

Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird

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Abstract

Most of Mesozoic bird diversity comprises species that are part of one of two major lineages, namely Ornithurae, including living birds, and Enantiornithes, a major radiation traditionally referred to as ‘opposite birds’. Here we report the largest Early Cretaceous enantiornithine bird from north-east China, which provides evidence that basal members of Enantiornithes share more morphologies with ornithurine birds than previously recognized. Morphological evolution in these two groups has been thought to be largely parallel, with derived members of Enantiornithes convergent on the ‘advanced’ flight capabilities of ornithurine birds. The presence of an array of morphologies previously thought to be derived within ornithurine and enantiornithine birds in a basal enantiornithine species provides evidence of the complex character evolution in these two major lineages. The cranial morphology of the new specimen is among the best preserved for Mesozoic avians. The new species extends the size range known for Early Cretaceous Enantiornithes significantly and provides evidence of forelimb to hind limb proportions distinct from all other known members of the clade. As such, it sheds new light on avian body size evolution and diversity, and allows a re-evaluation of a previously proposed hypothesis of competitive exclusion among Early Cretaceous avian clades.

Key words bird evolution; China; Early Cretaceous; Enantiornithes.

Systematic palaeontology

Aves Linnaeus, 1758

Enantiornithes Walker, 1981

***Pengornis houi* gen. et sp. nov**

Holotype specimen

IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China). V15336 comprises a nearly complete skeleton preserved in partial articulation (Figs 1–3) lacking only sternum and pelvic bones and parts of the distalmost left forelimb.

Etymology

‘Peng’ refers to a Chinese mythological bird, ‘ornis’ is Greek for bird, and ‘houi’ is in honour of Lianhai Hou, a pioneering palaeo-ornithologist.

Locality and horizon

Dapingfang, Chaoyang, Liaoning China; Jiufotang Formation, Early Cretaceous (He et al. 2004).

Diagnosis

Four characters are unambiguously optimized as local autapomorphies of the new species in the phylogenetic analysis: premaxillae unfused throughout their length, hooked scapular acromion, a globose humeral head that projects further proximally than the deltopectoral crest (Characters 1:0, 105:1, 107:1, 108:1; Appendices 1 and 2).

Description

The skull is preserved in left lateral view (Fig. 2A). The premaxillae are unfused throughout their lengths. One tooth in close association with the left premaxillary facial margin exposes a short, relatively blunt crown with a constricted waist and elongate root. The maxilla is broad with a well-developed dorsal process. Resorption pits above the maxillary tooth row and approximately 11 alveoli (with or without their associated teeth) are visible. Approximately 13 teeth are estimated to have been present in the exposed

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Fig. 1 Holotype of *Pengornis houi* gen. nov., sp. nov. (IVPP V15336). (A) Skeleton. (B) Line drawing. Anatomical abbreviations: cav, caudal vertebra; cv, cervical vertebra; dr, dorsal rib; dv, dorsal vertebra; fu, furcula; ga, gastralia; hy, hypocleidium; lco, left coracoid; lfe, left femur; lfi, left fibula; lhu, left humerus; lil, left ilium; lpu, left pubis; lra, left radius; lsc, left scapula; lti, left tibiotarsus; ltm, left tarsometatarsus; lul, left ulna; ma, mandible; mcl, major metacarpal; mcll, minor metacarpal; mtl, metatarsal I; phll-1, first phalanx of the major manual digit; py, pygostyle; rad, radiale; rco, right coracoid; rfe, right femur; rhu, right humerus; rpf, right pubic foot; rra, right radius; rsc, right scapula; rti, right tibiotarsus; rtm, right tarsometatarsus; rul, right ulna; sk, skull; sy, synsacrum; uln, ulnare; un, ungual.

left dentary. Dentary teeth, like those from the maxillae and premaxillae, are extremely small, with conical, nearly unrecurved crowns similar to those reported in *Archaeopteryx* (Elzanowski, 1996, 2002) and other Enantiornithes (Martin & Zhou, 1997). Those from the posteriormost section of the tooth row are largely blunt and appear to have wear facets (Fig. 2B). These morphologies indicate that dentary teeth in the jaw may be in various stages of replacement.

The nasals meet on the midline to exclude the premaxillae from contacting the frontals. At the posterior edge of the

maxilla–nasal contact there is a prominent ‘U’-shaped facet in the maxilla to receive the lacrimal. A facet of similar morphology is present in *Archaeopteryx* (Mayr et al. 2005) and other non-avian Maniraptora. The jugal is slender and appears to bear a short postorbital ramus preserved abutting the left quadrate. The postorbital is deflected anteriorly, and it is unclear if it contacted the jugal (Fig. 2A). The postorbital is relatively elongate, slender and tapering. In these morphologies, it is similar to that of an unnamed enantiornithine juvenile from the Lower Cretaceous of

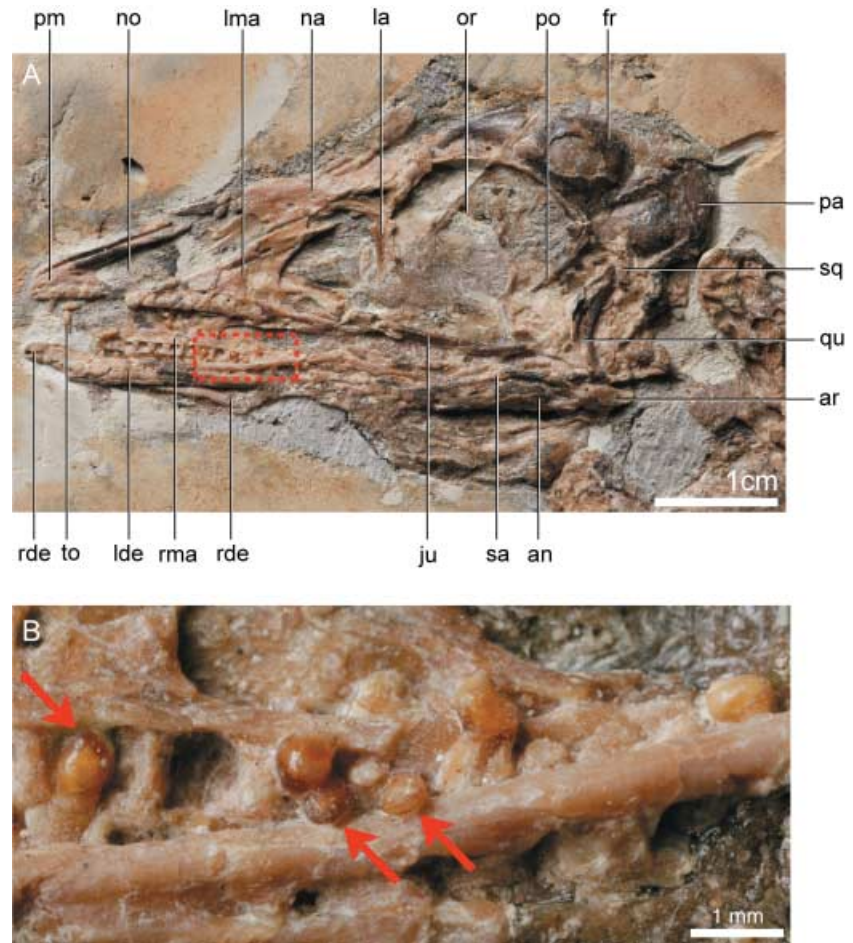


Fig. 2 (A) Skull of *Pengornis houi* gen. nov., sp. nov. (IVPP V15336). (B) Detail of the posterior dentary teeth. Anatomical abbreviations: an, angular; ar, articular; fr, frontal; ju, jugal; la, lachrymal; lde, left dentary; lma, left maxilla; na, nasal; no, nasal opening; or, orbit; pa, parietal; pm, premaxilla; po, postorbital; qu, quadrate; rde, right dentary; rma, right maxilla; sa, surangular; sq, squamosal; to, tooth. Arrows indicate possible wear facets.

Spain (Sanz et al. 1997). A postorbital has also been reported for *Protopteryx* (Zhang & Zhou, 2000).*

The anteriormost seven cervical vertebrae are ventrally exposed in articulation. Four posterior cervical vertebrae, also in articulation, lie near the right humerus. A complete arcus atlantis clasps the axis odontoid process (Fig. 3A,B). Heterocoelous articulations are clearly observed among neighbouring anterior cervical centra (Fig. 3C) while the more posterior cervicals transition into amphicoelous. Dorsal vertebrae bear deep lateral excavations and are amphicoelous. Unlike other described Enantiornithes, parapophyses are not centrally located; they are anteriorly positioned. Seven fused sacral and six caudal vertebrae are visible. The anteriormost synsacrum tip is, however, slightly obscured by overlying bone fragments. The pygostyle is elongate with transverse processes fused to each other throughout its length and lacks its distal end. It also has a dorsally projected and mediolaterally compressed blade

*It should also be noted that a putative enantiornithine '*Aberratiodontus wui*' lacks any proposed synapomorphies of Enantiornithes (Gong et al. 2004) and is considered to be a possible junior synonym of a previously named ornithurine taxon (*Yanornis*). A proposed postorbital could not be confirmed, and it is excluded from Enantiornithes by the enlarged anterior cnemial crest, for example.

unlike the more rod-like morphology in some Enantiornithes and in *Confuciusornis*. Gastralia are present.

The scapula preserves a large, tapering, and recurved acromion unlike any other enantiornithine birds but as seen in several ornithurine taxa (Clarke & Norell, 2002; Clarke, 2004). Both coracoids, preserved in ventral view, are strut-like and lack procoracoid processes. The lateral margin of the distal coracoid is slightly flared at its sternal end, which may represent an incipient lateral process. The furcula is V-shaped, and has extremely mediolaterally broad clavicular rami with shallow depressions along their posterodorsal surfaces. It preserves an elongate blade-like hypocleidium missing its distal end.

The forelimb is significantly longer than the hindlimb (with a ratio of 1.35: humerus + ulna + carpometacarpus/femur + tibiotarsus + tarsometatarsus; see Tables 1 and 2). The humerus has an oblate, globose head more proximally projected than any other enantiornithine. A ventral tubercle, and a deep capital incisure are developed. The dorsal projection of the deltopectoral crest approximates the humeral shaft width. It is dorsally rather than anteriorly directed. The distal humerus angles markedly ventrally. The ventral condyle is abraded but appears small and nearly terminal as in other enantiornithines and the ornithurine *Apsaravis ukhaana*

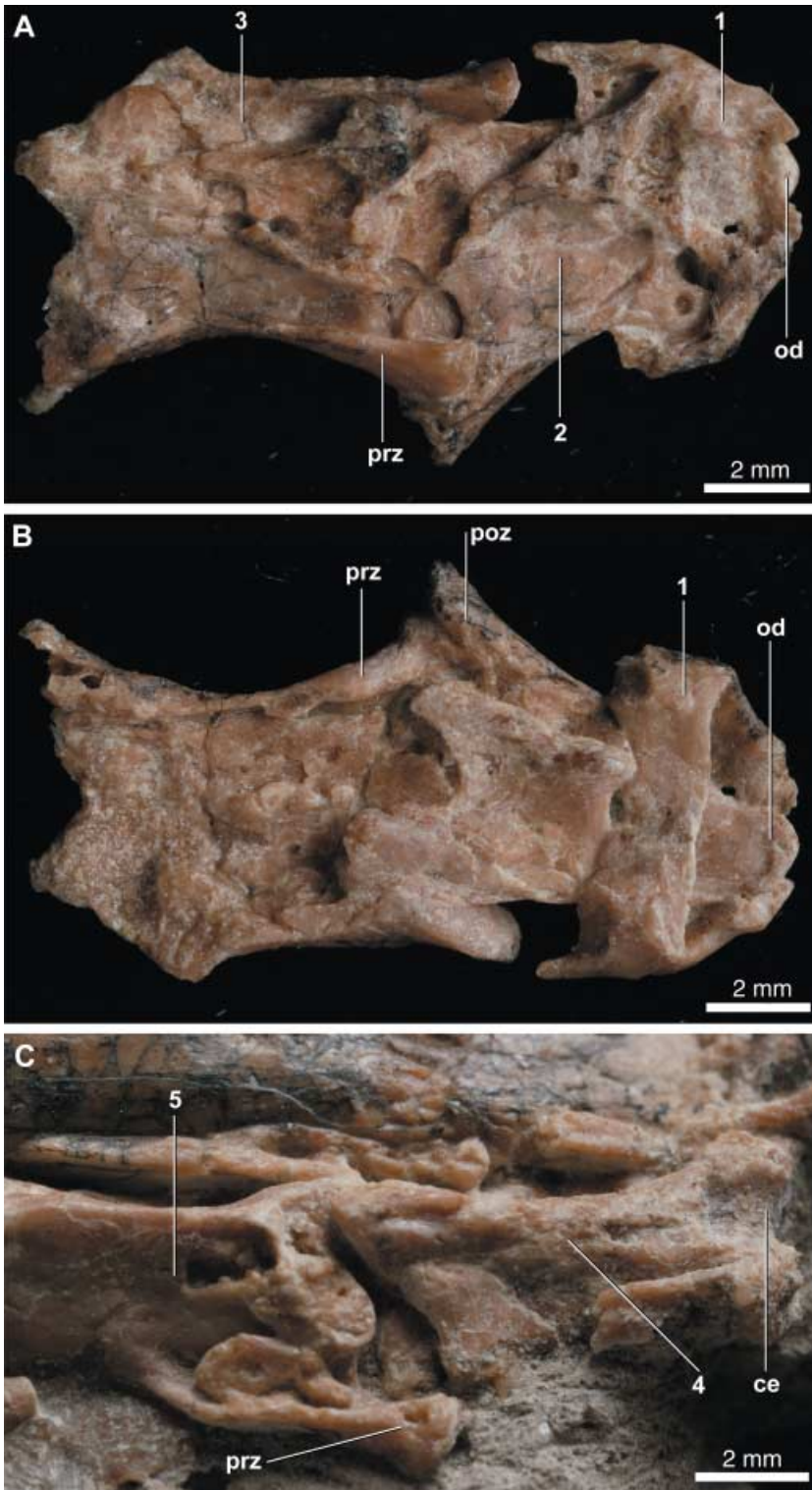


Fig. 3 Anterior cervicals of *Pengornis houi* gen. nov., sp. nov. (IVPP V15336). (A) 1st–3rd cervicals in ventral view. (B) 1st–3rd cervicals in dorsal view. (C) 4th–5th cervicals in ventrolateral view, showing heterocoelous articulations. Anatomical abbreviations: ce, centrum; od, odontoid process of the axis; poz, postzygopophysis; prz, prezygopophysis; 1–5, 1st–5th cervical vertebrae.

(Clarke & Norell, 2002). The dorsal condyle is orientated at a slightly higher angle from the long axis of the humerus than other basal birds but as in other enantiornithines and *Apsaravis*. The ulna is markedly longer than the humerus.

The ulnare and radialae are preserved with the ulnare differentiated into dorsal and ventral rami of approximately

equal length. Major and minor metacarpals are fused proximally with the semilunate carpal (Fig. 1), but the area of contact with the alular metacarpal is not preserved. No distal fusion is present. The minor metacarpal extends significantly further distally than the major metacarpal, as seen in other enantiornithines (Chiappe & Walker, 2002).

Table 1 Measurements of *Pengornis houi* gen. nov., sp. nov. (IVPP V15336)

Elements	Measurements (mm)
Skull length	54.7*
Skull height	26.6*
Orbit length	15.4*
Orbit height	15.0
Antorbital length	7.6
Antorbital height	5.0
Synsacrum length	27.1*
Synsacrum maximum width	19.8
Pygostyle length	19.4†
Scapula length	36.7†
Coracoid length (right)	37.9
Coracoid distal width (right)	18.8*
Furcula length	39.1†
Furcula proximal width	29.0
Furcula, hypocleidium length	10.8†
Humerus length (left)	64.3
Humerus, midshaft width (left)	6.2
Ulna length (left)	70.7
Ulna, midshaft width (left)	4.9
Radius length (left)	66.7
Radius, midshaft width (left)	3.5
Carpometacarpus length (right)	34.3
Major metacarpal length (right)	27.0
Minor metacarpal length (right)	31.1
Major digit phalanx-I length (right)	16.3
Pubis length	49.2*
Femur length (right)	48.0
Tibiotarsus length (right)	50.4
Fibula length (left)	44.5*
Tarsometatarsus length (left)	26.5
Metatarsal I length (left)	8.7
Pedal digit II-1 length (left)	5.9
Pedal digit II-2 length (left)	8.1
Pedal digit II-3 length (left)	12.4
Pedal digit III-1 length (left)	8.6
Pedal digit III-2 length (left)	7.9
Pedal digit III-3 length (left)	8.8
Pedal digit III-4 length (left)	11.7
Pedal digit IV-1 length (left)	5.2
Pedal digit IV-2 length (left)	3.8*
Pedal digit IV-3 length (left)	4.1
Pedal digit IV-4 length (left)	5.9
Pedal digit IV-5 length (left)	9.9

*Estimated, †preserved length.

The first phalanx of the major digit is subtriangular with no significant dorsoventral compression. Phalanx III: 1 preserves a well-developed distal articular surface, indicating at least two phalanges were present in this digit.

The pelvis is incompletely preserved. The distal pubis has a facet for a relatively elongate symphysis, as in *Confuciusornis*, and is terminally slightly flared (Fig. 1; Hou et al. 1995; Chiappe et al. 1999). The femur is bowed and just slightly shorter than the tibiotarsus (femur/tibiotarsus:

0.96). The proximal tarsals are fused to each other and to the tibia. The lateral distal condyle appears slightly wider than the medial condyle, a condition only so far reported in the ornithurine *Apsaravis ukhaana* (Clarke & Norell, 2002). The fibula is elongate and approaches the tarsal joint.

The distal tarsals fuse to each other and to the proximal metatarsals to form a tarsometatarsus. Metatarsals are unfused distally. The anterior surface of metatarsal II bears a prominent midline tubercle (m. tibialis cranialis tubercle; see Clarke & Norell, 2002), as developed in *Confuciusornis* and within other enantiornithines. Metatarsal IV is more slender than metatarsals II and III, while II is expanded distally. This condition, while originally identified as a synapomorphy of Enantiornithes, has a broader distribution in basal birds (e.g. *Confuciusornis*) and non-avian theropod outgroups. All unguis preserve impressions of their keratinous sheaths and are strongly curved. In digit II, phalanx 1 is shorter than 2, and its unguis is slightly larger than those of the other digits. No feather impressions are preserved.

Phylogenetic results and body size comparison

Phylogenetic analysis identifies *Pengornis* as a basal divergence within Enantiornithes (Fig. 4; Appendices 1 and 2). Three unambiguously optimized characters are found to support enantiornithine monophyly: two furcular features (posterior or dorsal excavation of the rami and presence of an elongate hypocleidium) and the distinctive scapula–coracoid articulation (Characters 82:2, 83:1, 87:1; Appendix 1). The scapula–coracoid articulation is the only character of these three so far unknown outside Enantiornithes and is unfortunately not exposed in *Pengornis*. Of these three features only an elongate hypocleidium is visible in *Pengornis*, although it exhibits several additional morphologies with a restricted distribution that represent previously proposed synapomorphies of the clade (e.g. metatarsal IV narrow, and minor metacarpal longer than major metacarpal; Chiappe & Walker, 2002).

An increase of only four steps from the most parsimonious tree length of 469 steps is required for *Pengornis* to be placed closer to Ornithurae rather than as a basal enantiornithine. Moreover, it only requires an increase of two steps for *Protopteryx* (Zhang & Zhou, 2000) to be so placed. If *Pengornis* was found with increased character and taxonomic sampling to be closer to Ornithurae rather than part of Enantiornithes, an array of characters found to diagnose Enantiornithes would be ambiguously optimized or as ancestral to a more inclusive avian clade.

Enantiornithes has the lowest bootstrap and Bremer support values of any recovered node (Fig. 4), although 27 features had been proposed as synapomorphies of this clade (Clarke & Norell, 2002; Chiappe & Witmer, 2002). *Pengornis* and other new taxa (e.g. *Hongshanornis*, *Vescornis*) show an increasing number of these characters

Table 2 Proportions of selected elements of *Pengornis houi* gen. nov., sp. nov. (IVPP VV15336) compared with other birds

Taxon	Hu	Ul	Cmc	Fe	Ti	Tmt	Fe/ti	Hu+ul+cmc/fe+ti+tmt
<i>Pengornis houi</i> (IVPP V15336)	64 (l.)	71 (l.)	27 (r.)	48 (r.)	50 (r.)	26	0.96	1.35
<i>Longipteryx chaoyangensis</i> (IVPP V12325)	45 (r.)	47 (r.)	19 (r.)	31 (r.)	32 (r.)	21 (r.)	0.97	1.32
<i>Eoenantiornis buhleri</i> (IVPP V11537)	35 (l.)	36 (l.)	17 (l.)	32 (l.)	38 (l.)	23 (l.)	0.84	0.95
<i>Longirostravis hani</i> (IVPP V12309)	24 (l.)	26 (l.)		20 (r.)	26 (r.)	14 (l.)	0.77	
<i>Cathayornis yandica</i> (IVPP V9769)	33 (l.)	34 (l.)	18 (l.)	28	34 (l.)	21* (l.)	0.82	1.14
<i>Archaeopteryx bavarica</i> (Solnhofen specimen)	83	72*	34†	70*	90	48	0.78	0.91
<i>Sapeornis chaoyangensis</i> (IVPP V12698)	127 (l.)	133 (l.)	57 (l.)	80 (l.)	84 (l.)	44 (l.)	0.95	1.52
<i>Confuciusornis sanctus</i> (IVPP V11619)	52 (r.)	47 (r.)	27 (r.)	47 (l.)	54 (l.)	25 (l.)	0.87	1.0
<i>Archaeorhynchus spathula</i> (IVPP V14287)	53 (l.)	56 (l.)	25 (l.)	37 (l.)	42 (l.)	20 (l.)	0.88	1.35
<i>Hongshanornis longicresta</i> (IVPP V14533)	26 (l.)	24 (l.)	13 (l.)	22 (l.)	38 (l.)	22 (l.)	0.58	0.79
<i>Yixianornis grabaui</i> (IVPP V12631)	49 (r.)	50 (r.)	21 (r.)	42 (r.)	54 (r.)	26 (r.)	0.78	0.98

*Estimated, †preserved length; l. and r. indicate left and right sides, respectively. Abbreviations: hu, humerus; ul, ulna; cmc, carpometacarpus; fe, femur; ti, tibiotarsus; tmt, tarsometatarsus.

to be alternatively present in other basal avians and, thus, ambiguously optimized or unambiguously primitive for a part of Aves (see Discussion).

Pengornis is approximately the size of the basal avian *Confuciusornis sanctus* (Hou et al. 1995; Chiappe et al. 1999) based upon comparisons of femoral length (Tables 1 and 2). *Pengornis* is similarly estimated to have been significantly larger than all previously described Early Cretaceous Enantiornithes including *Longipteryx* (see Zhang et al. 2001; Hou et al. 2004; Zhou et al. 2005; Table 2). Femoral length has been used in estimating body mass for avians and closely related theropods (e.g. Turner et al. 2007). With the discovery of *Pengornis*, there are similarly sized basal avians (e.g. *Confuciusornis*), Enantiornithes and stem Ornithurae (Table 2) in the Early Cretaceous.

Discussion

Pengornis significantly alters the distribution of characters considered uniquely diagnostic of Ornithurae. A globose humeral head, present in all extant birds, has been considered to diagnose Ornithurae and unambiguously optimized as having a single origin in the ornithurine stem lineage (Character 107:1). With the discovery of *Pengornis*, it is reported for the first time in Enantiornithes and currently optimized as convergently evolved in that taxon. A hooked acromion process on the scapula, which is prominent in *Pengornis*, is previously known only within Ornithurae as well (e.g. Lithornithids, *Apsaravis* and *Hongshanornis*). The heterocoelous articulations in the anterior cervical vertebrae of *Pengornis* (Fig. 3) as well as in the recently reported *Vescornis* (Zhang et al. 2005) constitute the first recognized occurrences of these saddle-shaped articulations in Enantiornithes. Previously, heterocoelous articulations were only known in taxa more closely related to extant birds than Enantiornithes (Clarke & Norell, 2002; Clarke et al. 2006). It is now ambiguously optimized whether this form of articulation seen in the cervical

vertebrae of all living birds may not have arisen phylogenetically earlier.

An elongate hypocleidium considered to diagnose Enantiornithes (or Euenantiornithes; Chiappe & Walker, 2002) is also now known from the ornithurine *Hongshanornis* (Zhou & Zhang, 2005), as well as in the more basal stem taxon *Sapeornis* (Zhou & Zhang, 2003, fig. 2). A tubercle-sized hypocleidium is now unambiguously optimized as ancestral from the divergence of *Sapeornis* to that of Enantiornithes. An elongate blade-like hypocleidium is currently optimized as having three separate origins.

The ulna is longer than the humerus in the ornithurine stem taxon *Archaeorhynchus* (Zhou & Zhang, 2006) as well as in several enantiornithines (e.g. *Longirostravis*) now including *Pengornis*. The ratio of these elements has been related to distinct flight styles in birds (Nudds et al. 2004; but see Gatesy & Middleton, 2007). Independent evolution of these proportions is currently indicated in the phylogenetic analysis. The newly overlapped distribution of humerus/ulna proportions in Early Cretaceous stem Ornithurae and basal Enantiornithes does not support the proposed exclusion of the former from niches by enantiornithines such as had been hypothesized from these ratio differences (Nudds et al. 2004). Similarly, with the discovery of *Pengornis*, a large-bodied Early Cretaceous enantiornithine, the body-size distributions for the clades now also overlap significantly.

Although future discoveries could support competitive exclusion of stem lineage ornithurines by enantiornithines (Wang et al. 2005; Zhou & Zhang, 2006, 2007), the morphology preserved in *Pengornis*, based on both proportional and absolute size metrics, casts doubt on the validity of this hypothesis during the Early Cretaceous. Moreover, *Pengornis* impacts our understanding of morphological evolution after the origin of flight. It confirms that cranial morphologies optimized as ancestral for Aves are retained in basal Enantiornithes and further increases ambiguity in support of a monophyletic Enantiornithes as currently recognized.

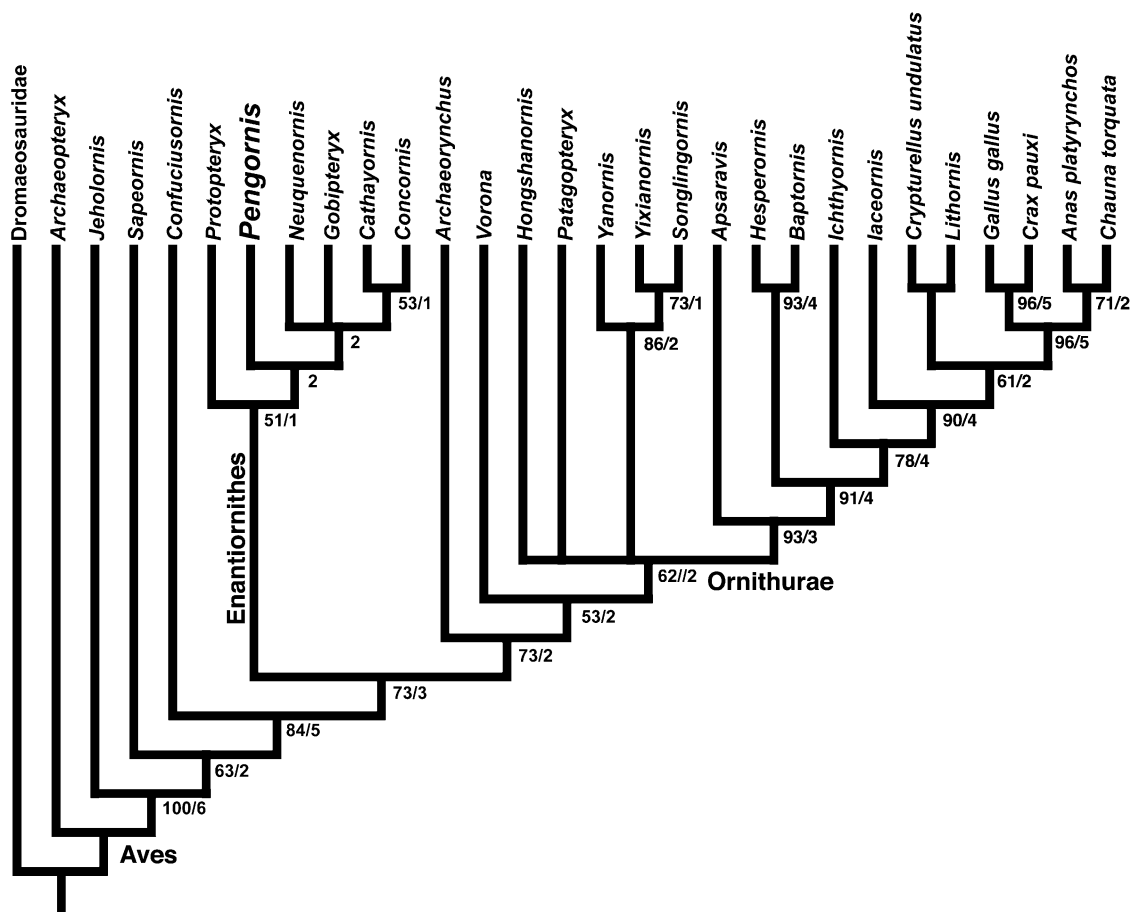


Fig. 4 The relationships of *Pengornis houi* gen. nov., sp. nov. in the strict consensus cladogram of three most-parsimonious trees recovered from the phylogenetic analysis (L: 469 CI: 0.57, RI: 0.80, RC: 0.46). Twenty-nine taxa were evaluated for 205 morphological characters from Clarke et al. (2006), 192 of which were parsimony-informative for the taxonomic sample analysed. Five of these characters were significantly modified from Clarke et al. (2006; see Appendix 1) and character states were reassessed (Appendix 2). The branch-and-bound algorithm was used and all analyses were performed using PAUP 4.0b10 (Swofford, 2002). Branches with a minimum length of 0 were collapsed. 3 trees of length 469 were recovered (CI: 0.57, RI: 0.80, RC: 0.46), the strict consensus of which is reported in Fig. 4. Bremer support values were calculated manually also using PAUP 4.0b10 (Swofford, 2001). One thousand bootstrap replicates (heuristic search, 10 random stepwise addition replicates each, with tbr) were also used to evaluate node support. Bremer support and percentage recovery of nodes in 1000 bootstrap replicates are given below nodes to the right and left, respectively.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Data matrix for the phylogenetic analysis.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-7580.2008.00880.x>
(This link will take you to the article abstract).

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Appendix 1 Character list modified from Clarke et al. (2006). In total, 205 morphological characters were used in the phylogenetic analysis. Several characters were significantly reworded and new states identified: 51, 82, 152, 157, 158, 194

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. Premaxillae at least partially edentulous: (0) absent, (1) present.
4. Maxillary teeth: (0) present, (1) absent.
5. Dentary teeth: (0) present, (1) absent.
6. Tooth crown serration: (0) present, (1) vestigial or absent.
7. Dentaries: (0) joined proximally by ligaments, (1) joined by bone.
8. Mandibular symphysis, two strong grooves forming an anteriorly-opening 'v' in ventral view: (0) absent, (1) present.
9. 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 1/2 facial margin, (2) maxillary process of the premaxilla extending more than 1/2 of facial margin (Ordered).
10. Nasal [frontal] process of premaxilla: (0) short, (1) long, closely approaching frontal.
11. Nasal process of maxilla, dorsal ramus: (0) prominent, exposed medially and laterally, (1) absent or reduced to slight medial, and no lateral, exposure.
12. 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 narial margin, (2) no dorsal projection of maxilla participates in anterior margin of the antorbital fenestra. (Ordered).
13. Osseous external naris: (0) considerably smaller than the antorbital fenestra, (1) larger.
14. Ectopterygoid: (0) present, (1) absent.
15. 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.
16. Palatine and pterygoid: (0) long, anteroposteriorly-overlapping, contact, (1) short, primarily dorsoventral, contact.
17. Palatine contacts: (0) maxillae only, (1) premaxillae and maxillae.
18. Vomer contacts premaxilla: (0) present, (1) absent.
19. Coronoid ossification: (0) present, (1) absent.
20. Projecting basisphenoid articulation with pterygoid: (0) present, (1) absent.
21. Basispterygoid processes: (0) long, (1) short (articulation with pterygoid sub-equal to, or longer than, amount projected from the basisphenoid rostrum).
22. Basisphenoid-ptyergoid 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).
23. Basisphenoid/ptyergoid articulation, orientation of contact: (0) anteroventral, (1) mediolateral, (2) entirely dorsoventral.
24. 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).
25. 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.
26. Osseous interorbital septum (mesethmoid): (0) absent, (1) present.
27. 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.
28. Eustachian tubes: (0) paired and lateral, (1) paired, close to cranial midline, (2) paired and adjacent on midline or single anterior opening.
29. Eustachian tubes ossified: (0) absent, (1) present.
30. 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.
31. 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.
32. Quadrate, orbital process: (0) pterygoid articulates with anterior-most tip, (1) pterygoid articulation does not reach tip, (2) pterygoid articulation with no extent up orbital process, restricted to quadrate corpus. (Ordered).
33. Quadrate/pterygoid contact: (0) as a facet, variably with slight anteromedial projection cradling base, (1) condylar, with a well-projected tubercle on the quadrate.
34. Quadrate, well-developed tubercle on anterior surface of dorsal process: (0) absent, (1) present.
35. Quadrate, quadratojugal articulation: (0) overlapping, (1) peg and socket articulation.
36. Quadrate, dorsal process, articulation: (0) with squamosal only, (1) with squamosal and prootic.
37. 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.'
38. Quadrate, mandibular articulation: (0) bicondylar articulation with mandible, (1) tricondylar articulation, additional posterior condyle or broad surface.

39. Quadrate, pneumaticity: (0) absent, (1) present.
40. Quadrate, cluster of pneumatic foramina on posterior surface of the tip of dorsal process: (0) absent, (1) present.
41. Quadrate, pneumatization, large, single pneumatic foramen: (0) absent, (1) posteromedial surface of corpus.
42. Articular pneumaticity: (0) absent, (1) present.
43. 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.
44. Splenial, anterior extent: (0) splenial stops well posterior to mandibular symphysis, (1) extending to mandibular symphysis, though non-contacting, (2) extending to proximal tip of mandible, contacting on midline.
45. Mandibular symphysis, anteroposteriorly extensive, flat to convex, dorsal-facing surface developed: (0) absent, concave, (1) flat surface developed.
46. Mandibular symphysis, symphyseal foramina: (0) absent, (1) present.
47. Mandibular symphysis, symphyseal foramen/foramina: (0) single, (1) paired.
48. Mandibular symphysis, symphyseal foramen/foramina: (0) opening on posterior edge of symphysis, (1) opening on dorsal surface of symphysis.
49. Meckel's groove: (0) not completely covered by splenial, deep and conspicuous medially, (1) covered by splenial, not exposed medially.
50. Anterior external mandibular fenestra: (0) absent, (1) present.
51. Postorbital: (0) present, variably contacting jugal (1) absent. REVISED
52. Frontal/parietal suture (0) open, (1) fused.
53. 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).
54. 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.)
55. Thoracic vertebrae, count: (0) 12 or more, (1) 11, (2) 10 or fewer. (Ordered).
56. 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.
57. Thoracic vertebrae, parapophyses: (0) rostral to transverse processes, (1) directly ventral to transverse processes (close to midpoint of vertebrae).
58. Thoracic vertebrae, centra, length, and midpoint width: (0) approximately equal in length and midpoint width, (1) length markedly greater than midpoint width.
59. Thoracic vertebrae, lateral surfaces of centra: (0) flat to slightly depressed, (1) deep, emarginate fossae, (2) central ovoid foramina.
60. Thoracic vertebrae with ossified connective tissue bridging transverse processes: (0) absent, (1) present.
61. Notarium: (0) absent, (1) present.
62. Sacral vertebrae, number ankylosed: (0) less than 7, (1) 7, (2) 8, (3) 9, (4) 10, (5) 11 or more, (6) 15 or more (Chiappe, 1996). (Ordered).
63. 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).
64. Free caudal vertebrae, number: (0) more than 8, (1) 8 or less.
65. Caudal vertebrae, chevrons, fused on at least one anterior caudal: (0) present, (1) absent.
66. Free caudals, length of transverse processes: (0) subequal to width of centrum, (1) significantly shorter than centrum width.
67. Anterior free caudal vertebrae: (0) elongate pre/post-zygapophyses, (1) pre- and post-zygapophyses short and variably non-contacting, (2) prezygapophyses clasping the posterior surface of neural arch of preceding vertebra, postzygapophyses negligible. (Ordered).
68. Distal caudals: (0) unfused, (1) fused.
69. Fused distal caudals, morphology: (0) fused element length equal or greater than 4 free caudal vertebrae, (1) length less than 4 caudal vertebrae, (2) less than 2 caudal vertebrae in length. (Ordered).
70. Ossified uncinat processes: (0) absent, (1) present and unfused to ribs, (2) fused to ribs. (Ordered).
71. Gastralia: (0) present, (1) absent.
72. Ossified sternal plates: (0) unfused, (1) fused, flat, (2) fused, with slightly raised midline ridge, (3) fused with projected carina. (Ordered).
73. Carina or midline ridge: (0) restricted to posterior half of sternum, (1) approaches anterior limit of sternum.
74. Sternum, dorsal surface, pneumatic foramen (or foramina): (0) absent, (1) present.
75. 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.
76. Sternum, coracoidal sulci spacing on anterior edge: (0) widely-separated mediolaterally, (1) adjacent, (2) crossed on midline.
77. Sternum, number of processes for articulation with the sternal ribs: (0) three, (1) four, (2) five, (3) six, (4) seven or more. (Ordered).
78. Sternum: raised, paired intermuscular ridges (linea intermuscularis, Baumel and Witmer, 1993) parallel to sternal midline: (0) absent, (1) present.
79. Sternum, posterior margin, distinct posteriorly projected medial and/or lateral processes: (0) absent (directly laterally projected zyphoid processes developed but not considered homologues as these are copresent with the posterior processes in the new clade), (1) with distinct posterior processes, (2) midpoint of posterior sternal margin connected to medial posterior processes to enclose paired fenestra. (Ordered).
80. Clavicles: (0) fused, (1) unfused.

81. Interclavicular angle (clavicles elongate): (0) greater than, or equal, to 90°, (1) less than 90°.
82. Furcula, hypocleideum: (0) absent, (1) a tubercle, (2) an elongate blade-like process (3) an elongate blade-like process that is over 1/2 the length of the clavicular rami. (Ordered). REVISED
83. Furcula, laterally excavated: (0) absent, (1) present.
84. Furcula, dorsal (omal) tip: (0) flat or blunt tip, (1) with a pronounced posteriorly pointed tip.
85. Furcula, ventral margin of apophysis: (0) curved, angling, (1) with a truncate or squared base.
86. Scapula and coracoid: (0) fused, (1) unfused.
87. 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.
88. Coracoid, procoracoid process: (0) absent, (1) present.
89. Coracoid: (0) height approximately equal mediolateral dimension, (1) height more than twice width, coracoid 'strut-like.'
90. Coracoid, lateral margin: (0) straight to slightly concave, (1) convex.
91. Coracoid, dorsal surface (= posterior surface of basal maniraptoran theropods): (0) strongly concave, (1) flat to convex.
92. Coracoid, pneumatized: (0) absent, (1) present.
93. Coracoid, pneumatic foramen: (0) proximal, (1) distal.
94. Coracoid, lateral process: (0) absent, (1) present.
95. Coracoid, ventral surface, lateral intermuscular line or ridge: (0) absent, (1) present.
96. Coracoid, glenoid facet: (0) dorsal to, or at approximately same level as, acrocoracoid process/'biceps tubercle', (1) ventral to acrocoracoid process.
97. Coracoid, acrocoracoid: (0) straight, (1) hooked medially.
98. Coracoid, n. supracoracoideus passes through coracoid: (0) present, (1) absent.
99. Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed): (0) strongly depressed, (1) flat to convex.
100. Angle between coracoid and scapula at glenoid: (0) more than 90°, (1) 90° or less.
101. Scapula, posterior end: (0) wider or approximately the same width as proximal dorsoventral shaft width, (1) tapering distally.
102. Scapula: (0) straight, (1) dorsoventrally curved.
103. Scapula, length: (0) shorter than humerus, (1) as long as or longer than the humerus.
104. Scapula, acromion process: (0) projected anteriorly to surpass the articular surface for coracoid (facies articularis coracoidea, Baumel and Witmer, 1993), (1) projected less anteriorly than the articular surface for coracoid.
105. Scapula, acromion process: (0) straight, (1) laterally hooked tip.
106. Humerus and ulna, length: (0) humerus longer than ulna, (1) ulna and humerus approximately the same length, (2) ulna significantly longer than humerus. (Ordered).
107. Humerus, proximal end, head in anterior or posterior view: (0) strap-like, articular surface flat, no proximal midline convexity, (1) head domed proximally.
108. Humerus, proximal end, proximal projection: (0) dorsal edge projected farthest, (1) midline projected farthest.
109. Humerus, ventral tubercle and capital incisure: (0) absent, (1) present.
110. Humerus, capital incisure: (0) an open groove, (1) closed by tubercle associated with a muscle insertion just distal to humeral head.
111. Humerus, anterior surface, well-developed fossa on midline making proximal articular surface appear v-shaped in proximal view: (0) absent, (1) present.
112. Humerus, 'transverse groove': (0) absent, (1) present, developed as a discreet, depressed scar on the proximal surface of the bicipital crest or as a slight transverse groove.
113. Humerus, deltopectoral crest: (0) projected dorsally (in line with the long axis of humeral head), (1) projected anteriorly.
114. Humerus, deltopectoral crest: (0) less than shaft width, (1) same width, (2) dorsoventral width greater than shaft width. (Ordered).
115. Humerus, deltopectoral crest, proximoposterior surface: (0) flat to convex, (1) concave.
116. Humerus, deltopectoral crest: (0) not perforate, (1) with a large fenestra.
117. Humerus, bicipital crest, pit-shaped scar/fossa for muscular attachment on anterodistal, distal or posterodistal surface of crest: (0) absent, (1) present.
118. 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.
119. 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).
120. Humerus, proximal end, one or more pneumatic foramina: (0) absent, (1) present.
121. Humerus, distal condyles: (0) developed distally, (1) developed on anterior surface of humerus.
122. Humerus, long axis of dorsal condyle: (0) at low angle to humeral axis, proximodistally orientated, (1) at high angle to humeral axis, almost transversely orientated.
123. Humerus, distal condyles: (0) sub-round, bulbous, (1) weakly defined, 'strap-like.'
124. 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).
125. Humerus, distal end, compressed anteroposteriorly and flared dorsoventrally: (0) absent, (1) present.
126. Humerus, brachial fossa: (0) absent, (1) present, developed as a flat scar or as a scar-impressed fossa.
127. Humerus, ventral condyle: (0) length of long axis of condyle less than the same measure of the dorsal condyle, (1) same or greater.
128. 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.

129. Humerus, distal end, posterior surface, groove for passage of m. scapulotriceps: (0) absent, (1) present.
130. Humerus, m. humerotricipitalis groove: (0) absent, (1) present as a ventral depression contiguous with the olecranon fossa.
131. Ulna, cotylae: (0) dorsoventrally adjacent, (1) widely separated by a deep groove.
132. Ulna, dorsal cotyla convex: (0) absent, (1) present.
133. Ulna, distal end, dorsal condyle, dorsal trochlear surface developed as a semilunate ridge: (0) absent, (1) present.
134. 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.
135. Ulna, bicipital scar: (0) absent, (1) developed as a slightly-raised scar, (2) developed as a conspicuous tubercle.
136. Ulna, brachial scar: (0) absent, (1) present.
137. Radius, ventroposterior surface: (0) smooth, (1) with muscle impression along most of surface, (2) deep longitudinal groove.
138. Ulnare: (0) absent, (1) present.
139. Ulnare: (0), 'heart-shaped,' little differentiation into short dorsal and ventral rami, (1) V-shaped, well-developed dorsal and ventral rami.
140. 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.
141. Semilunate carpal and metacarpals: (0) no fusion, (1) incomplete proximal fusion, (2) complete proximal fusion, (3) complete proximal and distal fusion. (Ordered).
142. Semilunate carpal, position relative to metacarpal I: (0) over 1/2 or more of proximal surface (1) over less than 1/2 proximal surface. (Ordered).
143. Metacarpal III, anteroposterior diameter as a percent of same dimension of metacarpal II: (0) approximately equal or greater than 50%, (1) less than 50%.
144. Metacarpal I, anteroproximally-projected muscular process: (0) absent no distinct process visible, (1) small knob at anteroproximal tip of metacarpal, (2) tip of process just surpasses the distal articular facet for phalanx 1 in anterior extent, (3) tip of extensor process conspicuously surpasses articular facet by approximately half the width of facet, producing a pronounced knob, (4) tip of extensor process conspicuously surpasses articular facet by approximately the width of facet, producing a pronounced knob. (Ordered).
145. Metacarpal I, anterior surface: (0) roughly hourglass-shaped proximally, at least moderately expanded anteroposteriorly, and constricted just before flare of articulation with phalanx 1, (1) anterior surface broadly convex.
146. Metacarpal I, distal articulation with phalanx I: (0) ginglymoid, (1) shelf.
147. Pisiform process: (0) absent, (1) present.
148. Carpometacarpus, ventral surface, supratrochlear fossa deeply excavating proximal surface of pisiform process: (0) absent, (1) present.
149. 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.
150. Carpometacarpus, distal end, metacarpals II and III, articular surfaces for digits: (0) metacarpal II sub-equal or surpasses metacarpal III in distal extent, (1) metacarpal III extends farther.
151. Intermetacarpal process or tubercle: (0) absent, (1) present as scar, (2) present as tubercle or flange. (Ordered).
152. Manual digit II, phalanx 1: (0) subcylindrical, not dorsoventrally compressed, (1) subtriangular, moderately dorsoventrally compressed, (2) flat posterior surface, strongly dorsoventrally compressed. (Ordered). REVISED
153. Manual digit II, phalanges: (0) length of phalanx II-1 less than or equal to that of II-2, (1) longer.
154. Manual digit II, phalanx 2, 'internal index process' (Stegmann, 1978) on posterodistal edge: (0) absent, (1) present (Clarke and Chiappe, 2001).
155. Ilium, ischium, pubis, proximal contact in adult: (0) unfused, (1) partial fusion (pubis not ankylosed), (2) completely fused. (Ordered).
156. Ilium/ischium, distal coossification to completely enclose the ilioischadic fenestra: (0) absent, (1) present.
157. Ischium, distal dorsal process: (0) present, (1) absent. REVISED
158. Ischium, proximal dorsal process: (0) absent, (1) present, does not contact ilium (2) present, does contact ilium. (Ordered). REVISED
159. Ischium and pubis: (0) not subparallel, pubis directed nearly directly ventrally, (1) subparallel, pubis posteriorly directed. REVISED
160. Laterally projected process on ischiadic peduncle (antitrochanter): (0) directly posterior to acetabulum, (1) posterodorsal to acetabulum.
161. Preacetabular pectineal process (Baumel and Witmer, 1993): (0) absent, (1) present as a small flange, (2) present as a well-projected flange. (Ordered).
162. Preacetabular ilium: (0) approach on midline, open, or cartilaginous connection, (1) coossified, dorsal closure of 'iliosynsacral canals'.
163. Preacetabular ilium extends anterior to first sacral vertebrae: (0) no free ribs overlapped, (1) one or more ribs overlapped.
164. Postacetabular ilium: (0) dorsoventrally orientated, (1) mediolaterally orientated.
165. Postacetabular ilium, ventral surface, renal fossa developed: (0) absent, (1) present.
166. Ilium, m. cuppedicus fossa as broad, mediolaterally-orientated surface directly anteroventral to acetabulum: (0) present, (1) surface absent, insertion variably marked by a small entirely lateral fossa anterior to acetabulum.
167. 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.
168. 207 Ischium, length relative to that of pubis: (0) 1/3 or greater total pubis length extends posterior to end of ishium, (1) less than 1/3 pubis extends farther than end of ishium.
169. Pubis: (0) sub-oval in cross section, (1) compressed mediolaterally.
170. Pubes, distal contact: (0) contacting, variably coossified into symphysis, (1) non-contacting.
171. Distal end of pubis: (0) expanded, flared, (1) straight, subequal, in proportion with rest of pubis.
172. Femur, fossa for insertion of lig. capitis femoris: (0) absent, (1) present.

173. 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 (Chiappe, 1991). (Ordered).
174. Femur, lesser and greater trochanters: (0) separated by a notch, (1) developed as a single trochanteric crest.
175. Femur, patellar groove: (0) absent, (1) present.
176. Femur: (0) ectocondylar tubercle and lateral condyle separated by deep notch, (1) ectocondylar tubercle and lateral condyle form single trochlear surface.
177. Femur, posterior projection of the lateral border of the distal end, continuous with lateral condyle: (0) absent, (1) present.
178. Laterally-projected fibular trochlea: (0) absent, (1) present, developed as small notch, (2) a shelf-like projection. (Ordered).
179. 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).
180. Calcaneum and astragalus: (0) unfused to each other or tibia in adult, (1) fused to each other, unfused to tibia, (2) complete fused to each other and tibia. (Ordered).
181. Tibia, cnemial crest (s): (0) lateral crest only, (1) lateral and anterior crests developed.
182. Tibia/tarsal formed condyles: (0) medial condyle projecting farther anteriorly than lateral, (1) equal in anterior projection.
183. Tibia/tarsal formed condyles, extensor canal: (0) absent, (1) an emarginate groove, (2) groove bridged by an ossified supratendinal bridge. (Ordered).
184. 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.
185. Tibia/tarsal formed condyles, mediolateral widths: (0) medial condyle wider, (1) approximately equal, (2) lateral condyle wider. (Ordered).
186. Tibia/tarsal formed condyles: (0) gradual sloping medial constriction of condyles, (1) no medial tapering of either condyle.
187. Tibia/tarsal formed condyles, intercondylar groove: (0) mediolaterally broad, approximately 1/3 width of anterior surface, (1) less than 1/3 width of total anterior surface.
188. Tibia, extension of articular surface for distal tarsals/tarsometatarsus: (0) no posterior extension of trochlear surface, or restricted to distal-most 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).
189. Tibia, distal-most mediolateral width: (0) wider than mid-point 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.
190. 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.
191. Distal tarsals and metatarsals, fusion: (0) distal tarsals fuse to metatarsals, (1) distal tarsals fuse to metatarsals and proximal metatarsals coossify, (2) distal tarsals fuse to metatarsals, and metatarsals fuse to each other proximally and distally, (3) extreme distal fusion, distal vascular foramen closed (Martin, 1983, Cracraft, 1986). (Ordered).
192. Metatarsal V: (0) present, (1) absent.
193. Metatarsal III: (0) proximally in plane with II and IV, (1) proximally displaced plantarly, relative to metatarsals II and IV.
194. Tarsometatarsus, intercotylar eminence: (0) absent, (1) a slight midline projection, (2) well developed, globose. (Ordered). REVISED.
195. Tarsometatarsus, projected surface 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).
196. Tarsometatarsus, proximal vascular foramen (foramina): (0) absent, (1) one, between metatarsals III and IV, (2) two. (Ordered).
197. Metatarsal I: (0) straight, (1) curved or distally deflected but not twisted, ventral surface convex 'J shaped', (2) deflected and twisted such that the ventromedial surface is concave proximal to trochlear surface for phalanx I. (Ordered).
198. 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).
199. 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).
200. Metatarsal II, articular surface for first phalanx: (0) ginglymoid, (1) rounded.
201. Metatarsals, relative mediolateral width: (0) metatarsal IV approximately the same width as metatarsals II and III, (1) metatarsal IV narrower than MII and MIII, (2) metatarsal IV greater in width than either metatarsal II or III.
202. 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.
203. Distal vascular foramen: (0) simple, with one exit, (1) forked, two exits (plantar and distal) between metatarsals III and IV.
204. 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.
205. 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).