A NEW ORNITHUROMORPH (AVES: ORNITHOTHORACES) BIRD FROM THE JEHOL GROUP INDICATIVE OF HIGHER-LEVEL DIVERSITY

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ABSTRACT—Basal Ornithuromorpha, until recently, was one of the most poorly documented segments of early avian evolution. The known species diversity of the ornithuromorph clade has increased rapidly with the addition of new discoveries from the Early Cretaceous deposits of northeastern China. Reported in this paper is the discovery of a new bird from the Lower Cretaceous Yixian Formation, Liaoning Province, China. The specimen represents a new species, *Longicrusavis houi*, but bears similarities to *Hongshanornis longicresta* from the same formation of Inner Mongolia. The two birds are comparable in size and share an unusual sigmoid mandible and elongate hindlimbs relative to their forelimbs. Together these taxa represent a clade (Hongshanornithidae, new taxon) of specialized 'shorebirds' whose elongate hindlimbs indicate ecological adaptations different from those of other Jehol ornithuromorphs. Phylogenetic relationships of Mesozoic birds are discussed based on the results of a comprehensive cladistic analysis. New morphological information on Ornithuromorpha is provided through the detailed description of the new taxon together with new information on *Hongshanornis*.

INTRODUCTION

Over the past two decades, the Jehol Biota has become world renowned for its diverse avifauna, with both enantiornithines and ornithuromorphs well represented alongside more basal taxa (Zhang et al., 2003; Zhou and Zhang, 2006; Chiappe, 2007). The sequence of alternating lacustrine and volcanic deposits provides an Early Cretaceous taphonomic setting ideal for preserving the delicate bones and feathers of small birds (Wang and Zhou, 2003), and thus presents a unique glimpse into the early evolution of Ornithuromorpha. Globally, the record of basal ornithuromorphs, those falling outside the ornithurine clade, consists primarily of partial skeletons of taxa including *Ambiortus dementjevi*, *Vorona berivotrensis*, and *Patagopteryx deferrariisi* (Kurochkin, 1982; Alvarenga and Bonaparte, 1992; Forster et al., 1996). From the Jehol Group in northern China, the discovery of well-preserved specimens of new species (*Yanornis martini*, *Yixianornis grabaui*, *Hongshanornis longicresta*, *Archaeorhynchus spathula*) has increased our knowledge of early ornithuromorph species-level diversity and our understanding of the early evolution of this clade (Zhou and Zhang, 2001; Zhou and Zhang, 2005; Zhou and Zhang, 2006). However, most of these species are known from a singular specimen or locality, yielding little information about Early Cretaceous avian paleogeographic and temporal ranges or higher-level diversity, although Clarke et al. (2006) suggest a higher clade relationship between *Songlingornis*, *Yanornis*, and *Yixianornis* (Hou, 1997). Here we describe a new taxon related to the previously described *Hongshanornis longicresta* (Zhou and Zhang, 2005) and erect a new clade, Hongshanornithidae, to include these taxa.

The new specimen (PKUP V1069) was collected from the Dawangzhangzi bed of the lower Yixian Formation, at a site near Lingyuan, Liaoning Province, China (Fig. 1). The Yixian Forma-

tion has produced a diverse array of birds including basal pygostylians such as *Confuciusornis sanctus* (Hou et al., 1995), long tailed birds such as *Jixiangornis orientalis* and *Zhongornis haoae* (Ji et al., 2002; Gao et al., 2008), and numerous ornithothoracines (Zhang and Zhou, 2003). The holotype specimen of *Hongshanornis* was collected from the Shifo locality 40 km northeast of Ningcheng, Inner Mongolia, on the western border with Liaoning, also from the lower Jehol Group member, the Yixian Formation (Fig. 1; Zhou and Zhang, 2005). The discovery of the new specimen from Lingyuan, approximately 60 km southwest of the Inner Mongolian locality, adds substantial new information on the diversity and evolution of basal ornithuromorph birds with unusual limb proportions.

Anatomical nomenclature mainly follows Baumel and Witmer (1993); certain structures not cited therein follow Howard (1929). Although the Latin terminology used by Baumel and Witmer (1993) is retained for muscles and ligaments, osteological structures are described using the English equivalents of the Latin terms.

Abbreviations

Anatomical Abbreviations—al, alular metacarpal; **al I**, first phalanx, alular digit; **al II**, second phalanx, alular digit; **cor**, coracoid; **crv**, cervical vertebrae; **den**, dentary; **dsp**, dorsal supracondylar process; **fem**, femur; **fib**, fibula; **fpp**, frontal processes, premaxilla; **fr**, frontal; **fur**, furcula; **hy?**, possible hyoid bones; **ili**, ilium; **isc**, ischium; **iso**, intersymphysial ossification; **ma**, major metacarpal; **ma I**, first phalanx, major digit; **ma II**, second phalanx, major digit; **ma III**, third phalanx, major digit; **max**, maxilla; **mi**, minor metacarpal; **mi I**, first phalanx, minor digit; **mi II**, second phalanx, minor digit; **mt I**, metatarsal one; **na**, nasal; **pmx**, premaxilla; **pub**, pubis; **qd?**, possible quadrate; **rad**, radius; **rib**, ribs; **sca**, scapula; **stn,** sternum; **sur**, surangular; **tbt**,
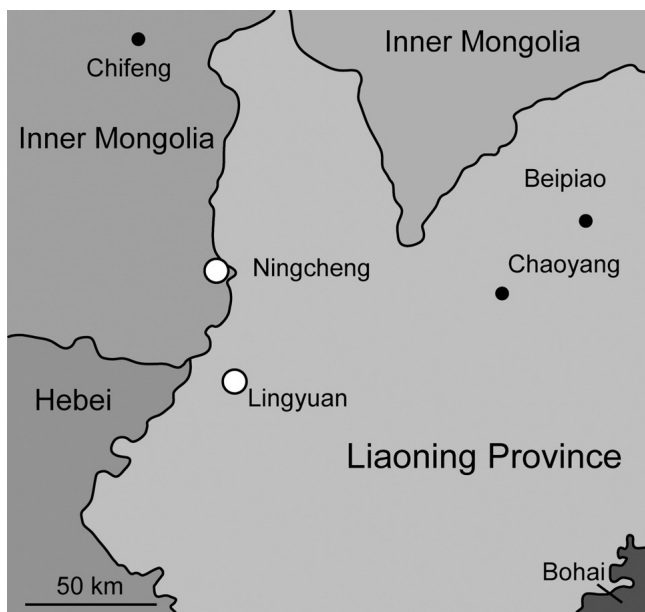
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FIGURE 1. Map showing the two known hongshanornithid localities; PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov., was found near Lingyuan and the holotype of *Hongshanornis longicresta* was found near Shifo, 40 km northeast of Ningcheng. Scale bar represents 50 km.

tibiotarsus; **thv**, thoracic vertebrae; **tmt**, tarsometatarsus; **uln**, ulna; **I–IV**, pedal digits.

Institutional Abbreviations—PKUP, Peking University Paleontological Collection, Beijing, China; **DNHM**, Dalian Natural History Museum, Dalian, Liaoning, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Subclass ORNITHUROMORPHA Chiappe, 2002a
Family HONGSHANORNITHIDAE, fam. nov.

Type Genus—*Hongshanornis* Zhou and Zhang, 2005.
Diagnosis—Small, phoebe-sized (*Sayornis*) ornithuromorph birds with hindlimbs proportionally much longer than their forelimbs (intermembral index less than 0.85); sigmoid mandibular rami such that the dorsal margin of each ramus is rostrally convex and caudally concave; manus longer than humerus; manual phalangeal formula 2–3-2-X-X; and lateral sternal trabecula lacking prominent distal expansions.

Phylogenetic Definition—The common ancestor of *Hongshanornis longicresta* and *Longicrusavis houi* plus all its descendants.

LONGICRUSAVIS HOUI, gen. et sp. nov.
(Figs. 2–4)

Holotype—PKUP V1069, a nearly complete, largely articulated adult individual preserved in light-grey tuffaceous shales, split into part (slab A; Figs. 2A, 3) and counterpart (slab B; Figs. 2B, 4) slabs. The skeletal elements are preserved as voids. Feathers are preserved as carbonized traces concentrated around the head and forelimbs.
Type Locality and Horizon—Dawangzhangzi near Lingyuan, Liaoning Province, China. Lower Cretaceous Yixian Formation (Zhang et al., 2006).

Etymology—*Longicrusavis*, Latin for 'long shin bird,' refers to the elongate hindlimb and, in particular, tibiotarsus that characterizes the taxon and the Hongshanornithidae in general. The specific epithet honors Lianhai Hou in recognition of his contribution to avian paleontology of the Jehol Group.
Diagnosis—Robust rostrum (relative to *Hongshanornis*); absence of a discreet medial trabecula on the distal sternum; dorsal supracondylar process present on distal humerus; lateral cnemial crest hooked; second and fourth metatarsals subequal in length.

DESCRIPTION

The holotype (PKUP V1069) consists of a nearly complete specimen exposed as part and counter-part of shale slabs. The remains of broken bones were prepared out and molds were made producing casts of the dorsal (slab A) and ventral (slab B) views.

Skull

The skull (Fig. 5) is preserved, laterally crushed, disarticulated from the postcranium, and displaced between the legs. The orbit is large and the skull roof consequently high with respect to the length of the rostrum, giving the skull an overall triangular shape in lateral view. The base of the rostrum is poorly preserved but it is not marked by a strong constriction of the skull, as in *Hongshanornis*, so that the dorsal margin of the skull is only slightly concave. In the morphologically similar *Hongshanornis longicresta*, the skull constricts abruptly into the rostrum so that the dorsal margin is strongly concave; consequently, the rostrum is dorsoventrally narrow and much more delicate than in the new taxon. The skull bones in both specimens are not obviously disarticulated in such a way to suggest that the observed difference in shape between taxa is an artifact of preservation, an interpretation supported by an unpublished specimen of *Hongshanornis longicresta* (DNHM D2945/6) preserving the same morphology as the holotype.

The premaxilla appears fused rostrally but unfused along the length of the slender frontal processes. These processes extend past the caudal margin of the external nares but are incomplete and it cannot be determined if they articulated with the frontals, as in Neornithes. The angle formed by the nasal and maxillary processes of the premaxilla is much larger in the new taxon compared to *Hongshanornis*, demarcating a more robust rostrum in the new taxon. The maxilla and premaxilla are unfused; the maxillary process of the premaxilla tapers caudally. The premaxillary and jugal processes of the maxilla are subequal, the jugal process being slightly longer. The short nasal process of the maxilla articulates with the nasal to contribute to the ventral margin of the external nares. The nasal has a short maxillary process that tapers to a sharp point and extends rostrally almost as far as the base of the nasal process of the maxilla.

The large external nares are teardrop-shaped, tapering rostrally. The rounded caudal margin of the naris is formed entirely by the nasal and reaches the rostral margin of the antorbital fossa. Virtually no anatomical details can be retrieved from the postorbital region; displaced onto the ventrocaudal border of the orbit, a fragmentary bone with a condylar structure may be part of the quadrate.

The mandibular symphysis appears to be unfused because the dentaries are preserved slightly offset from each other. There is a small bone located near the rostral contact between the two dentaries; an identical bone is also present in the ornithuromorphs *Hongshanornis*, *Yixianornis*, *Yanornis* (O'Connor and Chiappe, pers. observ.) and *Hesperornis regalis* (Martin, 1987). In *Hesperornis*, this ossification has been referred to as a predentary bone (Martin, 1987), but we believe this name is inappropriate because it implies a homology between this ossification and the predentary bone of ornithischian dinosaurs. The evolutionary origin of this element (intersymphysial ossification) in birds is

FIGURE 2. Photographs of PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov. **A**, slab A; **B**, slab B.

unknown, but it is possible that it contributed in strengthening the mandibular symphysis. The rostral half of the dentary is directed slightly ventrally so that the rostroventral margin is concave, accentuated by a ventral swelling of the distal end of the dentary. The caudal portion of the mandible is ventrally slightly convex whereas the dorsal margin of the surangular is slightly concave, giving the mandibular rami an overall sigmoidal shape in lateral view; this morphology is shared by *Hongshanornis*. Caudally, the dentary is not forked, lacking a dorsal process. The caudal portion of the mandible slopes caudoventrally. *Longicrusavis* lacks mandibular fenestrae, as does *Hongshanornis.*

There are no teeth preserved in PKUP V1069, though alveoli do appear to be present in the premaxilla and maxilla. *Hongshanornis* has been described as toothless (Zhou and Zhang, 2005), but in our observation of the holotype (IVPP V14533), we also noted alveoli in the premaxilla and maxilla; furthermore, the grooves and foramina observed in *Archaeorhynchus* (Zhou and Zhang, 2006) that indicate the presence of a beak are absent in *Hongshanornis* and *Longicrusavis*. The mandible in both *Hongshanornis* and *Longicrusavis* appears to have been edentulous

(Zhou and Zhang, 2005); however, this cannot be determined with absolute certainty.

Vertebral Column

There are at least seven articulated vertebrae of definitive cervical morphology with distinctly keeled ventral margins. These are laterally compressed and are exposed in ventral view in slab B (Fig. 4). The anterior most vertebrae are heterocoelous; posterior cervical articulations are not clear. The cranial articular surface of each vertebral body is greater in width than height and the caudal articular surface is greater in height than width, ovoid, and slightly concave. The prezygapophyses increase in length from the first preserved vertebra to the fourth. In the following two cervical vertebrae, the postzygapophyses are more dorsally oriented. Carotid processes are present in the cranial most preserved cervicals.

Two poorly preserved vertebrae following the articulated cervical series span the cervicodorsal transition. These vertebrae appear to have laterally compressed centra, excavated laterally on
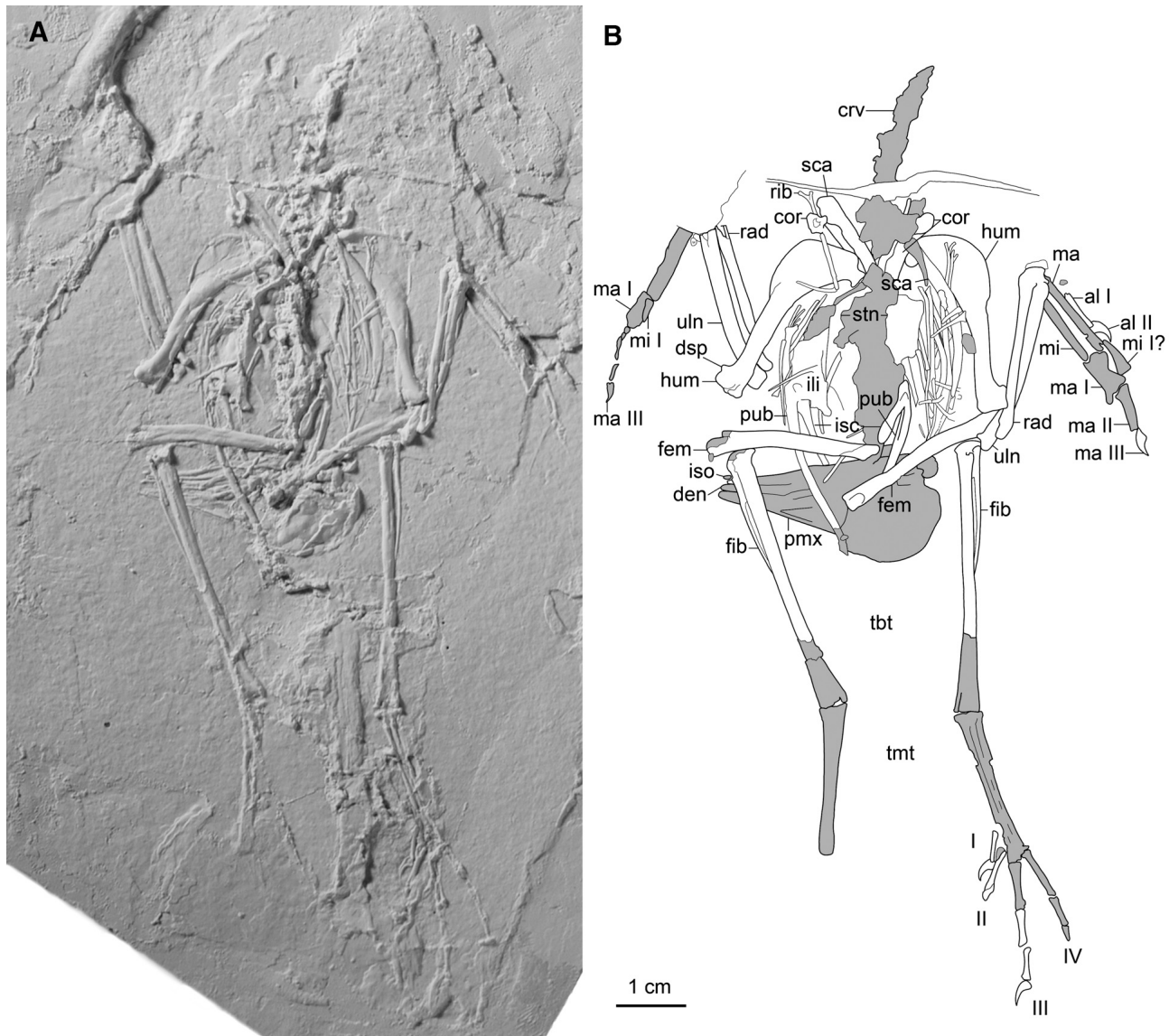
FIGURE 3.   Cast of slab A of PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov. **A**, photograph and **B**, camera lucida drawing. The cast was dusted with magnesium to highlight the bones.

both sides by deep fossae. Two disarticulated thoracic vertebrae, visible in slab B, are exposed in lateral view and displaced over the left side of the sternum (Fig. 4). These vertebrae also display deep, broad fossae on the lateral surfaces of their vertebral bodies. A large, round parapophysis is located toward the craniodorsal margin of the fossa. These vertebrae appear not to be heterocoelous, but more amphicoelous. Lying dorsal to the sternum is a longitudinal cluster of bone presumably comprised of more thoracic vertebrae and the synsacrum. These poorly preserved vertebrae yield no anatomical details. Neither free caudal vertebrae nor a pygostyle are preserved.

Gastralia and uncinate processes are not preserved.

Thoracic Girdle

The thoracic girdle is preserved nearly in its entirety. The scapula is thin, curved, and tapered distally. The proximal end of the scapula bears a short and cranially projecting acromion process. The length of the scapula exceeds two times the length of the coracoid (Table 1).

The coracoid is modern in appearance: strut-like with a procoracoid process. The sternolateral corner of the coracoid bears a lateral expansion that may be a rudimentary lateral process. The sternal articulation equals approximately one-half the total craniocaudal length of the coracoid, a greater proportion than that of *Apsaravis ukhaana*, a Mongolian ornithuromorph bird, in which it is only one-third the total length (Norell and Clarke, 2001), but less than that of other Jehol ornithuromorphs such as *Archaeorhynchus*, *Yixianornis*, and *Yanornis*, in which the sternal margin approaches the total length of the coracoid. The coracoid is very similar to that of *Hongshanornis*; in both taxa, its lateral margin is concave (contra Zhou and Zhang, 2005). There is no evidence of a supracoracoideus foramen. A deep socket forms the articular facet for the scapula, clearly evident in slab A.
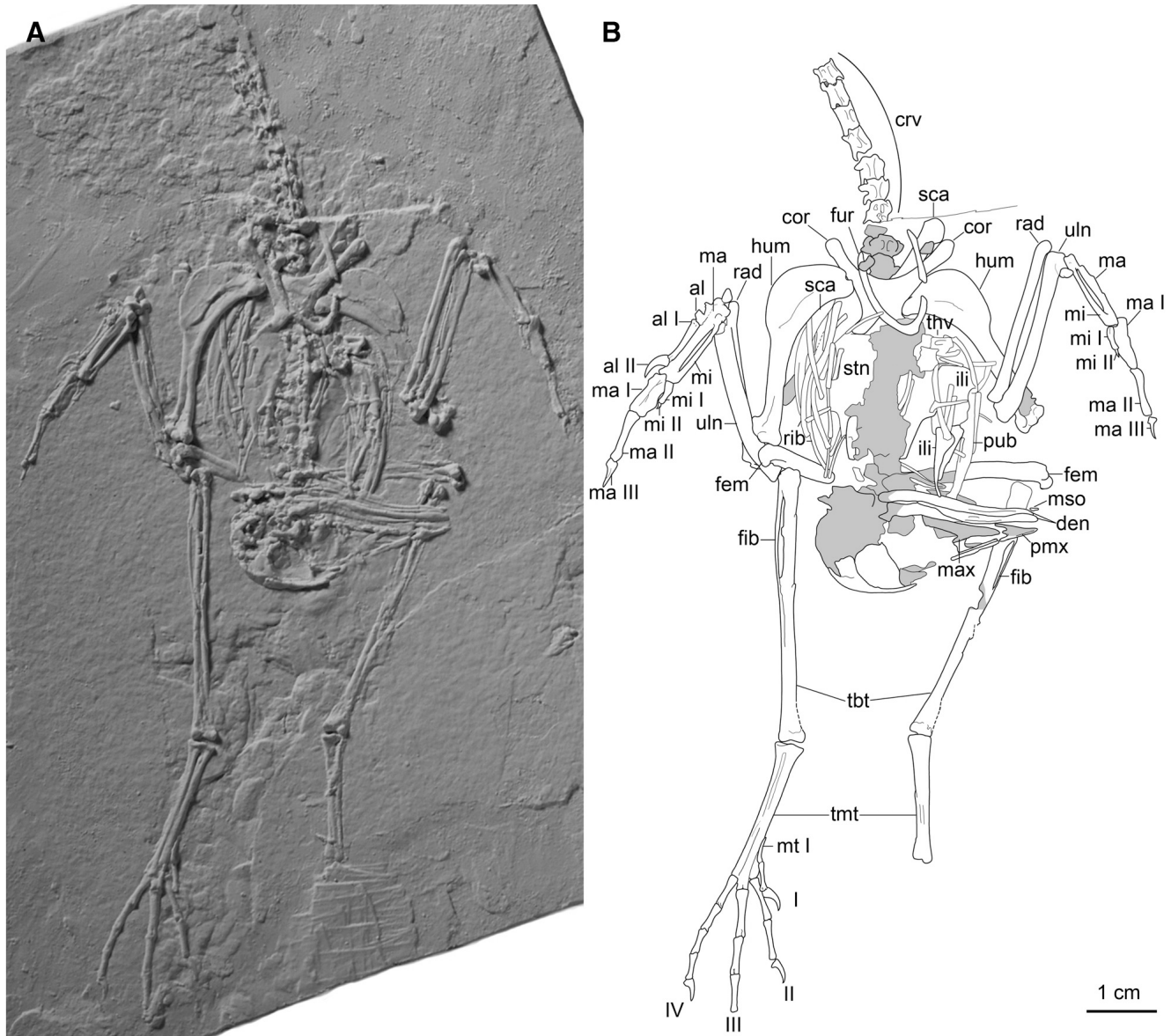
FIGURE 4. Cast of slab B of PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov. **A**, photograph and **B**, camera lucida drawing. The cast was dusted with magnesium to highlight the bones.

The furcula is broken but preserved almost in its entirety. The bone is U-shaped and has an interclavicular angle of 45° (measured as the angle between the medial edges of the sternal halves of the rami with the apex of the angle on the cranial edge of the clavicular symphysis). The omal tips curve medially. The thickness of the furcula is even throughout its length. The rami are oval in cross-section, with the long axis oriented obliquely to the sagittal plane in such a way that the ventral border of the furcula is more exposed laterally than the dorsal border. The furcula lacks a prominent hypocleideum, possessing only a small tubercle, whereas *Hongshanornis* appears to possess a short tapered hypocleidium (Zhou and Zhang, 2005).

The sternum (Fig. 6A) is badly crushed and covered by the pelvic girdle, making it difficult to interpret. The overall shape appears rectangular, with the long axis oriented craniocaudally; the cranial margin is broadly parabolic. An ossified carina is present,

extending the entire length of the sternum. The sternum possesses sternocoracoidal and zyphoid processes, as in *Yixianornis*, but lacks the strongly developed lateral projection of these processes present in the latter taxon (Fig. 6C). Well-defined processes, like those present in *Yixianornis* and *Longicrusavis*, are absent in *Hongshanornis*; instead the craniolateral margins are rounded and the middle third of the lateral margin bulges laterally. Caudally, the sternum is deeply notched; the lateral trabecula appears to be strap-like, and slightly angled medially. The lateral trabeculae in *Hongshanornis* are not strap-like but curved medially (Fig. 6B). A discrete medial trabecula, like that present in *Hongshanornis*, appears to be absent. The caudomedial margins of the sternum converge on the midline, so that the caudal margin (xiphial area; Howard, 1929) forms a wide V, the apex of which is not clearly preserved. The sterna of *Hongshanornis* and *Longicrusavis*, though distinct, are more similar to each other
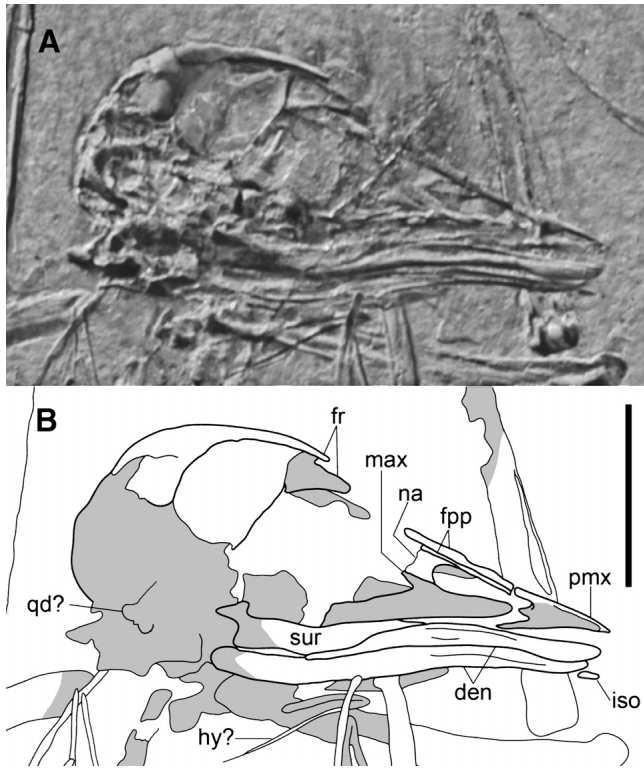
FIGURE 5. Skull of PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov. **A**, photograph and **B**, camera lucida drawing.

TABLE 1. Selected measurements of *Longicrusavis houi* holotype specimen (PKUP-V1069) in mm.

	Right	Left
Skull, length	30.7	
Dentary	23.7*	
Furcula	12.7*	
Coracoid		12.7
Scapula	23.1	
Humerus		26
Ulna		25
Radius		24
Carpometacarpus	13.1	
Alular metacarpal		2.7*
Phalanx 1		6.9
Claw		4.3
Major metacarpal	11.5	
Phalanx 1		7
Phalanx 2		7.3
Claw		3.4
Minor metacarpal		11.1
Phalanx 1		3.2
Phalanx 2		0.8
Ilium		(11.7)
Ischium	(10.7)	
Pubis		31*
Femur		24.3
Tibiotarsus		37.6
Fibula		16.6*
Tarsometatarsus	21.5	
Metatarsal I		4
Phalanx 1		4.1
Phalanx 2		3.3
Metatarsal II		19.2
Phalanx 1		6.3
Phalanx 2		5.4
Phalanx 3		3.3
Metatarsal III		21
Phalanx 1		6.8
Phalanx 2		5.7
Phalanx 3		5.1
Phalanx 4		—
Metatarsal IV		19.6
Phalanx 1		4*
Phalanx 2		4.1
Phalanx 3		3.7
Phalanx 4		3.8
Phalanx 5		3

The asterisk denotes estimated lengths; parentheses represent incomplete elements.

than to those of sympatric ornithuromorphs, like *Yanornis* and *Yixianornis*, that bear a pair of caudal fenestrae (Clarke et al., 2006), or enantiornithines, which typically possess an elongate xiphoid process (*Eoenantiornis*, *Longipteryx*; Hou et al., 1999, Zhang et al., 2001).

Thoracic Limb

The humerus is curved proximally, but not twisted so the proximal and distal ends are more or less in the same plane. The proximal head is globose and the bicipital tubercle is separated from the head by a deep capital incisure. The area distal to the ventral tubercle is partially obscured by other bones, thus the existence of either a pneumotricipital fossa or pneumatic foramen cannot be determined; however, if they indeed existed
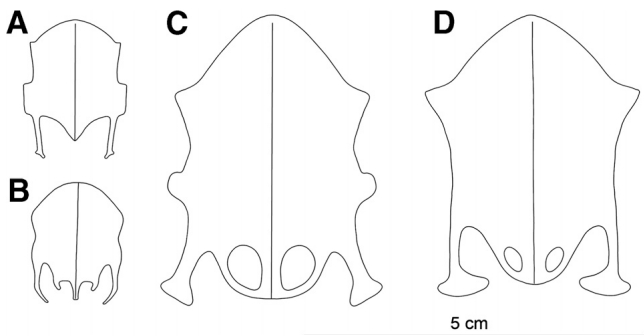

FIGURE 6. Comparative drawings of the sterna of Early Cretaceous ornithuromorphs from the Jehol Biota, China. **A**, PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov.; **B**, *Hongshanornis longicresta*; **C**, *Yixianornis grabaui*; **D**, *Yanornis martini*.

in this specimen, they could not have been very extensive, limited only to the immediate area of the ventral tubercle. In cranial view, the deltopectoral crest extends entirely in the dorsoventral plane without cranial deflection. The crest, though distinct, is not very extensive, spanning only two-fifths the total length of the humerus, as opposed to the robust crest in *Archaeorhynchus*, which extends for more than one-third the humeral length. The bicipital crest projects cranioventrally; the ventral surface of the crest possesses a small, ovoid fossa for muscle attachment, possibly the M. scapulohumeralis caudalis (Clarke, 2004). Slightly distal to the humeral head, there is a shallow, rounded fossa similar to those observed in other Cretaceous birds such as *Concornis*, *Patagopteryx*, and *Apsaravis* (Fig. 7; Sanz et al., 1995; Chiappe, 2002a); this feature cannot be identified in *Hongshanornis*.

The distal end of the humerus is depressed, consistent with a brachial depression, but whether or not a discrete scar existed for the attachment of the M. brachialis cannot be determined due to the preservation. Proximal to the distal condyles lies a dorsal supracondylar process for the origin of the M. extensoris metacarpi radialis, as is present in some charadriiforms (Fig. 3). The distal condyles are globular and well defined; the

dorsal condyle is slightly larger than the ventral. A distinct trough separates the prominent ventral epicondyle from the ventral condyle. The flexor process extends only slightly past the ventral tubercle so that the distal margin of the humerus is still more or less perpendicular to the shaft. A distinct olecranon fossa embays the caudal surface. The distal surface is smooth, lacking evidence of tricipital grooves.

The ulna is slightly longer than the humerus and has a midshaft thickness almost double that of the radius. The ulna is slightly bowed proximally and has a poorly developed olecranon process. The dorsal cotyle is ovoid and the ventral cotyle is flat. The two cotyla are not separated by a groove, a condition recognized in some enantiornithine taxa (*Enantiornis*). Quill knobs (papillae) are absent. The radius is straight and its shaft smooth. The ulnare and radiale appear to be sub-equal in size. The radiale is triangular, while the outline of the ulnare cannot be clearly observed.

The carpometacarpus is completely fused. The manus possesses the following phalangeal formula: 2–3-2-X-X. The alular metacarpal is small and rectangular; the presence of an extensor process cannot be determined due to incomplete preservation. The first phalanx of the alular digit is long and tapers distally. The major metacarpal is straight; the minor metacarpal is slightly bowed, creating a moderate intermetacarpal space. The former element is twice as thick and slightly longer than the latter, opposite the enantiornithine condition where the minor metacarpal projects distally farther than the major metacarpal (Chiappe and Walker, 2002). In ventral view, the carpometacarpus possesses a cranioventrally oriented pisiform process. Proximally, there is a distinct infratrochlear fossa. The proximal section of the minor metacarpal is craniocaudally compressed; distally the bone becomes rounded in cross-section. There is a distinctly thicker segment of the minor metacarpal located distal to the pisiform process.

The alular digit extends distally further than the distal end of the major metacarpal, slightly longer than the alular digit in *Hongshanornis*, which ends approximately level with the distal end of the major metacarpal. The first phalanx of the major digit is broad, robust, and compressed dorsoventrally; it is one-half the length and twice the thickness of the major metacarpal, as in *Hongshanornis*. The intermediate phalanx is longer than the first, but less than half the thickness. The ungual phalanx is smaller and less recurved than that of the alular digit; both unguals possess rounded flexor tubercles. The minor digit has only two phalanges. The proximal phalanx is reduced, less than half the length of the intermediate phalanx of the major digit, and bowed so that it is concave craniocaudally. The second phalanx is extremely reduced, less than one-fifth the size of the first.

Pelvic Girdle

The pelvic girdle is badly crushed and displaced cranially so that it overlaps the sternum. The left side is preserved in articulation, whereas the right side is unclear. The preacetabular wing of the ilium appears rounded. The postacetabular wing, as observed in slab B, is long, narrow, and tapered distally. The ilium bears a prominent antitrochanter. Both ischia are preserved in slab A, though slightly damaged by the process of splitting the shale slabs. The bone is strap-like, lacking both dorsal and obturator processes, as in *Hongshanornis*. The bone tapers distally, but the distal end is incomplete. The pubis is in articulation and appears to have been oriented caudally. The pubis is similar in length to the femur; the shaft lacks lateral compression. The distal ends are not preserved, although the two pubes approach each other as if to form a symphysis. The articulated pelvic girdle of *Hongshanornis* does not provide much anatomical detail; however, the retroverted pubes contact distally, forming a symphysis approximately one-quarter the length of the pubis.

Pelvic Limb

The femur is slightly longer than the tarsometatarsus. The femoral shaft is slightly curved craniocaudally, and thickens distally. The lateral condyle projects farther caudally than the medial condyle. The lateral condyle appears mediolaterally compressed; it cannot be determined if a fibular condyle is present.

The tibiotarsus is completely fused and is nearly twice the length of the tarsometatarsus. The proximal articular surface is craniocaudally inclined. The tibiotarsus has two cnemial crests: the lateral cnemial crest has a slightly hooked profile, as opposed to the medial crest, which forms a short vertical ridge. A prominent fibular crest extends less than one-fifth the length of the tibia. The distal condyles are separated by a wide intercondylar incisure. The lateral condyle is round whereas the smaller medial condyle is triangular, tapering toward the midline. The cranially projecting portion of the lateral condyle is broader than that of the medial condyle. A supratendinal bridge is absent, although various grooves scar the craniodistal end of the tibiotarsus. Whether these grooves are a taphonomic artifact or part of an extensor groove complex is unclear. No detail can be discerned from the distal tibiotarsus of *Hongshanornis*. Distally, the medial and lateral tibiotarsal margins form caudally projected ridges, presumably coinciding with the edges of the cartilaginous portion of the tibial trochlea.

The very slender fibula extends more than halfway down the tibiotarsus. The area between the proximal articulation and the iliofibular tubercle is substantially wider craniocaudally than the splint-like distal portion of the fibula. The iliofibular tubercle is level with the distal end of the fibular crest of the tibiotarsus. Just distal to the tubercle, the shaft of the fibula bows (becoming laterally convex), creating a space between the fibula and tibiotarsus that is approximately three times the width of the fibula itself. This space extends slightly more than one-third the length of the fibula. The distal portion of the fibula contacts the tibiotarsus.

Metatarsals II through IV are all sub-equal in width, and completely fused to the distal tarsals to form a tarsometatarsus. The proximal end is marked by a weak but distinct intercotylar prominence. Proximally, metatarsal III is plantarly displaced from metatarsals II and IV, forming a deep extensor groove that continues distally as a shallow groove between metatarsals III and IV. Proximally, within this fossa on the dorsal surface of metatarsal II at its contact with metatarsal III, lies an elliptical tubercle for the attachment of the M. cranialis tibialis. Also within this fossa, a lateral proximal vascular foramen pierces the contact between metatarsals III and IV, although it is unclear whether the foramen traverses through the tarsometatarsus.

On the distal end of the tarsometatarsus, a slit-like distal vascular foramen opens between metatarsals III and IV. The distal end of metacarpal III extends the farthest; the proximal end of its distal trochlea lies distal to the trochlea of metatarsals II and IV. Metatarsals II and IV are subequal, though metatarsal IV projects distally slightly farther than metatarsal II, as in *Archaeorhynchus*. The distal trochleae of metatarsals II–IV are roughly subequal in width. The trochlea of metatarsal III is ginglymous, but it is unclear if those of metatarsals II and IV shared this condition. The plantar surface of the tarsometatarsus is poorly preserved, but medial and lateral plantar crests are visible. The first metatarsal is straight, strongly compressed laterally, and tapers proximally. Metatarsal I articulates with the medial surface of metatarsal II; the distal trochlear surface is elevated with respect to the distal trochlea of the metatarsal II so that the two do not overlap.

The pedal digits are long and slender; the phalanges are roughly symmetrical with well-formed distal ginglymous trochleae and distinct pits for the attachment of the collateral ligaments. The foot appears to have the following phalangeal
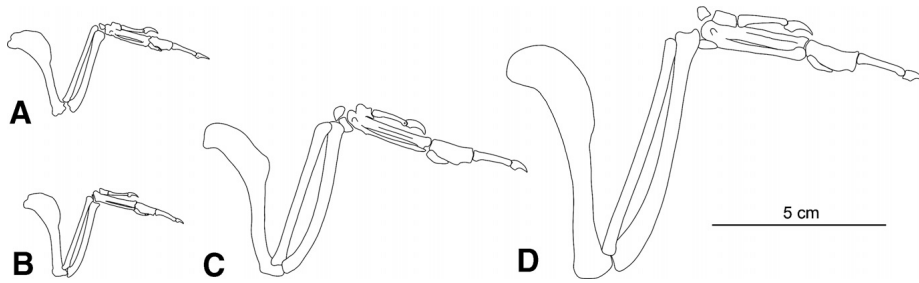
FIGURE 7. Comparative drawings of the forelimbs of Early Cretaceous ornithuromorphs from the Jehol biota, China. **A**, PKUP V1069, holotype of *Longicrusavis houi*, gen. et sp. nov.; **B**, *Hongshanornis longicresta*; **C**, *Yixianornis grabaui*; **D**, *Yanornis martini*.

formula: 2–3–4–5-X; the distal phalanx of digit III is not preserved. The proximal phalanx is the longest in each digit; subsequent phalanges gradually reduce in length distally. The hallux is very short: the distal end of its ungual does not extend beyond the distal end of the proximal phalanx of the second digit. The claw of the hallux is more recurved than those of digits II and IV; all the pedal claws are less recurved than those of the manus. The claws are all similar in size to each other and to that of the major digit of the wing. The third digit is the longest, followed by the fourth and then the second. The configuration in *Hongshanornis* is similar, but the trochlea of metatarsal II is slightly more elevated so that the fourth digit is markedly longer than the second digit (Fig. 8).

PHYLOGENETIC ANALYSIS

The phylogenetic analysis was performed using the Gao et al. (2008) data set, which is a highly modified version of the Chiappe (2002b) data set, with the incorporation of *Longicrusavis* (see Supplementary Information). The clade Neornithes was represented by *Anas platyrhynchos* and *Gallus gallus*; the family Dromaeosauridae was scored as the outgroup. An analysis of 213 characters (31 ordered; 29 uninformative characters removed, see Supplementary Information) was evaluated for 29 taxa using NONA (Goloboff, 1993); optimal trees were identified using five random addition sequence replications of taxa, each followed by Tree Bisection Reconnection (TBR) branch-swapping and 100 iterations of jackknife ratchet, collapsing the trees on TBR rearrangements. The analysis resulted in six most parsimonious trees (MPTs) of 582 steps, which differ only within the enantiornithine clade.

The strict consensus tree (Fig. 9) places *Longicrusavis* within Ornithuromorpha. *Zhongornis*, *Jeholornis*, and *Archaeopteryx* form consecutive outgroups of Pygostylia with the confuciusornithid clade and *Sapeornis* as basal-most pygostylians. *Sapeornis* forms the outgroup to Ornithothoraces, recovered as more derived than Confuciusornithidae (contra Zhou and Zhang, 2002, Clarke et al., 2006, and Zhou et al., 2008; as in Gao et al., 2008).

A large ornithothoracine clade is formed by Enantiornithes and Ornithuromorpha. The 'longirostrine' enantiornithines (*Longipteryx*, *Longirostravis*, DNHM D1878, and DNHM D2522; Morschhauser et al., 2009; O'Connor et al., 2009) form a basal clade within enantiornithines, with *Longirostravis* and DNHM D2522 forming a more exclusive relationship
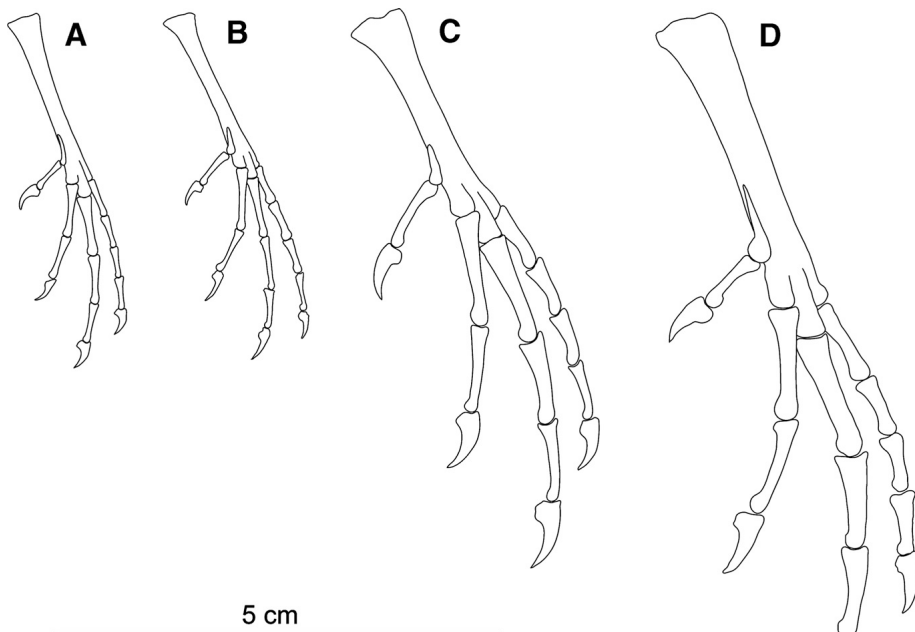

FIGURE 8. Comparative drawings of the feet of Early Cretaceous ornithuromorphs from the Jehol biota, China. **A**, PKUP 1069, holotype of Longicrusavis *houi*, gen. et sp. nov.; **B**, *Hongshanornis longicresta*; **C**, *Yixianornis grabaui*; **D**, *Yanornis martini*.
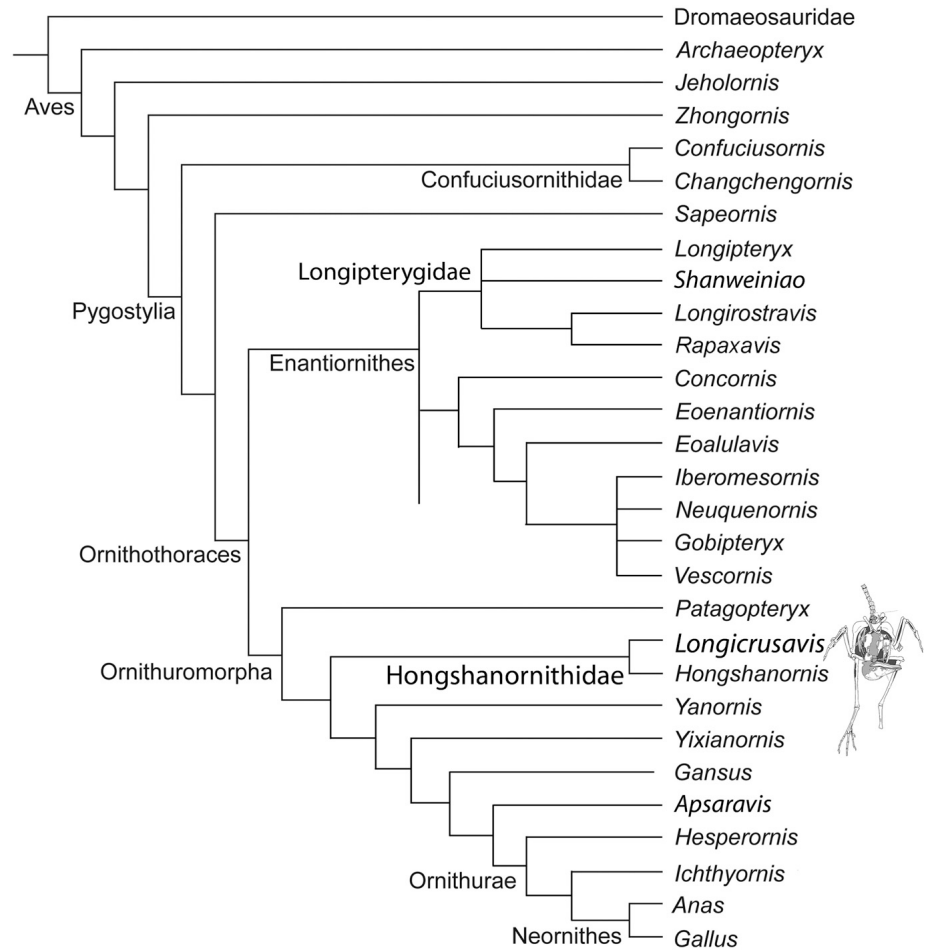
FIGURE 9. Strict consensus cladogram illustrating the phylogenetic position of *Longicrusavis houi*. Tree length: 582 steps, consistency = 48, consistency index = 0.48, retention index = 0.68.

within this larger clade (Morschhauser et al., 2009; O'Connor et al., in press). Remaining enantiornithine taxa form a large clade in which *Concornis*, *Eoalulavis* (Sanz et al., 1996), and *Eoenantiornis* are successive outgroups to a polytomy formed by *Neuquenornis*, *Iberomesornis*, *Gobipteryx*, and *Vescornis* (Elzanowski, 1974; Sanz et al., 1988; Chiappe, 1991; Zhang et al., 2004). The relationships presented here differ greatly from those derived from other matrices (Clarke et al., 2006; Cau and Arduini, 2008; Zhou et al., 2008), reflecting the need for a detailed inspection of the phylogenetic relationships of this clade.

Hongshanornis and *Longicrusavis* cluster together within Ornithuromorpha, supporting the monophyly of the newly recognized clade Hongshanornithidae. The node is supported by four unambiguous synapomorphies (see Supplementary Information): the presence of sigmoidal mandibular rami (43:1); the absence of a prominent distal expansion in the outermost trabecula of the sternum (112:0, reversal); length of manus less than length of humerus (175:0, reversal); and an intermembral index between 0.7 and 0.9 (176:1, reversal).

The remaining ornithuromorph relationships largely agree with previous work (Chiappe, 2002b; Clarke et al., 2006; Zhou and Zhang, 2006). *Ichthyornis* is placed as sister taxon to Neornithes, whereas *Hesperornis, Apsaravis, Gansus, Yixianornis, Yanornis,* Hongshanornithidae (*Hongshanornis longicresta + Longicrusavis houi*) and *Patagopteryx* form a series of successive outgroups (see Supplementary Information). *Patagopteryx* maintains a basal position as in previous analyses (Chiappe,

2002b; Clarke et al., 2006; Cau and Arduini, 2008). Zhou et al. (2008) found *Patagopteryx* to be more derived than *Hongshanornis*. The relatively higher position of *Hongshanornis* within the analysis presented here may reflect the new data available on this taxon in this publication; *Patagopteryx* holds its basal position based on the absence of eight apomorphies: procoracoid process on the coracoid (89:1), sternum with a well-developed keel (108:3), globe-shaped humeral head (121:1), a brachial depression on the distal humerus (134:1), a craniocaudally expanded first phalanx of the major digit (168:1), a caudodorsally directed antitrochanter (184:0, reversal), and the absence of a cranial cnemial crest (211:1). A close relationship between *Yixianornis* and *Yanornis*, as proposed by Clarke et al. (2006), is not supported here.

DISCUSSION

Relationships of the Hongshanornithidae

Longicrusavis possesses several ornithuromorph synapomorphies, such as a U-shaped furcula, craniocaudally elongate sternum, derived manus with a robust, craniocaudally expanded first phalanx in the major digit and reduced minor digit, and a completely fused tarsometatarsus lacking a reduced metatarsal IV. The new taxon is morphologically very similar to *Hongshanornis*, from the Yixian Formation of Inner Mongolia near the border with Liaoning Province (Zhou and Zhang, 2005). Both birds are small, comparable in size to a phoebe (*Sayornis*), possess

sigmoid mandibular rami, and have elongate hindlimbs relative to the forelimb, with intermembral indices of 0.81 (humerus + radius/femur + tibiotarsus). The new specimen possesses several autapomorphies and a unique suite of morphologies that justify the erection of a new taxon, *Longicrusavis houi*, diagnosed by the following characteristics: dorsal margin of skull lacking a strong constriction at the base of the rostrum; rostrum longer and more robust than in *Hongshanornis*; absence of a medial sternal process; presence of a dorsal supracondylar process on the humerus; femur is proportionally shorter than in *Hongshanornis*; and the trochleae of metatarsals II and IV are nearly level.

The results of our phylogenetic analysis indicate that *Longicrusavis* and *Hongshanornis* are sister taxa, and supports their position within a common higher taxon, Hongshanornithidae, a clade of basal ornithuromorphs here defined as the common ancestor of *Hongshanornis longicresta* and *Longicrusavis houi* plus all its descendants. Both these taxa come from the Yixian Formation of northern China. The outcrops near Ningcheng, Inner Mongolia, have been correlated with the Dawangzhangzi bed at Lingyuan (Wang et al., 2000). The Lingyuan deposits have been constrained between 125 and 122 Ma (Ji, 2004; Zhang et al., 2006), which is approximately the estimated age for the Yixian Formation (Yang et al., 2007). The overlying Jiufotang Formation has been dated at 120 Ma (He et al., 2004); therefore, present knowledge of Hongshanornithidae constrains the family temporally to a period of less than 5 Ma and geographically to the same Early Cretaceous lake system, separated by a distance of approximately 60 kilometers (Yang et al., 2007).

Integument

Feather preservation in the hongshanornithids provides key evidence about the plumage of basal ornithuromorphs. Although a crest of feathers located on the dorsal surface of the holotype skull of *Hongshangornis longicresta* was reported by Zhou and Zhang (2005), we were unable to determine if this 'crest' is indeed an attribute or a preservational artifact. Reliable information, however, is preserved in the wings and tail of these birds. The contour feathers of the wing in PKUP V1069 are not preserved in great detail (individual barbs and barbules cannot be discerned) and it appears that some of the integument has been displaced from its original position. Nevertheless, five primaries and seven secondaries can be clearly identified in the left wing of slab A, and organic residue suggests that more were present. The three medial-most primaries are extremely long; on the basis of the preserved feathers, the wingspan of *Longicrusavis houi* is estimated to be nearly 26 cm.

The tail plumage of PKUP V1069 is not preserved, but the holotype of *Hongshanornis longicresta* preserves a long tail composed of more than two feathers, similar to that observed in the younger *Yixianornis* (Clarke et al., 2006). A minimum of eight long rectrices are preserved in the *Yixianornis* holotype. They are arranged in a graduated manner, with lengths ranging from 7.2 to 9.5 cm (Clarke et al., 2006). In *Hongshanornis*, there are at least four feathers, approximately 5 cm in length, preserved distal to the pygostyle. The vanes are directed toward the pygostyle and pubis and angled with respect to the vanes of the primaries. Based on their orientation, these feathers appear to be in situ, and not displaced primaries, suggesting the presence of a long, feathered tail. The distal ends of the tail feathers are broad and rounded. The central two feathers are slightly longer than the feathers on either side, suggesting a graded pattern of distribution. *Hongshanornis* is the earliest known taxon to have possessed a fan-shaped tail composed of rectrices, a condition that likely increased lift and thus flying ability (Gatesy and Dial, 1996).

Paleoecology

Elongate hindlimbs in birds are commonly associated with aquatic 'shorebird'/littoral ecological niches (Zeffer et al., 2003). The presence of a dorsal supracondylar structure in *Longicrusavis*, together with the proportions of the legs (elongate tibiotarsus) and feet (elongate proximal phalanges, short hallux), suggests that hongshanornithids occupied such a niche. Wading 'shorebird' taxa are known from the Late Cretaceous; the enantiornithine *Lectavis bretincola* from the South American Lecho Formation is suggested to have filled this niche based on the long and gracile nature of its tarsometatarsus (Chiappe, 1993). Ostensible charadriiform taxa, such as *Cimolopteryx maxima*, *Graculavus velox*, and *Telmatornis priscus*, have been reported mostly from the Late Cretaceous of North America (Hope, 2002); however, these taxa are fragmentary and their referral to Charadriiformes is questionable. The Early Cretaceous record of aquatic taxa is limited to the exceptional *Gansus yumenensis* and inconclusive trackways from Asia and Europe (Lockley et al., 1992; Fuentes Vidarte, 1996; You et al., 2006). The hongshanornithids thus expand our knowledge of Early Cretaceous specializations within the aquatic niche. The Hongshanornithidae are known from lakes located relatively close to the coast, in contrast to the younger more phylogenetically derived *Gansus*, which is known from inland deposits in northern Gansu Province, China. As more ornithuromorph taxa are described, it is becoming increasingly clear that a majority of species have aquatic specializations such as elongate hindlimbs and pedal digits and proximally projecting cnemial crests on the tibiotarsus (*Yanornis*, *Gansus*, *Hongshanornis*). *Longicrusavis* also possesses specializations for a littoral environment, and together with *Hongshanornis*, reveals an early diversification of wading birds.

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