive to Aves (Clarke, 2002), the tubercles associated with the m. tibialis cranialis are less pronounced and are located on the anteromedial edge of metatarsal II and/or on the anterior surface of metatarsal III. In *Apsaravis ukhaana*, a single tubercle is visible on the medial edge of metatarsal III (fig. 21).

A deep, subcircular fossa excavates the proximal surface of the lateral condyle (figs. 20, 21) of the tibiotarsus. A similar fossa has been described for *Vorona berivotrensis* and Enantiornithes (Forster et al., 1996), and it is very faintly developed or absent in *Ichthyornis dispar* and Aves. The intercondylar groove is shallow and located far medially. It is also narrow; its width is less than a third of that of the distal tibiotarsus, unlike the comparatively broad groove in *Patagopteryx deferrariisi*, *Hesperornis regalis*, *Ichthyornis dispar*, and Aves, for example (Chiappe, 1996; Marsh, 1880).

Neither distal condyle of the tibiotarsus tapers medially, which gives the distal tibiotarsus in *Apsaravis ukhaana* the “barrel-shaped” aspect found only in some Enantiornithes (e.g., *Nanantius eos*; Molnar, 1986) and *Vorona berivotrensis* (Forster et al., 1996). However, the latter taxa, *Patagopteryx deferrariisi*, and other basal avialans share

the condition seen in nonavian theropods where the medial condyle is broader than the lateral one (Chiappe, 1996; Forster et al., 1996). In contrast, in *Apsaravis ukhaana* the opposite is true; the lateral condyle is more than twice the width of the medial one (fig. 20). In Hesperornithes, *Ichthyornis dispar*, and most Aves, the condyles are approximately equal in width, or the lateral is slightly larger. The extreme difference in condylar proportions in *Apsaravis ukhaana* is also similar to the condition in *Vorona berivotrensis* (Forster et al., 1996) and *Nanantius eos* (Molnar, 1986) and is more marked than seen in nonavian theropods (e.g., Norell and Makovicky, 1999), *Confuciusornis sanctus* (Chiappe et al., 1999), and *Patagopteryx deferrariisi* (Chiappe, 1996), for example.

In *Apsaravis ukhaana*, the cartilage-covered distal articular surface of the tibiotarsus extends up its posterior surface to approximately even with the proximal edge of the condyles. This surface is demarcated by pronounced posteriorly projected medial and lateral edges as well as a slight difference in bone texture. A large, similarly demarcated, posterior trochlear surface is also seen in Aves. In Aves, this surface (trochlea cartilaginosa tibialis; Baumel and Witmer, 1993) serves as the articular surface for the tibial cartilage. The condition in *Apsaravis ukhaana* and Aves is derived (see character 185) relative to the condition in more basal theropods where there is no indication of a posterior component to the distal articular surface and textured bone is limited to the distal end of the tibia and distal surfaces of the proximal tarsals (e.g., *Velociraptor mongoliensis*; Norell and Makovicky, 1999).

The edges of this posterior surface of the tibiotarsus (trochlea cartilaginosa tibialis; Baumel and Witmer, 1993) are developed as extremely pronounced wings in *Apsaravis ukhaana*. The medial wing of this surface is conspicuously more strongly projected than the corresponding lateral wing, and its distal edge is prominently notched (figs. 1, 21). These hypertrophied wings of the posterodistal tibiotarsus are identified as an autapomorphy of *Apsaravis ukhaana* (see diagnosis).

Metatarsals II through IV are fused with the distal tarsals and to each other throughout

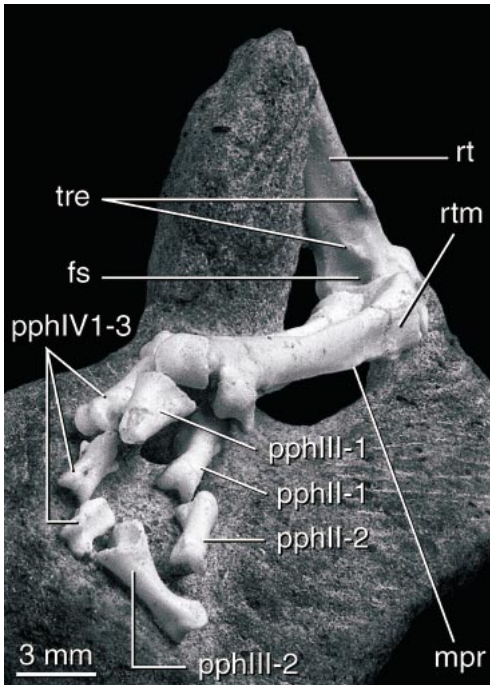


Fig. 22. Oblique distal view of the right tarsometatarsus. Note pronounced medial wing on distal trochlea of metatarsal II. See appendix 1 for anatomical abbreviations.

their lengths; they ankylose distally to enclose the distal vascular foramen (figs. 21, 22). However, the edges of the shafts of the metatarsals remain distinguishable throughout their lengths (fig. 21) unlike the condition in *Ichthyornis dispar*, *Hesperornis regalis*, and most Aves. Metatarsal V is absent. The proximal end of metatarsal III is displaced posteriorly (fig. 21), a derived condition also seen in *Hesperornis regalis* (Marsh, 1880), *Ichthyornis dispar* (Marsh, 1880), and Aves (e.g., Baumel and Witmer, 1993). Proximally, intercotylar eminence is not developed. The lateromedial width of the medial cotyla is approximately one-third that of the lateral cotyla. However, the anterior edge of this medial cotyla is projected farther proximally than that of the lateral cotyla (fig. 21).

A single proximal vascular foramen is developed between metatarsals III and IV (fig. 21). In the position of an avian hypotarsus in *Apsaravis ukhaana* is a flat, weakly projected, discrete area similar to that of *Hesperornis regalis* (Marsh, 1880) and *Patagopteryx*

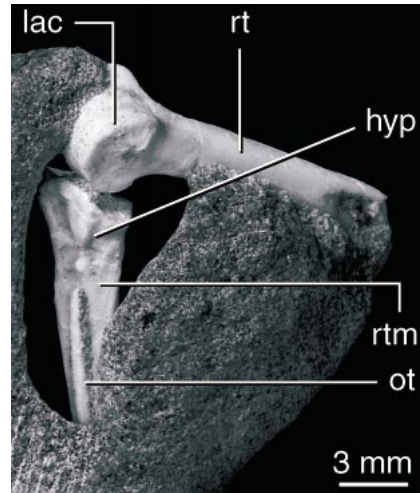


Fig. 23. Posterolateral view of right tibiotarsus and tarsometatarsus. Note flat hypotarsus and prominent ossified tendon. See appendix 1 for anatomical abbreviations.

deferrariisi (Chiappe, 1996; fig. 23). This surface is considered the topological equivalent of the hypotarsus in Aves where at least one well-developed hypotarsal crest or groove is present on this surface. In *Apsaravis ukhaana*, this surface has relatively little distal extent and is defined distally by a midline depression of the shaft. A conspicuous ossified tendon extends down the midline of the tarsometatarsus distal to the hypotarsus in both the right and left foot (fig. 23). This ossified tendon may correspond to that of the m. flexor digitorum longus in Aves (Hutchinson, in press). As such, it would be the earliest known occurrence of an ossified tendon associated with this muscle (Hutchinson, in press). Plantar crests are visible bordering a slightly depressed flexor sulcus (fig. 22).

The distal vascular foramen angles obliquely ventrodistally and exits in a small depression on the plantar surface. This foramen has only one distal exit, whereas in Aves two exits are present: one is plantar (that present, for example, in *Apsaravis ukhaana* and *Ichthyornis dispar* [Clarke, 2002]) and the second is directly distal, between metatarsals III and IV. Digit I is not preserved and may not have been present. If this absence is not an artifact, then lack of

digit I in *Apsaravis ukhaana* represents the phylogenetically earliest known such loss among avialans. Loss of digit I in Aves occurs in some ground-dwelling birds (e.g., some ratites; Baumel and Witmer, 1993; Stidham, personal commun.) as well as an array of other avians of highly varied ecologies (Raikow, 1985).

Metatarsal III is the longest, and metatarsal II is the shortest in *Apsaravis ukhaana*. Metatarsal II projects only as far as the base of the trochlea of metatarsal IV. Livezey (1997b) found a short metatarsal II to be derived within Aves (e.g., within Anseriformes); however, no outgroups of Aves were included in that analysis. In *Hesperornithes* (Marsh, 1880; Martin and Tate, 1976), *Ichthyornis dispar* (Marsh, 1880), *Gansus yumenensis*, and *Apsaravis ukhaana*, metatarsal II is shorter than metatarsal IV (i.e., it extends only as far as approximately the base of metatarsal IV). This condition is derived in Avialae but is optimized as primitive for Aves; having metatarsal II equal in length to metatarsal IV is optimized as a derived condition in some basal avians (Clarke, 2002; contra Livezey, 1997b).

Metatarsal II projects plantar to metatarsals III and IV and has a well-developed wing on the medial edge of its trochlear surface (fig. 22). A correspondingly developed lateral wing is also present on the lateral plantar trochlear surface of metatarsal IV. The trochlea of metatarsal III is widest, and those of metatarsals II and IV are approximately equal in width (fig. 21).

Phalanges are associated with both tarsometatarsi; some are in partial articulation. Phalangeal length appears to decrease distally in digits II–IV as typical in birds that spend at least part of their time on the ground (e.g., Hopson, 2001). The first phalanx of digit II has strong flexor keels, with the lateral keel better developed than the medial one. Small collateral ligament pits are present. Both articular surfaces of the shorter second phalanx of digit II are ginglymoid, and the collateral ligament pits are large, taking up most of the medial and lateral surfaces of the distal end.

The proximal end of the first phalanx and the complete second phalanx of digit III are preserved in partial articulation with the right

tarsometatarsus (figs. 21, 22). Only the complete first phalanx of digit III is preserved in articulation with the left (fig. 1). The shaft of the phalanx tapers distally. The third and fourth phalanges of digit III are visible and associated with the left foot. On the third phalanx of digit III, collateral ligament pits are not visible and are either absent or extremely weakly developed. The fourth phalanx is slightly broken distally but would have been approximately equal in length to the third phalanx. It is recurved with vascular grooves and a large flexor tubercle.

The proximal three phalanges of digit IV are preserved in partial articulation on the right pes (figs. 21, 22). The first phalanx has well-developed flexor keels, with the medial keel better developed than the lateral one. The second phalanx is approximately one-half the length of the first. The third phalanx (IV:3) is slightly shorter than the second phalanx. All of the preserved unguals are recurved, including three preserved in a separate (and unfigured) block.

PHYLOGENETIC ANALYSES

Phylogenetic analysis of 17 ingroup terminal taxa and two outgroups were scored for 202 characters (listed in appendices 2 and 3; from Clarke, 2002); 185 of them were parsimony informative for the included taxa (a subset of the taxa included in Clarke, 2002).

Five species exemplars were chosen for Aves (sensu Gauthier, 1986; Gauthier and de Queiroz, 2001). *Crypturellus undulatus* (YPM 11564), one of the forest-dwelling tinamous that have been placed as basal within Tinamidae (S. Bertelli, personal commun.), was used as the exemplar for Palaeognathae. Of Neognathae, *Chauna torquata* (YPM 6046, AMNH 3616) and *Anas platyrhynchos* (YPM 2230, YPM 14369, YPM 14344, AMNH 5847) were used for Anseriformes; and *Crax pauxi* (YPM 2104) and *Gallus gallus* (YPM 2106, YPM 6705) were used for Galliformes. These exemplars were chosen to sample both basal divergences (i.e., *Crypturellus*, *Chauna*, and *Crax*) and deeply nested taxa (i.e., *Anas* and *Gallus*) from within the three included avian subclades based on previous phylogenetic hypotheses (e.g., Holman, 1964; Cracraft, 1974; Sibley and

Ahlquist, 1990; Livezey, 1997a, 1997b). No neoavian exemplars were included, because there remains no resolution of the basal relationships within this clade (recently reviewed in Cracraft and Clarke, 2001). The same five avian exemplars were used in Norell and Clarke (2001).

The terminals *Lithornis* and *Vorona berivotrensis* were added to the taxa included in Norell and Clarke (2001). *Lithornis* was scored from study of *Lithornis plebius* (USNM 336534, AMNH 21902), *Lithornis promiscuus* (USNM 336535, USNM 424072, AMNH 21903), and *Lithornis celetius* (USNM 290601, USNM 290554, USNM 336200, YPM-PU 23485, YPM-PU 23484, YPM-PU 23483, YPM-PU 16961) and was supplemented by the description of this material provided in Houde (1988). The paraphyly of the “Lithornithidae” has been proposed (Houde, 1988). However, the “Lithornithidae” included *Paracathartes* and *Pseudocrypturus*, as well as *Lithornis*; the monophyly of *Lithornis* itself has not been disputed. *Paracathartes* and *Pseudocrypturus* material was not used in the current analysis. *Vorona berivotrensis* was scored from the holotype and referred specimen described in Forster et al. (1996).

The *Ichthyornis dispar* terminal was scored from all YPM material assessed to be part of that species in Clarke (2002), as well as from SMM 2305 and BMNH A905. Clarke (2002) offered evidence in support of the referral of these specimens to *Ichthyornis dispar* and for the recognition of a single species of *Ichthyornis* rather than the eight previously named. Elements that had previously been considered dubiously referable (e.g., Elzanowski, 1995) to *Ichthyornis dispar*, and problems of the association of other *Ichthyornis dispar* material (Clarke, 1999, 2000), were addressed in Clarke (2002). Only material determined to be part of *Ichthyornis dispar* in Clarke (2002) was scored for the *Ichthyornis dispar* terminal in the current analysis. *Hesperornis regalis* was scored primarily from study of the holotype (YPM 1200) and referred YPM specimens (YPM 1206, YPM 1207, YPM 1476), as well as from the description of that taxon in Marsh (1880), Witmer and Martin (1987), Bühler et al. (1988), and Witmer (1990). *Baptornis advenus* was scored from the holotype speci-

TABLE 1
Measurements of the Holotype of
Apsaravis ukhaana (in mm)

Vertebral column:	
Length of posteriormost presacral centrum	4.50
Width of distal end of posteriormost presacral centrum	2.00
Length of sacrum	28.60
Length of third free caudal centrum	2.04
Width of third free caudal centrum	1.57
Pectoral girdle and limb:	
Coracoid	
Maximum length	29.25
Width at sternum	11.10
Width at narrowest point	2.30
Length of glenoid facet	4.92
Scapula	
Length (estimated)	52.50
Humerus	
Maximum length	48.43
Dorsoventral width at midpoint of deltopectoral crest	16.70
Ulna	
Maximum length	45.69
Midpoint width	2.27
Radius	
Maximum length	43.11
Midpoint width	1.51
Carpometacarpus	
Maximum anteroposterior width	7.70
Phalanx II:1	
Length (estimated)	9.62
Pelvic girdle and limb:	
Ilium	
Maximum length	31.50
Ischium	
Length from center of acetabulum	30.14
Pubis	
Length from center of acetabulum	30.14
Anterior width	1.65
Femur	
Length (estimated)	40.90
Tarsometatarsus	
Maximum length	28.70

men (YPM 1465) and Martin and Tate (1976). *Patagopteryx deferrariisi* was scored from MACN-N-03 (holotype), MACN-N-10, MACN-N-11, and MACN-N-14, as well as from Chiappe (1996). *Vorona berivotrensis* was scored from Forster et al. (1996). *Con-*

fuciusornis sanctus was scored from study of numerous IVPP and GMV specimens referenced in Hou (1997) and Chiappe et al. (1999).

Enantiornithes (sensu Sereno, 1998) was represented by taxa referred to it by previous authors (e.g., Zhou et al., 1992; Chiappe and Calvo, 1994; Sanz et al., 1995; Chiappe, 1995, 1996; Zhou, 1995; Hou, 1997; Norell and Clarke, 2001). Unfortunately, because relationships among Enantiornithes remain largely unresolved (e.g., Padian and Chiappe, 1998; Chiappe, 2001), sampling taxa basal to the clade, as recommended in exemplar choice (e.g., Prendini, 2001 and references therein), was problematic. The four taxa exemplars used were chosen because they (1) are known from relatively complete and/or multiple specimens, (2) sample Early and Late Cretaceous parts of the clade, and (3) are, together, geographically and morphologically diverse. The four exemplar taxa used are the following: *Cathayornis yandica* (Zhou et al., 1992) was scored from the holotype specimen (IVPP V-9769A, B) and two referred specimens (IVPP 10890, IVPP 10916). *Concornis lacustris* (Sanz and Bussaloni, 1992; Sanz et al., 1995) was scored from the holotype specimen, LH 2814, and from Sanz et al. (1995). *Neuquenornis volans* was scored from Chiappe and Calvo (1994). *Gobipteryx minuta* was scored from Elzanowski (1974, 1977, 1995), Chiappe et al. (2001), as well as from the description of the holotype of "*Nanantius valifanovi*" (Kurochkin, 1996), a junior synonym of *Gobipteryx minuta* (Chiappe et al., 2001).

Of the outgroup terminals, *Archaeopteryx lithographica* was scored based on study of the London and Berlin specimens, and from descriptions provided in Wellnhofer (1974, 1993), Ostrom (1976), Witmer (1990), and Elzanowski and Wellnhofer (1996). *Dromaeosauridae* (sensu Gauthier, 1986) was represented primarily by studied specimens of *Deinonychus antirrhopus*, *Dromaeosaurus albertensis*, and *Velociraptor mongoliensis* cited in Ostrom (1969), Norell et al. (1992), Colbert and Russell (1969), Currie (1995), and Norell and Makovicky (1997, 1999), as well as from descriptions provided in those publications.

Of the 202 characters scored, 200 were

employed in the primary analysis. The two additional characters, 89 and 97, were swapped in to replace 88 and 98, respectively, to consider the effect of a previous interpretation and scoring of two morphologies of the coracoid as also briefly discussed in Norell and Clarke (2001). The result of this exchange is discussed below. Of the 202 characters, 36 are ordered; these are listed in appendix 2. Our rationale for ordering characters follows those of Merck (1999) and Slowinski (1993). Note that unordering all characters does not affect the topology, or number, of most parsimonious trees (see below).

All searches were branch and bound and performed using PAUP*4.0b8 (PPC; Swofford, 2001). Several settings were altered from the PAUP* defaults in the analyses: "amb-" in the "Parsimony Settings" menu was selected such that internal branches with a minimum length of 0 were collapsed to form a soft polytomy; by contrast, the PAUP* default is to collapse only internal branches with a maximum length of 0. Additionally, when interpreting entries with more than one state, ambiguity (e.g., "state 1 or 2") was distinguished from polymorphism (e.g., "states 1 and 2").

Bootstrap support values from 1000 replicates (10 random sequence additions per replicate) were computed in PAUP* with the same settings as for the other analyses (given above). Values greater than 50% are reported in figure 24. Bremer support values were calculated manually in PAUP* and are also reported in figure 24.

RESULTS

Analysis of the 19 included taxa produced 2 most parsimonious trees of 392 steps including uninformative characters with CI of 0.68, RI of 0.81, and RC of 0.55 (fig. 24). Excluding uninformative characters, tree length was 379 steps (CI = 0.67, RI = 0.81, and RC = 0.55). These two trees differ only in enantiornithine interrelationships. The strict consensus of these trees is reported in figure 24. Other polytomies in the shortest trees are present because internal nodes with a minimum branch length of 0 were collapsed (see above). If 0-length internal

branches were allowed, more most parsimonious topologies would have resulted. Running the analysis with all characters unordered did not affect the topology or number of most parsimonious trees, only tree length and statistics (with uninformative characters: length 383, CI = 0.70, RI = 0.80, RC = 0.56; without uninformative characters: length 366, CI = 0.68, RI = 0.80, RC = 0.55).

Apsaravis ukhaana is placed as the sister taxon of Hesperornithes + Aves (fig. 24). The analyses of Norell and Clarke (2001) previously placed this taxon within Hesperornithes + Aves. They noted, however, that there was only a two-step difference in tree length for *Apsaravis ukhaana* to be outside of this clade. The six characters supporting Hesperornithes + Aves relative to *Apsaravis ukhaana* are as follows: (85:1) procoracoid process; (88:1) dorsal surface of coracoid flat to convex rather than deeply excavated; (180:1) extensor groove on tibiotarsus; (191:1) intercotylar eminence; (193:2) two proximal vascular foramina in tarsometatarsus; (196:1) fossa "metatarsal I" present.

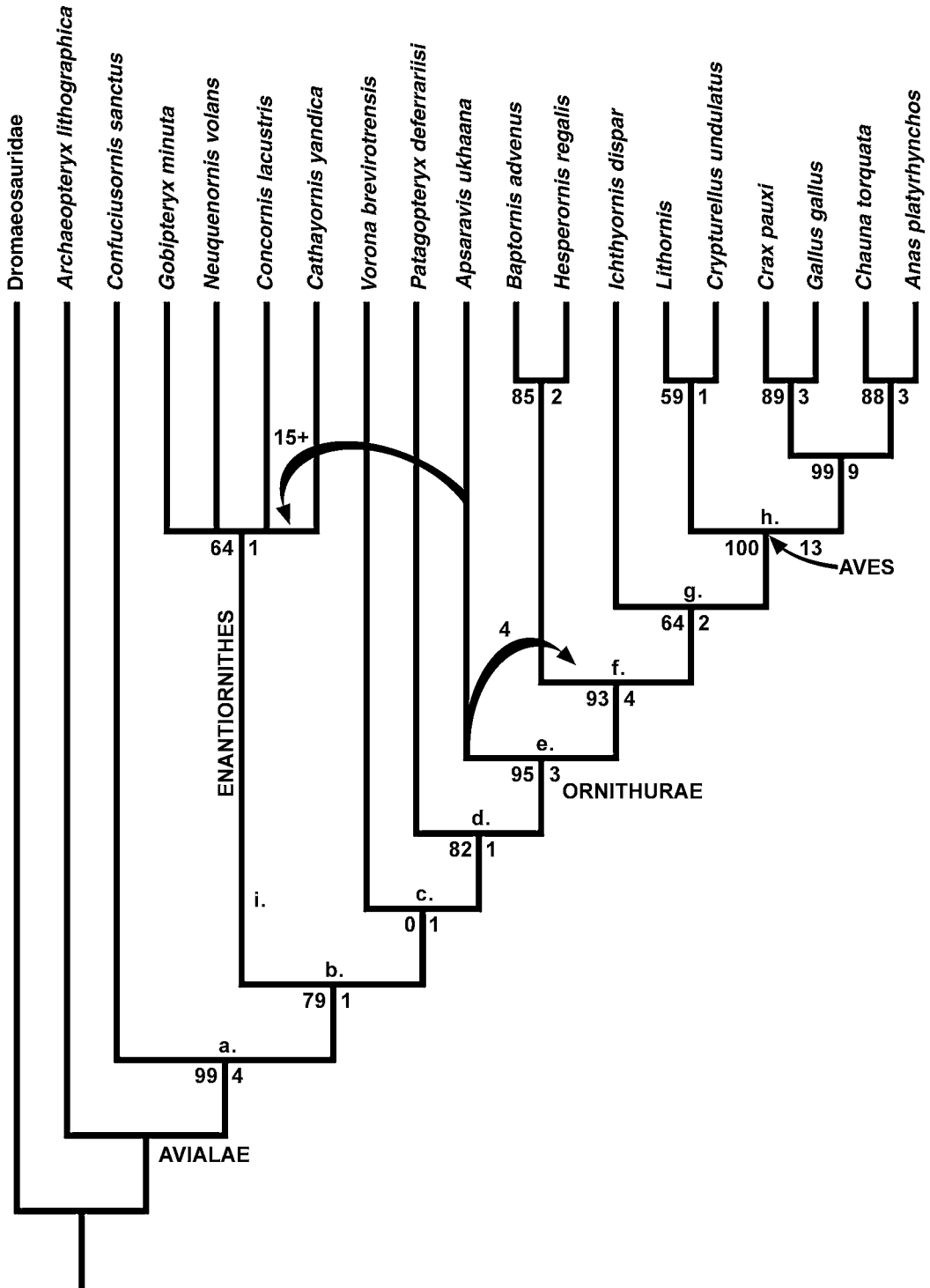
Of these characters, the scoring of *Baptornis advenus* for character 85 has been changed from Norell and Clarke (2001), who considered this taxon to lack a procoracoid process. Norell and Clarke (2001) followed Elzanowski (1995) in considering the small flange present in *Baptornis advenus* to be of questionable equivalence with a procoracoid process; however, that assessment has been changed here. *Apsaravis ukhaana* clearly lacks a procoracoid process (Norell and Clarke, 2001). Further, the scoring of both *Ichthyornis dispar* and *Hesperornis regalis* for character 193 has also changed from Norell and Clarke (2001). Material from these two taxa was re-prepared and revealed the presence of two proximal vascular foramina (Clarke, 2002). *Apsaravis ukhaana* has only one proximal vascular foramen (Norell and Clarke, 2001).

For *Apsaravis ukhaana* to be part of Hesperornithes + Aves, four additional steps would have to be added (fig. 24). *Apsaravis ukhaana* is placed as more closely related to Aves than *Patagopteryx deferrariisi* by 11 unambiguous synapomorphies (i.e., 54:2, 61:

4, 106:1, 135:1, 141:1, 150:1, 158:1, 166:1, 172:1, 182:1, 190:1).

Apsaravis ukhaana is easily differentiated from two other Cretaceous avialans from Mongolia and inner Mongolia, China (*Ambiortus dementjevi* and *Otogornis genghisi*), which have been proposed to be ornithurines (e.g., Kurochkin, 1985a, 1985b, 1999; though see Sereno and Rao, 1992, and Hou, 1997). For example, *Apsaravis ukhaana* is differentiated from *Ambiortus dementjevi* (Kurochkin, 1985a, 1985b, 1999) by the lack of procoracoid and lateral processes of the coracoid. It is differentiated from *Otogornis genghisi* (Hou, 1994, 1997) by having, for example, a globose humeral head and an elongate recurved acromion on the scapula, both of which are absent in *Otogornis genghisi*. These taxa were not included in the phylogenetic analysis because, in addition to being represented by fragmentary single specimens, conflicting statements had been made about the anatomy of *Ambiortus dementjevi* (Kurochkin, 1985a and 1985b vs. 1999; scored from the literature), and *Otogornis genghisi* is not an ornithurine (Clarke, Zhou, and Zhang, in prep.).

The other results of this analysis concerning avialan phylogenetic relationships are consistent with the results of the analyses of Norell and Clarke (2001) and Clarke (2002). Additionally, *Lithornis*, from the Paleocene and Eocene of North America and Europe (Houde, 1988), is placed as the sister taxon of *Crypturellus undulatus* (fig. 24). This placement is consistent with *Lithornis* being either the sister taxon of crown clade palaeognaths or a part of that clade. *Lithornis* has been placed in several positions within a paraphyletic Palaeognathae (Houde, 1988) or, alternatively, as the sister taxon to Aves (Clarke and Chiappe, 2001). Both of these analyses involved small datasets, and the position of *Lithornis* was weakly supported in both. Also consistent with results in Clarke (2002), *Vorona berivotrensis* from the Late Cretaceous of Madagascar (Forster et al., 1996) is placed as the sister taxon of *Patagopteryx deferrariisi* + Aves (fig. 24). *Vorona berivotrensis* was previously placed in an unresolved trichotomy with Enantiornithes and the lineage leading to Aves (Forster et al., 1996), or in an unresolved trichotomy



with *Patagopteryx deferrariisi* and the lineage leading to Aves (Chiappe, 2001).

CONCLUSIONS

We originally noted three areas of avialan evolution illuminated by the discovery of *Apsaravis ukhaana* (Norell and Clarke, 2001; Clarke and Norell, 2001): (1) proposed restriction of Mesozoic ornithurines to a shorebird habitus (e.g., Feduccia, 1995, 1996, 1999), (2) diagnosis of, and character support for, enantiornithine monophyly, and (3) the evolution of flight after its origin. These conclusions are revisited and elaborated on here, in light of the phylogenetic analyses presented above.

Of “Transitional Shorebirds” and Ornithurine Ecology

In Norell and Clarke (2001) and Clarke and Norell (2001) we responded to Feduccia’s (e.g., 1995, 1996, 1999) statements regarding the ecology of ornithurine birds (sensu Martin, 1983). For example, Feduccia (1999: 152) wrote, “Given the near absence of ornithurine birds in Late Cretaceous continental deposits and their near exclusive occurrence as ‘transitional shorebirds’, ichthyornithiforms and hesperornithiforms, it is tempting to speculate that ornithurines may have been more or less restricted to shoreline and marine deposits during this time”. Feduccia’s (1995, 1996, 1999) statements are the latest avatar of an oft-discussed, but often nebulous, hypothesis concerning the “shorebird ecology” of Mesozoic avialan taxa placed as basal parts of, or close to, Aves.

Martin (1987: 17) attributed to Brodkorb

the idea that “[a]ll of the Mesozoic birds that have affinities with Cenozoic birds are also recognized to have basically charadriiform postcranial skeletons”. Brodkorb, in his *Catalogue of Fossil Birds* (Brodkorb, 1967), indeed included Mesozoic taxa such as *Ichthyornis*, *Apatornis*, the “Graculavidae”, and Cimolopterygidae with Charadriiformes, the crown clade taxon referred to as “shorebirds”. Martin (1983: 311) later identified *Ichthyornis dispar* and *Apatornis celer* (as well as Hesperornithes) as outgroups of the avian crown clade (contra Brodkorb, 1967). Despite that these taxa were no longer placed with crown shorebirds, Martin emphasized that they, and, in fact, “[a]ll Mesozoic Ornithurae are aquatic in one way or another” (Martin, 1983: 311). He also commented of ornithurines, “The basic adaptive zone of the group seems to be wading along the shoreline. This is still an important avian adaptive zone and one for which few other Mesozoic vertebrates would have been well suited” (Martin, 1983: 311). The characters used to place these Mesozoic taxa with Charadriiformes (e.g., Brodkorb, 1967), and what constituted the perceived “key” ecological “variable” (e.g., aquatic lifestyle or wading) in common amongst ornithurines (Martin, 1983, 1987), were not articulated.

In 1987, Martin elaborated, “I think that this situation will be maintained as the Mesozoic record becomes better known and that the entire modern avian radiation had its origin within these so-called ‘basal charadriiforms’. In this case, it is probably better to think of these as primitive charadriiform-like birds but perhaps not really members of the

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Fig. 24. Strict consensus cladogram of two most parsimonious topologies (including uninformative characters: L = 392, CI = 0.68, RI = 0.81, RC = 0.55; excluding uninformative characters: L = 379, CI = 0.67, RI = 0.81, RC = 0.55). These two topologies differ only in enantiornithine interrelationships (fig. 24). Unambiguous apomorphies for nodes “a–i” are as follows: **a.** 1:1, 2:1, 9:1, 12:1, 34:1, 35:1, 48:1, 52:1, 57:1, 61:1, 63:1, 67:1, 71:1/2, 86:1, 112:0, 114:1, 119:1, 128:1, 133:2, 134:1, 136:1, 139:1, 140:1, 153:1, 157:1, 170:1, 171:1, 173:1, 175:1, 176:1, 177:1/2, 181:1, 187:1, 193:1, 194:1. **b.** 61:2/3, 71:3, 83:1, 99:1, 100:1, 108:1, 111:1, 117:1, 131:1, 139:2, 145:1, 179:1. **c.** 188:2. **d.** 188:3, 192:1. **e.** 54:2, 61:4, 106:1, 135:1, 141:1, 150:1, 158:1, 166:1, 172:1, 182:1, 190:1. **f.** 85:1, 88:1, 180:1, 191:1, 193:1, 196:1. **g.** 59:1, 62:1, 73:1, 92:1, 98:1. **h.** 3:1, 6:1, 8:1, 18:2, 37:1, 40:1, 61:6, 74:1, 77:1, 90:1, 112:1, 113:0, 114:0, 118:1, 142:2/3, 161:1, 179:0, 197:1, 200:1. **i.** 81:1, 135:2, 198:1, 199:1. Bootstrap support values greater than 50% are shown to the right below the node to which they refer; Bremer support values are listed to the left.

modern order Charadriiformes, and all modern orders may be post-Mesozoic in age” (Martin, 1987: 17). In these statements, Martin (1983, 1987) further developed the ideas that (1) ornithurines are occupying, perhaps exclusively, a “shorebird adaptive zone”, and (2) that “modern” or crown clade birds had their “origin in” (Martin, 1987: 17) taxa with a “shorebird ecology”. Feduccia (1995, 1996, 1999) went further, positing the existence of a “bottleneck of avian morphotypes transcending the K/T boundary, like mammalian insectivores” (Feduccia, 1995: 638), and suggested the competitive exclusion of ornithurines from other “continental” environments by enantiornithines, which he has referred to as “the dominant land birds of the Cretaceous” (e.g., Feduccia, 1995: 637; see also Feduccia, 1999).

Olson and Parris (1987) took a different stance in their evaluation of the Late Cretaceous Hornerstown birds (e.g., parts of “Graculavidae”) often cited (e.g., Feduccia, 1995; Chiappe, 1995) as evidence of Cretaceous crown (or “modern”) orders. These authors wrote: “As far as can be determined, all of the birds in this assemblage were probably marine or littoral in habits. We certainly would not interpret this as an indication that waterbirds are primitive and that they gave rise to land birds . . . (Olson, 1985)” (Olson and Parris, 1987: 19). These authors, while agreeing that these birds had marine or littoral ecologies, apparently differed in their interpretation of the implications of these data (Olson, 1985; Olson and Parris, 1987).

Finally, Feduccia (2001; contra Feduccia, 1995, 1996, 1999; Martin, 1983, 1987), described ornithurine taxa as abundant and well known from continental deposits, including those with “no particular adaptations for near-shore habitats” (Feduccia, 2001: 507). He further commented, “What correlation is there between the distribution of shorebirds (waders; Charadriiformes) and the marine shoreline deposits of the continental margins? These birds are quite cosmopolitan . . .” (Feduccia, 2001: 507).

For the point of argument, we accepted (Norell and Clarke, 2001) that previously described Mesozoic ornithurines were identified as exhibiting an “ecological” restriction to littoral or marine habitats based on evi-

dence of some kind, either (1) from their depositional environment or (2) from morphology. Inferring ecology from either form of evidence is complex and often problematic (e.g., Anderson, 2001; Behrensmeier, 2001; Kidwell, 2001; Skelton, 2001). Further, it remains unclear what ecological character was interpreted (Martin, 1983, 1987; Feduccia, 1995, 1996, 1999) as held in common among, for example, *Ichthyornis* (with an ecology likened to that of a tern; Marsh, 1880), *Hesperornis* (a highly modified flightless diver (Marsh, 1880), and, for example, the filter-feeding, wading, anseriform *Presbyornis* (Olson and Feduccia, 1980). However, these points were not the basis for our argument.

We accepted that the ornithurines that formed the basis for the “shorebird hypothesis” had been described from littoral, marine, or lacustrine deposits, and that formed part of the evidence used to argue that they were restricted to these environments (Martin, 1983; Feduccia, 1996, 1999). In contrast to these taxa, we pointed out that *Apsaravis ukhaana* is from a semi arid dunefield (Loope et al., 1998; Norell and Clarke, 2001), data not easily construed as supporting evidence of a restriction of ornithurines to shorebird habitats.

Although morphological evidence is also used to infer ecology, the often discussed “shorebird morphologies” are notoriously hard to define. Livezey (1997b) aptly remarked in reviewing the “transitional shorebird” hypothesis (in the context of the phylogenetic relationships of *Presbyornis pervetus*) that even identifying derived morphologies diagnosing Charadriiformes (i.e., crown clade “shorebirds”) remains problematic (e.g., Strauch, 1978; Chu, 1995). Further, the presence of morphologies convergently seen in extant Charadriiformes in taxa supported as outgroups of the crown clade, does make these taxa shorebirds, or these morphologies indicative of a shorebird ecology. Indeed, several morphologies that have been considered characteristic of Charadriiformes (e.g., the presence of fewer sacral vertebrae, prominent lateral excavations of the thoracic vertebrae and an unpneumatized humerus) are optimized as plesiomorphic for much more inclusive avialan subclades (e.g., Or-

nithurae) as well as derived within Aves and present in Charadriiformes (as well as other neoavians; Clarke, 2002). Further, although there are several characters that are optimized specifically as convergently present in some Charadriiformes and *Ichthyornis dispar* (Clarke, 2002), these morphologies are not seen in *Apsaravis ukhaana*.

No morphological or paleoenvironmental data from *Apsaravis ukhaana* support its identity as a shorebird even if we accept the kinds of evidence used by proponents of the “ecological bottle neck” hypothesis (Clarke and Norell, 2001). However, as illustrated in Feduccia (2001), there are general problems with the testability of this hypothesis and the style of argumentation used to support it. For example, Feduccia (2001: 507) wrote, “Because shoreline habitats were as common in continental interiors as on continental margins during the Late Cretaceous and shorebirds are equally at home in freshwater and marine environments, *Apsaravis* has no bearing on the habitat of Late Cretaceous birds”. If this position is taken, then no paleoenvironmental data can be used to corroborate or test the shorebird hypothesis. It cannot be deemed exceptionable only in the case of *Apsaravis ukhaana*. If any fossil could be a cryptic shorebird regardless of depositional environment and morphology, how is this shorebird hypothesis able to be investigated?

We (Clarke and Norell, 2001) proposed optimizing ecology on a phylogeny of Aves and its near outgroups as a potential test of this hypothesis. We used a phylogeny supported by morphological and molecular data (reviewed in Cracraft and Clarke, 2001), in which Palaeognathae and Galloanserae are, respectively, two of the basalmost divergences within the avian crown clade. Charadriiformes (“shorebirds”) are placed as part of Neoaves, the sister taxon of Galloanserae, which includes all other non-galloanserine neognaths in what is essentially an unresolved polytomy (reviewed in Cracraft and Clarke, 2001). We (Clarke and Norell, 2001) attempted to roughly “bracket” (e.g., Witmer, 1995) the ecology basal to Aves considering extant taxa for which ecology can be observed. No extant palaeognaths or galloanserines have been considered to have a “shorebird ecology” and Neoaves would be

polymorphic for such a character (Clarke and Norell, 2001). Even if *Ichthyornis dispar* is considered to have a “shorebird ecology”, (e.g., per Marsh, 1880), this ecology cannot parsimoniously optimize as primitive to Aves (Clarke and Norell, 2001). It is optimized as independently derived within Neoaves and for *Ichthyornis dispar*. For this rough optimization, *Hesperornis regalis* and *Apsaravis ukhaana* were not considered to evidence a “shorebird ecology”.

Feduccia (1996, 1999, 2001) has also commented that several Paleogene taxa described as “shorebird mosaics” were further evidence that a shorebird ecology was primitive to the avian crown. For example, he wrote “the basal status of the transitional shorebirds . . . is evidenced not only by the presence of numerous latest Cretaceous and early Paleocene fossils of transitional shorebirds but by the discovery of a number of shorebird-modern order mosaics in the Eocene: *Juncitarsus*, *Presbyornis* and *Rhynchaeites* . . .” (Feduccia, 1999: 165). Of these three taxa, *Presbyornis* has been placed most basally within Aves (in Galloanserae; Ericson, 1997; Livezey, 1997b), but, because of its position nested within extant Anseriformes, it cannot alone affect the optimization of ecology primitive to Galloanserae, let alone for all of Aves. However, more inclusive analyses of fossil and extant parts of Aves and its near outgroups are the necessary next step toward further investigation of these issues.

Here, and in Clarke and Norell (2001), we outlined an approach that places the ornithurine ecological restriction argument in a testable frame, in marked contrast to the intuitive approach taken by others (e.g., Feduccia, 1995, 1996, 1999, 2001). Future work optimizing the ecological characters ancestral to Aves will be particularly effected by (1) inclusion of Tertiary fossil taxa on the stem lineages of subclade crowns, (2) resolution of neoavian relationships, and (3) the discovery, phylogenetic placement, and inferred ecology of other new near-outgroups of Aves. Finally, it is essential to rigorously discriminate the various ecological variables referred to collectively as a “shorebird ecology” for potential inclusion in, or optimization on, such a phylogeny.

Diagnosis of Enantiornithes

While 27 characters have been proposed as derived morphologies of Enantiornithes (e.g., Walker, 1981; Chiappe, 1991, 1996, 2001; Kurochkin, 1996; Sereno et al., 2002; listed in the supplementary information of Norell and Clarke, 2001), in the current analysis, only 4 characters support monophyly in both most parsimonious trees. The strict consensus of these is presented in figure 24. Enantiornithine monophyly collapses with a tree length one step longer than the most parsimonious topologies.

As noted in Norell and Clarke (2001), as further avialan taxa, such as *Apsaravis ukhaana*, are described, many previously proposed unique enantiornithine morphologies are discovered to have a broader distribution within Avialae. They are optimized as having alternatively homoplastic distributions or as primitive to an avialan subclade including Aves and Enantiornithes (see two examples discussed below). One implication of the more complex known distributions of these characters is that the identification of isolated elements as part of Enantiornithes (e.g., *Nanantius eos*; Molnar, 1986) based on the presence of one, or a few, such characters need to be reevaluated. For example, the narrow intercondylar groove and barrel-shaped aspect of the condyles of the tibiotarsus used to refer *Nanantius eos* to Enantiornithes (Molnar, 1986) are also seen in *Apsaravis ukhaana* and *Vorona berivotrensis*. Such fragmentary fossils may be found to be part of Enantiornithes, but further analyses of their phylogenetic relationships that include recently discovered taxa, such as *Apsaravis ukhaana*, are recommended.

Two examples of characters that, with the discovery of *Apsaravis ukhaana* and our increasing knowledge of the morphology of basal avialans, are no longer optimized as unique to Enantiornithes are from the coracoid (Norell and Clarke, 2001). The condition in which the dorsal surface of the coracoid is strongly concave versus flat to convex throughout the majority of the shaft has been considered a derived feature of Enantiornithes (Walker, 1981; Chiappe, 1991, 1996). However, as discussed in Norell and

Clarke (2001), the dorsal surface of the coracoid in Dromaeosauridae is broadly concave, and it is deeply concave in *Confuciusornis sanctus* and *Apsaravis ukhaana* (Norell and Clarke, 2001). It appears that it is the loss of the depression or fossa, rather than its presence, that is derived within Avialae.

Further, in both *Apsaravis ukhaana* and *Neuquenornis volans* (Chiappe and Calvo, 1994) the posterodorsal opening of the supracoracoideus nerve foramen lies in the depressed dorsal surface, or dorsal fossa, of the coracoid. The medial opening of the supracoracoideus nerve foramen being developed in a groove was also considered a derived feature of Enantiornithes (Chiappe, 1991). However, in Dromaeosauridae, this medial opening of the foramen lies into a broad depression on the anteromedial surface of the coracoid. In *Neuquenornis volans*, *Concornis lacustris*, *Cathayornis yandica*, *Gobipteryx minuta*, as well as *Apsaravis ukhaana*, the medial opening of the foramen lies in an elongate groove that we consider the topological equivalent of the broad depression in Dromaeosauridae. In *Confuciusornis sanctus*, the morphology of the supracoracoideus nerve foramen is unknown. Previous descriptions of this morphology (see excluded character 97) considered the dromaeosaurid condition equivalent to that in the avian crown clade as state "0" for purposes of analysis (e.g., Chiappe and Calvo, 1994). However, while the foramen lies in a depression in Dromaeosauridae, it lies on a flat surface in Aves.

To consider the effect of the previous interpretation of these coracoidal morphologies, characters 89 and 97 were swapped in to replace 88 and 98. When 89 and 97 were included (and 88 and 98 removed), two most parsimonious trees resulted that were two steps longer (length = 394; CI = 0.68; RI = 0.81; RC = 0.55) than the analysis including 88 and 98 (and excluding 89 and 97). In neither of these trees do characters 89 and 97 optimize as synapomorphies of Enantiornithes. Given that a "dorsal fossa" (89:1) is present in *Confuciusornis sanctus* and in *Apsaravis ukhaana*, this feature optimizes as a synapomorphic gain of *Confuciusornis sanctus* + Aves followed by a loss outside of

Hesperornithes + Aves. In the case of the medial opening of the supracoracoideus nerve foramen into an elongate groove (97: 1), it is equally parsimoniously gained at Enantiornithes + Aves and lost in Hesperornithes + Aves as it is independently gained in Enantiornithes and in *Apsaravis ukhaana*.

Assembly of the Avian Flight Stroke

We noted in Norell and Clarke (2001) that *Apsaravis ukhaana* provides insight into the assembly of the avian flight apparatus, as the basalmost avialan with an avian extensor process. In Aves, a strong, anteriorly projected “extensor” process on metacarpal I is developed at the insertion of the m. extensor metacarpi radialis and the propatagial ligaments (e.g., Ostrom, 1976). The m. extensor metacarpi radialis functions to “automate” extension of the manus with extension of the forearm in Aves (Vasquez, 1994). This automation has been considered a “key innovation” in the origin of flight (e.g., Ostrom, 1995) and has been proposed to be present in nonavialan theropods (Ostrom, 1995; Gishlick, 2001).

We argued (Norell and Clarke, 2001) that the strongest inference of the point of origin of avian automatic extension of the forelimb is at the *Apsaravis* + Aves node because *Apsaravis ukhaana* is the phylogenetically earliest avialan to have a morphology of metacarpal I associated with m. extensor metacarpi radialis function in extant parts of Aves. Here, we elaborate ideas presented in that paper (Norell and Clarke, 2001).

In *Apsaravis ukhaana*, a muscular process developed on the anterior tip of metacarpal I is pointed and extends well past the anterior tip of the articular surface for phalanx I:1 (fig. 2). The degree of projection (see above) and pointed morphology in *Apsaravis ukhaana* is seen in *Ichthyornis dispar* and optimized as primitive to Aves (Clarke, 2002). However, they are not seen in more basal avialans with this region preserved. In *Archaeopteryx lithographica* and nonavialan theropods (to varying degrees), the proximoanterior edge of metacarpal I flares slightly but does not extend past the anterior limit of the articular surface for phalanx I:1. In *Confuciusornis sanctus* and enantiornithines,

the entire surface of metacarpal I is bowed, or broadly convex, anteriorly (Clarke and Chiappe, 2001). Additionally, two new basal avialan taxa were recently described from China (Zhou and Zhang, 2002a, 2002b). Both lack the convex anterior edge of metacarpal I seen in *Confuciusornis sanctus* and Enantiornithes, having instead an hourglass-shaped anterior surface like that seen in *Archaeopteryx lithographica* and nonavialan outgroups. However, metacarpal I projects more in these taxa than in *Archaeopteryx* and nonavialan theropods but less than in *Apsaravis ukhaana*, *Ichthyornis*, and Aves. Because the degree of projection thus appears continuously variable, at what point the “key innovation” in the development of the avian function might be identified is unclear.

We proposed that at the *Apsaravis* + Aves node, where a morphology associated with “automatic” extension in Aves is optimized as first present, constitutes the best supported (and most conservative) inference of its point of origin. Avian “automatic” extension may have originated earlier, either associated with the unusual morphologies of metacarpal I seen in *Confuciusornis sanctus* and enantiornithines, in more basal avialans, or perhaps in nonavialan theropods (Gishlick, 2001); however, this inference awaits further support.

For example, it has so far not been explained how avian automatic extension would have functioned in nonavialan theropods without morphological features that participate in the avian “automated” extension kinematic chain (Vasquez, 1994). These morphologies include a radiale with a depression to receive the end of the radius, a V-shaped ulnare, and anteriorly located humeral condyles. All of these features are present in *Apsaravis ukhaana* and can be bracketed for at least the *Apsaravis* + Aves node (e.g., Chiappe, 1996; Sereno and Rao, 1992; Norell and Clarke, 2001; Norell et al., 2001) in addition to the derived metacarpal I process.

That precursors to the avian flight stroke developed in nonflighted outgroups of Avialae makes evolutionary sense. This conclusion is also supported by abundant fossil evidence (e.g., Gauthier and Padian, 1985; Padian and Chiappe, 1999). However, the pro-

posal that specifically the “automatic” extension seen in living birds was present in these taxa (Gishlick, 2001) requires further investigation. In conclusion, we do not propose that the shift to the morphology seen in *Apsaravis* + Aves node is the “key innovation” in the origin of automatic extension, but that it is this point that is the most justifiable minimal estimate of its origin. Generally, focusing on key innovations may often obscure, more than it illuminates, the complex assembly of avian flight. The inferred “key” points of origin of many such identified novelties are often harder to defend with denser taxon sampling and can appear increasingly like arbitrarily defined points in continuous variation.

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APPENDIX 1

ANATOMICAL ABBREVIATIONS

(The “r” and “l” prefixes combined with the abbreviations listed below indicate right and left, respectively.)

a	acromion	dfs	dorsal fossa
aas	anterior articular surface	dl	dorsal lip of sternum
acf	anterior carpal fovea	dp	dorsal process
acr	acrocrocoracoid	ep	extensor process
an	antitrochanter	f	femur
bc	bicipital crest	fh	femoral head
bt	bicipital tubercle	fl	ischial flange
c	coracoid	fp	flexor process
cf	capital fossa	fpt	pneumotricipital fossa
cg	coracoidal groove	fs	fossa
cm	carpometaacarpus	g	groove
cr	cranium	gf	glenoid facet
crv	cervical vertebrae	h	humerus
ct	carpal trochlea	hyp	hypotarsal area
ctb	carpal tubercle of ulna	il	ilium
cv	caudal vertebrae	is	ischium
cvIII	third free caudal vertebra	j?	jugal?
cvIV	fourth free caudal vertebra	lac	lateral condyle
cvV	fifth free caudal vertebra	le	lateral excavation
d	dentary	m	mandibula
dc	dorsal condyle	mc	medial condyle
dct	dorsal cotyla	mdr	midline ridge
df	distal vascular foramen	mpr	medial plantar ridge
		ms	mandibular symphysis
		mw	medial wing of sulcus cartilaginis tibialis
		n?	notarium?

ole	olecranon	saf	sternal articular facet
or	orbit	scl	sclerotic ossicles
ot	ossified tendon	shg	scapulohumeralis groove
p	pubis	snf	supracoracoideus nerve foramen
pas	posterior articular surface	sno	spinal nerve openings
pp	pisiform process	spc	scapular cotyla
phII-1	phalanx 1, manual digit II	st	sternum
pphII-1	phalanx 1, pedal digit II	svI	sacral vertebra I
pphII-2	phalanx 2, pedal digit II	svII	sacral vertebra II
pphIII-1	phalanx 1, pedal digit III	t	tibiotarsus
pphIII-2	phalanx 2, pedal digit III	tct	m. tibialis cranialis tubercles
pphIV-1	phalanx 1, pedal digit IV	tf	transverse foramen
pphIV-2	phalanx 2, pedal digit IV	tm	tarsometatarsus
pphIV-3	phalanx 3, pedal digit IV	trc	trochanteric crest
ptf	pneumotricipital fossa	tre	extensor retinaculum tubercles
pvf	proximal vascular foramen	tub	tubercle
py	pygostyle	tv	thoracic vertebrae
q	quadrate	u	ulna
r	radius	ue	ulnare
rdg?	lateral ridge of Norell and Makovicky (1999)?	vc	ventral condyle
re	radiale	vct	ventral cotyla
ri	ribs	vf	vascular foramen
s	scapula	vp	ventral process

APPENDIX 2

CHARACTER LIST

A list of the 202 morphological characters used in the phylogenetic analyses (from Clarke, 2002). All characters are unordered except the following 36: 1, 8, 11, 23, 31, 52, 54, 61, 62, 66, 68, 69, 71, 76, 80, 105, 113, 117, 139, 142, 149, 153, 159, 170, 175, 177, 180, 182, 185, 188, 192, 193, 194, 195, 196, and 202. The “PV” associated with characters 89 and 97 indicates these are the “previous versions” of characters 88 and 98, respectively, which were excluded from the primary analysis (see text).

1. **Premaxillae:** (0) unfused in adults; (1) fused anteriorly in adults, posterior nasal (frontal) processes not fused to each other; (2) frontal processes completely fused as well as anterior premaxillae. (ORDERED)
2. **Premaxillary teeth:** (0) present, (1) absent.
3. **Maxillary teeth:** (0) present, (1) absent.
4. **Dentary teeth:** (0) present, (1) absent.
5. **Tooth crown serration:** (0) present, (1) vestigial or absent.
6. **Dentaries:** (0) joined proximally by ligaments, (1) joined by bone.
7. **Mandibular symphysis, two strong grooves forming an anteriorly opening**

“V” in ventral view: (0) absent, (1) present.

8. **Facial margin:** (0) primarily formed by the maxilla, with the maxillary process of the premaxilla restricted to the anterior tip; (1) maxillary process of the premaxilla extending one-half of facial margin; (2) maxillary process of the premaxilla extending more than one-half of facial margin. (ORDERED)
9. **Nasal (frontal) process of premaxilla:** (0) short; (1) long, closely approaching frontal.
10. **Nasal process of maxilla, dorsal ramus:** (0) prominent, exposed medially and laterally; (1) absent or reduced to slight medial, and no lateral, exposure.
11. **Nasal process of maxilla, participation of ventral ramus in anterior margin of antorbital fenestra in lateral view:** (0) present, extensive; (1) small dorsal projection of the maxilla participates in the anterior margin of the antorbital fenestra, descending process of the nasals contacts premaxilla to exclude maxilla from nasal margin; (2) no dorsal projection of maxilla participates in anterior margin of the antorbital fenestra. (ORDERED)
12. **Osseous external naris:** (0) considerably

- smaller than the antorbital fenestra, (1) larger.
13. **Ectopterygoid:** (0) present, (1) absent.
 14. **Articulation between vomer and pterygoid:** (0) present, well developed; (1) reduced, narrow process of pterygoid passes dorsally over palatine to contact vomer; (2) absent, pterygoid and vomer do not contact.
 15. **Palatine and pterygoid:** (0) long, antero-posteriorly overlapping contact; (1) short, primarily dorsoventral contact.
 16. **Palatine contacts:** (0) maxillae only, (1) premaxillae and maxillae.
 17. **Vomer contacts premaxilla:** (0) present, (1) absent.
 18. **Coronoid ossification:** (0) present, (1) absent.
 19. **Projecting basisphenoid articulation with pterygoid:** (0) present, (1) absent.
 20. **Basipterygoid processes:** (0) long, (1) short (articulation with pterygoid subequal to, or longer than, amount projected from the basisphenoid rostrum).
 21. **Basisphenoid/pterygoid articulations:** (0) located basal on basisphenoid, (1) located markedly anterior on basisphenoid (parasphenoid rostrum) such that the articulations are subadjacent on the narrow rostrum (the “rostrompterygoid articulation” of Weber, 1993).
 22. **Basisphenoid/pterygoid articulation, orientation of contact:** (0) anteroventral, (1) mediolateral, (2) entirely dorsoventral.
 23. **Pterygoid, articular surface for basisphenoid:** (0) concave “socket”, or short groove enclosed by dorsal and ventral flanges; (1) flat to convex; (2) flat to convex facet, stalked, variably projected. (ORDERED)
 24. **Pterygoid, kinked:** (0) present, surface for basisphenoid articulation at high angle to axis of palatal process of pterygoid; (1) absent, articulation in line with axis of pterygoid.
 25. **Osseous interorbital septum (mesethmoid):** (0) absent, (1) present.
 26. **Osseous interorbital septum (mesethmoid):** (0) restricted to posterior or another just surpassing premaxillae/frontal contact in rostral extent does not surpass posterior edge of external nares in rostral extent; (1) extending rostral to posterior extent of frontal processes of premaxillae and rostral to posterior edge of external nares.
 27. **Eustachian tubes:** (0) paired and lateral; (1) paired, close to cranial midline; (2) paired and adjacent on midline or single anterior opening.
 28. **Eustachian tubes ossified:** (0) absent, (1) present.
 29. **Squamosal, ventral or “zygomatic” process:** (0) variably elongate, dorsally enclosing otic process of the quadrate and extending anteroventrally along shaft of this bone, dorsal head of quadrate not visible in lateral view; (1) short, head of quadrate exposed in lateral view.
 30. **Orbital process of quadrate, pterygoid articulation:** (0) pterygoid broadly overlapping medial surface of orbital process (i.e., “pterygoid ramus”); (1) restricted to anteromedial edge of process.
 31. **Quadrate, orbital process:** (0) pterygoid articulates with anteriormost tip; (1) pterygoid articulation does not reach tip; (2) pterygoid articulation with no extent up orbital process, restricted to quadrate corpus. (ORDERED)
 32. **Quadrate/pterygoid contact:** (0) as a facet, variably with slight anteromedial projection cradling base; (1) condylar, with a well-projected tubercle on the quadrate.
 33. **Quadrate, well-developed tubercle on anterior surface of dorsal process:** (0) absent, (1) present.
 34. **Quadrate, quadratojugal articulation:** (0) overlapping, (1) peg-and-socket articulation.
 35. **Quadrate, dorsal process, articulation:** (0) with squamosal only, (1) with squamosal and prootic.
 36. **Quadrate, dorsal process, development of intercotylar incisure between prootic and squamosal cotylae:** (0) absent, articular surfaces not differentiated; (1) two distinct articular facets, incisure not developed; (2) incisure present, “double headed”.
 37. **Quadrate, mandibular articulation:** (0) bicondylar articulation with mandible; (1) tricondylar articulation, additional posterior condyle or broad surface.
 38. **Quadrate, pneumaticity:** (0) absent, (1) present.
 39. **Quadrate, cluster of pneumatic foramina on posterior surface of the tip of dorsal process:** (0) absent, (1) present.
 40. **Quadrate, pneumatization, large, single pneumatic foramen:** (0) absent, (1) posteromedial surface of corpus.
 41. **Articular pneumaticity:** (0) absent, (1) present.
 42. **Dentary strongly forked posteriorly:** (0)

- unforked, or with a weakly developed dorsal ramus; (1) strongly forked with the dorsal and ventral rami approximately equal in posterior extent.
43. **Splenic, anterior extent:** (0) splenic stops well posterior to mandibular symphysis; (1) extending to mandibular symphysis, though noncontacting; (2) extending to proximal tip of mandible, contacting on midline.
 44. **Mandibular symphysis, anteroposteriorly extensive, flat to convex, dorsal-facing surface developed:** (0) absent, concave; (1) flat surface developed.
 45. **Mandibular symphysis, symphyseal foramina:** (0) absent, (1) present.
 46. **Mandibular symphysis, symphyseal foramen/foramina:** (0) single, (1) paired.
 47. **Mandibular symphysis, symphyseal foramen/foramina:** (0) opening on posterior edge of symphysis, (1) opening on dorsal surface of symphysis.
 48. **Meckel's groove:** (0) not completely covered by splenic, deep and conspicuous medially; (1) covered by splenic, not exposed medially.
 49. **Anterior external mandibular fenestra:** (0) absent, (1) present.
 50. **Jugal/postorbital contact:** (0) present, (1) absent.
 51. **Frontal/parietal suture:** (0) open, (1) fused.
 52. **Cervical vertebrae:** (0) variably dorsoventrally compressed, amphicoelous ("biconcave": flat to concave articular surfaces); (1) anterior surface heterocoelous (i.e., mediolaterally concave, dorsoventrally convex), posterior surface flat; (2) heterocoelous anterior (i.e., mediolaterally concave, dorsoventrally convex) and posterior (i.e., mediolaterally convex, dorsoventrally concave) surfaces. (ORDERED)
 53. **Thoracic vertebrae (with ribs articulating with the sternum), one or more with prominent hypapophyses:** (0) absent, (1) present. (This character does not address the presence of hypapophyses on transitional vertebrae, or "cervicothoracics", that do not have associated ribs that articulate with the sternum [e.g., Gauthier, 1986; Chiappe, 1996]. In contrast, in Aves, well-developed hypapophyses are developed well into the thoracic series, on vertebrae with ribs articulating with the sternum.)
 54. **Thoracic vertebrae, count:** (0) 12 or more, (1) 11, (2) 10 or fewer. (ORDERED)
 55. **Thoracic vertebrae:** (0) at least part of series with subround, central articular surfaces (e.g., amphicoelous/opisthocoelous) that lack the dorsoventral compression seen in heterocoelous vertebrae; (1) series completely heterocoelous.
 56. **Thoracic vertebrae, parapophyses:** (0) rostral to transverse processes, (1) directly ventral to transverse processes (close to midpoint of vertebrae).
 57. **Thoracic vertebrae, centra, length, and midpoint width:** (0) approximately equal in length and midpoint width, (1) length markedly greater than midpoint width.
 58. **Thoracic vertebrae, lateral surfaces of centra:** (0) flat to slightly depressed; (1) deep, emarginate fossae; (2) central ovoid foramina.
 59. **Thoracic vertebrae with ossified connective tissue bridging transverse processes:** (0) absent, (1) present.
 60. **Notarium:** (0) absent, (1) present.
 61. **Sacral vertebrae, number ankylosed:** (0) less than 7, (1) 7, (2) 8, (3) 9, (4) 10, (5) 11 or more, (6) 15 or more. (ORDERED)
 62. **Sacral vertebrae, series of short vertebrae, with dorsally directed parapophyses just anterior to the acetabulum:** (0) absent; (1) present, three such vertebrae; (2) present, four such vertebrae. (ORDERED)
 63. **Free caudal vertebrae, number:** (0) more than 8, (1) 8 or less.
 64. **Caudal vertebrae, chevrons, fused on at least one anterior caudal:** (0) present, (1) absent.
 65. **Free caudals; length of transverse processes:** (0) approximately equal to, or greater than, centrum width; (1) significantly shorter than centrum width.
 66. **Anterior free caudal vertebrae:** (0) elongate pre/postzygapophyses; (1) pre- and postzygapophyses short and variably noncontacting; (2) prezygapophyses clasping the posterior surface of neural arch of preceding vertebra, postzygapophyses negligible. (ORDERED)
 67. **Distal caudals:** (0) unfused, (1) fused.
 68. **Fused distal caudals, morphology:** (0) long, more than length of 4 free caudal vertebrae; (1) medium, less than the length of 4 caudal vertebrae; (2) short, less than 2 caudal vertebrae in length. (ORDERED)
 69. **Ossified uncinat processes:** (0) absent, (1) present and unfused to ribs, (2) fused to ribs. (ORDERED)
 70. **Gastralia:** (0) present, (1) absent.
 71. **Ossified sternal plates:** (0) unfused; (1)

- fused, flat; (2) fused, with slightly raised midline ridge; (3) fused with projected carina. (ORDERED)
72. **Carina or midline ridge:** (0) restricted to posterior half of sternum, (1) approaches anterior limit of sternum.
73. **Sternum, dorsal surface, pneumatic foramen (or foramina):** (0) absent, (1) present.
74. **Sternum, pneumatic foramina in the depressions (loculi costalis; Baumel and Witmer, 1993) between rib articulations (processi articularis sternocostalis; Baumel and Witmer (1993):** (0) absent, (1) present.
75. **Sternum, coracoidal sulci spacing on anterior edge:** (0) widely separated mediolaterally, (1) adjacent, (2) crossed on midline.
76. **Sternum, number of processes for articulation with the sternal ribs:** (0) three, (1) four, (2) five, (3) six, (4) seven or more. (ORDERED)
77. **Sternum: raised, paired intermuscular ridges (linea intermuscularis; Baumel and Witmer, 1993) parallel to sternal midline:** (0) absent, (1) present.
78. **Clavicles:** (0) fused, (1) unfused.
79. **Interclavicular angle (clavicles elongate):** (0) greater than 90°, (1) less than 90° degrees.
80. **Furcula, hypocleideum:** (0) absent, (1) a tubercle, (2) an elongate process. (ORDERED)
81. **Furcula, laterally excavated:** (0) absent, (1) present.
82. **Furcula, dorsal (omal) tip:** (0) flat or blunt tip, (1) with a pronounced posteriorly pointed tip.
83. **Scapula and coracoid:** (0) fused, (1) unfused.
84. **Scapula and coracoid articulation:** (0) pit-shaped scapular cotyla developed on the coracoid, and coracoidal tubercle developed on the scapula (“ball-and-socket” articulation); (1) scapular articular surface of coracoid convex; (2) flat.
85. **Coracoid, procoracoid process:** (0) absent, (1) present.
86. **Coracoid:** (0) height approximately equal to mediolateral dimension; (1) height more than twice width, coracoid “strut-like”.
87. **Coracoid, lateral margin:** (0) straight to slightly concave, (1) convex.
88. **Coracoid, dorsal surface (= posterior surface of basal maniraptoran theropods):** (0) strongly concave, (1) flat to convex.
89. **PV. Coracoid, dorsal surface, deep fossa:** (0) absent, (1) present.
90. **Coracoid, pneumatized:** (0) absent, (1) present.
91. **Coracoid, pneumatic foramen:** (0) proximal, (1) distal.
92. **Coracoid, lateral process:** (0) absent, (1) present.
93. **Coracoid, ventral surface, lateral intermuscular line or ridge:** (0) absent, (1) present.
94. **Coracoid, glenoid facet:** (0) dorsal to acrocoracoid process/“biceps tubercle”, (1) ventral to acrocoracoid process.
95. **Coracoid, acrocoracoid:** (0) straight, (1) hooked medially.
96. **Coracoid, n. supracoracoideus passes through coracoid:** (0) present, (1) absent.
97. **PV. Coracoid, passage of n. supracoracoideus foramen opening into a medial groove:** (0) absent, (1) present.
98. **Coracoid, medial surface, area of the n. supracoracoideus foramen (when developed):** (0) strongly depressed, (1) flat to convex.
99. **Angle between coracoid and scapula at glenoid:** (0) more than 90°, (1) 90° or less.
100. **Scapula:** (0) posterior tip wider than proximal dorsoventral shaft width, (1) tapering distally.
101. **Scapula:** (0) straight, (1) dorsoventrally curved.
102. **Scapula, length:** (0) shorter than humerus, (1) as long as or longer than humerus.
103. **Scapula, acromion process:** (0) projected anteriorly surpassing the articular surface for coracoid (facies articularis coracoidea; Baumel and Witmer, 1993), (1) projected less anteriorly than the articular surface for coracoid.
104. **Scapula, acromion process:** (0) straight, (1) laterally hooked tip.
105. **Humerus and ulna, length:** (0) humerus longer than ulna, (1) ulna and humerus approximately the same length, (2) ulna significantly longer than humerus. (ORDERED)
106. **Humerus, proximal end, head in anterior or posterior view:** (0) straplike, articular surface flat, no proximal midline convexity; (1) head domed proximally.
107. **Humerus, proximal end, proximal projection:** (0) dorsal edge projected farthest, (1) midline projected farthest.
108. **Humerus, ventral tubercle and capital incisure:** (0) absent, (1) present.

109. **Humerus, capital incisure:** (0) an open groove, (1) closed by tubercle associated with a muscle insertion just distal to humeral head.
110. **Humerus, anterior surface, well-developed fossa on midline making proximal articular surface appear V-shaped in proximal view:** (0) absent, (1) present.
111. **Humerus, “transverse groove”:** (0) absent; (1) present, developed as a discrete, depressed scar on the proximal surface of the bicipital crest or as a slight transverse groove.
112. **Humerus, deltopectoral crest:** (0) projected dorsally (in line with the long axis of humeral head), (1) projected anteriorly.
113. **Humerus, deltopectoral crest:** (0) less than shaft width, (1) same width, (2) dorsoventral width greater than shaft width. (ORDERED)
114. **Humerus, deltopectoral crest, proximoposterior surface:** (0) flat to convex, (1) concave.
115. **Humerus, bicipital crest, pit-shaped scar/fossa for muscular attachment on anterodistal, distal, or posterodistal surface of crest:** (0) absent, (1) present.
116. **Humerus, bicipital crest, pit-shaped fossa for muscular attachment:** (0) anterodistal on bicipital crest, (1) directly ventrodistal at tip of bicipital crest, (2) posterodistal, variably developed as a fossa.
117. **Humerus, bicipital crest:** (0) little or no anterior projection; (1) developed as an anterior projection relative to shaft surface in ventral view; (2) hypertrophied, rounded tumescence. (ORDERED)
118. **Humerus, proximal end, one or more pneumatic foramina:** (0) absent, (1) present.
119. **Humerus, distal condyles:** (0) developed distally, (1) developed on anterior surface of humerus.
120. **Humerus, long axis of dorsal condyle:** (0) at low angle to humeral axis, proximodistally oriented; (1) at high angle to humeral axis, almost transversely oriented.
121. **Humerus, distal condyles:** (0) subround, bulbous; (1) weakly defined, “straplike”.
122. **Humerus, distal margin:** (0) approximately perpendicular to long axis of humeral shaft; (1) ventrodistal margin projected significantly distal to dorsodistal margin, distal margin angling strongly ventrally (sometimes described as a well-projected flexor process).
123. **Humerus, distal end, compressed anteroposteriorly and flared dorsoventrally:** (0) absent, (1) present.
124. **Humerus, brachial fossa:** (0) absent; (1) present, developed as a flat scar or as a scar-impressed fossa.
125. **Humerus, ventral condyle:** (0) length of long axis of condyle less than the same measure of the dorsal condyle, (1) same or greater.
126. **Humerus, demarcation of muscle origins (e.g., m. extensor metacarpi radialis in Aves) on the dorsal edge of the distal humerus:** (0) no indication of origin as a scar, a pit, or a tubercle; (1) indication as a pit-shaped scar or as a variably projected scar-bearing tubercle or facet.
127. **Humerus, distal end, posterior surface, groove for passage of m. scapulotriceps:** (0) absent, (1) present.
128. **Humerus, m. humerotricipitalis groove:** (0) absent, (1) present as a well-developed ventral depression contiguous with the olecranon fossa.
129. **Ulna, cotylae:** (0) dorsoventrally adjacent, (1) widely separated by a deep groove.
130. **Ulna, dorsal cotyla convex:** (0) absent, (1) present.
131. **Ulna, distal end, dorsal condyle, dorsal trochlear surface developed as a semilunate ridge:** (0) absent, (1) present.
132. **Ulna, distal end, dorsal condyle, dorsal trochlear surface, extent along posterior margin:** (0) less than transverse measure of dorsal trochlear surface, (1) approximately equal in extent.
133. **Ulna, bicipital scar:** (0) absent, (1) developed as a slightly raised scar, (2) developed as a conspicuous tubercle.
134. **Ulna, brachial scar:** (0) absent, (1) present.
135. **Radius, ventroposterior surface:** (0) smooth, (1) with muscle impression along most of surface, (2) deep longitudinal groove.
136. **Ulnare:** (0) absent, (1) present.
137. **Ulnare:** (0), “heart-shaped”, little differentiation into short dorsal and ventral rami; (1) V-shaped, well-developed dorsal and ventral rami.
138. **Ulnare, ventral ramus (crus longus, Baumel and Witmer, 1993):** (0) shorter than dorsal ramus (crus brevis); (1) same length as dorsal ramus, (2) longer than dorsal ramus.
139. **Semilunate carpal and metacarpals:** (0) no fusion, (1) incomplete proximal fusion,

- (2) complete proximal fusion, (3) complete proximal and distal fusion. (ORDERED)
140. **Semilunate carpal, position relative to metacarpal I:** (0) over entire proximal surface, (1) over less than one-half proximal surface.
141. **Metacarpal III, anteroposterior diameter as a percentage of same dimension of metacarpal II:** (0) approximately equal or greater than 50%, (1) less than 50%.
142. **Metacarpal I, extensor process:** (0) absent, no anteroproximally projected muscular process; (1) present, tip of extensor process just surpassed the distal articular facet for phalanx 1 in anterior extent; (2) tip of extensor process conspicuously surpasses articular facet by approximately half the width of facet, producing a pronounced knob; (3) tip of extensor process conspicuously surpasses articular facet by approximately the width of facet, producing a pronounced knob. (ORDERED)
143. **Metacarpal I, anterior surface:** (0) roughly hourglass-shaped proximally, at least moderately expanded anteroposteriorly, and constricted just before flare of articulation for phalanx 1; (1) anterior surface broadly convex.
144. **Metacarpal I, distal articulation with phalanx I:** (0) ginglymoid, (1) shelf.
145. **Pisiform process:** (0) absent, (1) present.
146. **Carpometacarpus, ventral surface, supratrochlear fossa deeply excavating proximal surface of pisiform process:** (0) absent, (1) present.
147. **Intermetacarpal space (between metacarpals II and III):** (0) reaches proximally as far as the distal end of metacarpal I, (1) terminates distal to end of metacarpal I.
148. **Carpometacarpus, distal end, metacarpals II and III, articular surfaces for digits:** (0) metacarpal II subequal or surpasses metacarpal III in distal extent; (1) metacarpal III extends farther.
149. **Intermetacarpal process or tubercle:** (0) absent, (1) present as scar, (2) present as tubercle or flange. (ORDERED)
150. **Manual digit II, phalanx 1:** (0) subcylindrical to subtriangular; (1) strongly dorsoventrally compressed, flat posteriorly.
151. **Manual digit II, phalanges:** (0) length of phalanx II-1 less than or equal to that of II-2, (1) longer.
152. **Manual digit II, phalanx 2, "internal index process" (Stegmann, 1978) on posterodistal edge:** (0) absent, (1) present.
153. **Ilium, ischium, pubis, proximal contact in adult:** (0) unfused, (1) partial fusion (pubis not ankylosed), (2) completely fused. (ORDERED)
154. **Ilium/ischium, distal co-ossification to completely enclose the ilioischialic fenestra:** (0) absent, (1) present.
155. **Ischium:** (0) forked (dorsal process present); (1) straight, no dorsal process.
156. **Ischium, dorsal process:** (0) does not contact ilium, (1) contacts ilium.
157. **Ischium and pubis:** (0) not subparallel, pubis directed nearly directly ventrally; (1) subparallel, pubis posteriorly directed.
158. **Laterally projected process on ischiadic peduncle (antitrochanter):** (0) directly posterior to acetabulum, (1) posterodorsal to acetabulum.
159. **Praecetabular pectineal process (Baumel and Witmer, 1993):** (0) absent, (1) present as a small flange, (2) present as a well-projected flange. (ORDERED)
160. **Praecetabular ilium:** (0) approach on midline, open, or cartilaginous connection; (1) co-ossified, dorsal closure of "iliosynsacral canals".
161. **Praecetabular ilium extends anterior to first sacral vertebrae:** (0) no free ribs overlapped, (1) one or more ribs overlapped.
162. **Postacetabular ilium:** (0) dorsoventrally oriented, (1) mediolaterally oriented.
163. **Postacetabular ilium, ventral surface, renal fossa developed:** (0) absent, (1) present.
164. **Ilium, m. cuppedicus fossa as broad, mediolaterally oriented surface directly anteroventral to acetabulum:** (0) present; (1) surface absent, insertion variably marked by a small entirely lateral fossa anterior to acetabulum.
165. **Ischium, posterior demarcation of the obturator foramen:** (0) absent; (1) present, developed as a small flange or raised scar contacting/fused with pubis and demarcating the obturator foramen distally.
166. **Pubis:** (0) suboval in cross section, (1) compressed mediolaterally.
167. **Pubes, distal contact:** (0) contacting, variably co-ossified into symphysis; (1) noncontacting.
168. **Distal end of pubis:** (0) expanded, flared into a pubic boot; (1) straight, approximately the same width as the rest of pubis (pubic boot absent).

169. **Femur, fossa for insertion of lig. capitis femoris:** (0) absent, (1) present.
170. **Femur, posterior trochanter:** (0) present, developed as a slightly projected tubercle or flange; (1) hypertrophied, "shelf-like" conformation (in combination with development of the trochanteric shelf; see Hutchinson, 2001); (2) absent. (ORDERED)
171. **Femur, lesser and greater trochanters:** (0) separated by a notch, (1) developed as a single trochanteric crest.
172. **Femur, patellar groove:** (0) absent, (1) present.
173. **Femur:** (0) ectocondylar tubercle and lateral condyle separated by deep notch, (1) ectocondylar tubercle and lateral condyle form single trochlear surface.
174. **Femur, posterior projection of the lateral border of the distal end, continuous with lateral condyle:** (0) absent, (1) present.
175. **Laterally projected fibular trochlea:** (0) absent; (1) present, developed as small notch; (2) a shelflike projection. (ORDERED)
176. **Femur, popliteal fossa:** (0) a groove open distally and bounded medially and laterally by narrow condyles, (1) closed distally by expansion of both condyles (primarily the medial).
177. **Calcaneum and astragalus:** (0) unfused to each other or tibia in adult, (1) fused to each other, unfused to tibia; (2) completely fused to each other and tibia. (ORDERED)
178. **Tibia, cnemial crest(s):** (0) lateral crest only, (1) lateral and anterior crests developed.
179. **Tibia/tarsal-formed condyles:** (0) medial condyle projecting farther anteriorly than lateral, (1) equal in anterior projection.
180. **Tibia/tarsal-formed condyles, extensor canal:** (0) absent, (1) an emarginate groove, (2) groove bridged by an ossified supratendinal bridge. (ORDERED)
181. **Tibia/tarsal-formed condyles, tuberositas retinaculi extensoris (Baumel and Witmer, 1993) indicated by short medial ridge or tubercle proximal to the condyles close to the midline and a more proximal second ridge on the medial edge:** (0) absent, (1) present.
182. **Tibia/tarsal-formed condyles, mediolateral widths:** (0) medial condyle wider, (1) approximately equal, (2) lateral condyle wider. (ORDERED)
183. **Tibia/tarsal-formed condyles:** (0) gradual sloping medial constriction of condyles, (1) no medial tapering of either condyle.
184. **Tibia/tarsal-formed condyles, intercondylar groove:** (0) mediolaterally broad, approximately one-third width of anterior surface, (1) less than one-third width of total anterior surface.
185. **Tibia, extension of articular surface for distal tarsals/tarsometatarsus:** (0) no posterior extension of trochlear surface, or restricted to distalmost edge of posterior surface; (1) well-developed posterior extension, sulcus cartilaginis tibialis of Aves (Baumel and Witmer, 1993), distinct surface extending up the posterior surface of the tibiotarsus; (2) with well-developed, posteriorly projecting medial and lateral crests. (ORDERED)
186. **Tibia, distalmost mediolateral width:** (0) wider than midpoint of shaft, giving distal profile a weakly developed triangular form; (1) approximately equal to shaft width, no distal expansion of whole shaft, although condyles may be variably splayed mediolaterally.
187. **Fibula:** (0) reaches tarsal joint articulating into distinct socket formed between the proximal tarsals and the tibia, (1) reduced in length, does not reach tarsal joint.
188. **Distal tarsals and metatarsals, fusion:** (0) distal tarsals fuse to metatarsals; (1) distal tarsals fuse to metatarsals and proximal metatarsals co-ossify; (2) distal tarsals fuse to metatarsals, and metatarsals fuse to each other proximally and distally; (3) extreme distal fusion, distal vascular foramen closed. (ORDERED)
189. **Metatarsal V:** (0) present, (1) absent.
190. **Metatarsal III:** (0) proximally in plane with metatarsals II and IV; (1) proximally displaced plantarly, relative to metatarsals II and IV.
191. **Tarsometatarsus, intercotylar eminence:** (0) absent; (1) well developed, globose.
192. **Tarsometatarsus, projected surface and/or grooves on proximoposterior surface (associated with the passage of tendons of the pes flexors in Aves; hypotarsus):** (0) absent; (1) developed as posterior projection with flat posterior surface; (2) projection, with distinct crests and grooves; (3) at least one groove enclosed by bone posteriorly. (ORDERED)
193. **Tarsometatarsus, proximal vascular fo-**

- ramen(foramina):** (0) absent; (1) one, between metatarsals III and IV; (2) two. (ORDERED)
194. **Metatarsal I:** (0) straight; (1) curved or distally deflected but not twisted, ventral surface convex “J-shaped”; (2) deflected and twisted to such an extent that the ventromedial surface is concave proximal to trochlear surface for phalanx I. (ORDERED)
195. **Metatarsal II tubercle (associated with the insertion of the tendon of the m. tibialis cranialis in Aves):** (0) absent; (1) present, on approximately the center of the proximodorsal surface of metatarsal II; (2) present, developed on lateral surface of metatarsal II, at contact with metatarsal III or on lateral edge of metatarsal III. (ORDERED)
196. **Metatarsal II, distal plantar surface, fossa for metatarsal I (fossa metatarsi I; Baumel and Witmer, 1993):** (0) absent, (1) shallow notch, (2) conspicuous ovoid fossa. (ORDERED)
197. **Metatarsal II, articular surface for first phalanx:** (0) ginglymoid, (1) rounded.
198. **Metatarsals, relative mediolateral width:** (0) metatarsal IV approximately the same width as metatarsals II and III, (1) metatarsal IV narrower than metatarsals II and III, (2) metatarsal IV greater in width than either metatarsal II or III.
199. **Metatarsals, comparative trochlear width:** (0) II approximately the same size as III and/or IV, (1) II wider than III and/or IV, (2) II narrower than III and/or IV.
200. **Distal vascular foramen:** (0) simple, with one exit; (1) forked, two exits (plantar and distal) between metatarsals III and IV.
201. **Metatarsal III, trochlea in plantar view, proximal extent of lateral and medial edges of trochlea:** (0) absent, trochlear edges approximately equal in proximal extent; (1) present, lateral edge extends farther.
202. **Metatarsal II, distal extent of metatarsal II relative to metatarsal IV:** (0) approximately equal in distal extent; (1) metatarsal II shorter than metatarsal IV; but reaching distally farther than base of metatarsal IV trochlea, (2) metatarsal II shorter than metatarsal IV, reaching distally only as far as base of metatarsal IV trochlea. (ORDERED)

APPENDIX 3
(Continued)

	101	110	120	130	140	150
<i>Anas platyrhynchos</i>	1 0 0 0	1 1 0 0	1 1 0 0	1 1 0 0	1 1 2 3	1 1 0 1
<i>Chauna torquata</i>	1 0 1 0	2 1 1 0	2 0 1 0	1 0 1 0	1 1 2 3	1 1 3 0
<i>Gallus gallus</i>	1 1 0 0	1 1 1 0	1 0 0 0	1 0 1 0	1 1 1 1	1 1 3 0
<i>Crax pauxi</i>	1 1 0 0	1 1 1 0	1 0 0 0	1 0 1 0	1 1 1 1	1 1 3 0
<i>Crypturellus undulatus</i>	1 1 0 0	1 1 1 0	1 0 0 0	1 0 1 0	1 1 1 1	1 1 3 0
<i>Lithornis</i>	1 2 0 1	1 1 0 0	1 1 0 0	1 0 1 0	1 1 1 1	1 2 0 1
<i>Ichthyornis dispar</i>	1 1 1 0	1 1 1 0	1 0 0 0	1 0 1 0	1 1 1 1	1 1 1 0
<i>Hesperornis regalis</i>	1 0 2 0	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2
<i>Baptornis advenus</i>	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2
<i>Patagopteryx deferrariisi</i>	1 0 0 1	0 2 2 0	0 0 0 0	0 0 1 0	0 0 1 0	0 0 2 2
<i>Cathayornis yandica</i>	0 0 0 1	0 1 0 0	1 1 1 0	1 1 1 0	2 1 0 1	1 1 0 1
<i>Concornis lacustris</i>	0 2 2 0	0 1 1 0	2 2 1 0	2 2 1 0	2 2 2 2	2 2 2 2
<i>Neuquenornis volans</i>	0 2 2 0	1 2 2 0	1 2 2 0	1 2 2 0	1 2 2 0	1 2 2 0
<i>Gobipteryx minuta</i>	0 2 2 0	1 2 2 0	1 2 2 0	1 2 2 0	1 2 2 0	1 2 2 0
<i>Vorena berivotrensis</i>	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2
<i>Apsaravis ukhaana</i>	1 1 0 1	1 1 0 1	1 1 0 1	1 1 0 1	2 3 1 1	1 1 0 1
<i>Confuciusornis sanctus</i>	0 0 2 0	0 0 2 0	0 0 2 0	0 0 2 0	1 1 0 1	0 0 2 0
<i>Archaeopteryx lithographica</i>	0 0 2 0	0 0 2 0	0 0 2 0	0 0 2 0	0 0 2 0	0 0 2 0
<i>Dromaeosauridae</i>	0 0 2 0	0 0 2 0	0 0 2 0	0 0 2 0	0 0 2 0	0 0 2 0

	151	160	170	180	190	200
<i>Anas platyrhynchos</i>	1 0 2 1	1 1 1 1	1 1 1 1	1 1 0 2	1 1 0 2	1 0 0 2
<i>Chauna torquata</i>	1 0 2 1	1 1 1 1	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 1
<i>Gallus gallus</i>	1 0 2 1	1 1 1 1	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 1
<i>Crax pauxi</i>	1 0 2 1	1 1 1 1	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 1
<i>Crypturellus undulatus</i>	1 0 2 0	1 1 2 0	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 1
<i>Lithornis</i>	1 0 2 0	1 1 2 0	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 1
<i>Ichthyornis dispar</i>	2 2 0 0	1 1 0 0	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 2
<i>Hesperornis regalis</i>	2 2 0 0	1 1 0 0	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 2
<i>Baptornis advenus</i>	0 2 0 1	0 0 0 0	0 1 1 1	0 2 0 0	0 2 0 0	0 2 0 2
<i>Patagopteryx deferrariisi</i>	1 0 1 0	1 2 2 0	1 1 2 0	1 1 2 0	1 1 2 0	1 0 0 0
<i>Cathayornis yandica</i>	1 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2
<i>Concornis lacustris</i>	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2
<i>Neuquenornis volans</i>	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2
<i>Gobipteryx minuta</i>	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2	2 2 2 2
<i>Apsaravis ukhaana</i>	2 2 0 1	1 1 0 1	1 1 1 1	1 0 2 1	1 0 2 1	1 0 0 0
<i>Confuciusornis sanctus</i>	0 0 1 0	0 0 0 0	0 0 1 0	0 0 2 0	0 0 2 0	0 0 2 0
<i>Archaeopteryx lithographica</i>	0 0 0 0	0 0 0 0	0 0 0 0	0 0 2 0	0 0 2 0	0 0 2 0
<i>Dromaeosauridae</i>	0 0 0 0	0 0 0 0	0 0 0 0	0 0 2 0	0 0 2 0	0 0 2 0