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A new species of Early Cretaceous ornithuromorph with an elongate rostrum is described from the Sihedang locality of the Lower Cretaceous Yixian Formation in north-eastern China. Like the longipterygid enantiornithines, rostral elongation in *Dingavis longimaxilla* gen. et sp. nov. is achieved primarily through the maxilla, whereas neornithines elongate the premaxilla and rostralization is far more extreme than observed in early birds. Notably, in the rostrum of *Xinghaiornis*, the most 'longirostrine' Early Cretaceous ornithuromorph, the premaxilla and maxilla contribute to the rostrum equally. These lineages together highlight the diversity of configurations in which early birds experimented with rostralization of the skull. The 65% upper limit in rostral proportions of Early Cretaceous taxa with elongate maxillae and the fact that this morphology was abandoned in more derived taxa suggests that in Aves this skull configuration provided less structural stability.

http://zoobank.org/urn:lsid:zoobank.org:pub:9D8A429F-BBA7-47EF-BFD0-ADFB7118833A

Keywords: Ornithothoraces; Cretaceous; Jehol; Mesozoic birds; skull

Introduction

The rostrum (facial skeleton) is the most variable portion of the archosaur skull and extant birds cover nearly the entire spectrum of viable skull morphospace (Marugán-Lobón & Buscalioni 2003). In neornithines, the rostrum is defined by the premaxilla (Baumel & Witmer 1993) and the maxilla is heavily reduced and fused to the premaxilla, not significantly contributing to the facial skeleton, but in non-avian theropods and basal birds the rostrum is formed by both the premaxilla and maxilla. Here we use the term 'rostrum' to refer to the facial skeleton following Marugán-Lobón & Buscalioni (2003). In extant avian theropods, the neornithines, the contribution of the rostrum to the skull varies from 30 to <85%, and the beak encompasses a huge variety of morphologies (Marugán-Lobón & Buscalioni 2003; Gill 2007). The rostrum and its horny beak, together with the jaw musculature, form the avian feeding mechanism. While tooth morphology can be used to infer diet in mammals, neornithines lack teeth and have adapted the shape of their rostra to suit a diversity of feeding habits (e.g. carnivorous, filter-feeding, mud-probing, seed-eating), allowing them to access a wide variety of trophic resources (Gill 2007). However, thus far this diversity appears to be largely a characteristic of Neornithes despite the fact that Cretaceous pterosaurs

achieved extreme rostral proportions (Marugán-Lobón & Buscalioni 2003). Rostral proportions in early birds as far as we know are much more conservative (O'Connor & Chiappe 2011). The earliest bird, the Late Jurassic *Archaeopteryx*, has a mesorostrine skull (rostral contribution 50–70%) in which the rostrum accounts for roughly half the total length (rostral length is very difficult to precisely measure from most fossil specimens). Mesorostral proportions also represent the plesiomorphic condition within both Archosauria and Theropoda (Marugán-Lobón & Buscalioni 2003). Similar proportions were retained in other basalmost birds *Jeholornis* (52%), *Confuciusornis* (55%) and *Sapeornis* (53%), lineages all found only in the Early Cretaceous Jehol Biota (130.7–120 Ma) (Z. Zhou 2006; Z.-H. Zhou & Zhang 2006). Only in the most diverse clade, the Enantiornithes, were significant excursions in rostral proportions observed (Zhang *et al.* 2000; Hou *et al.* 2004; Morschhauser *et al.* 2009; O'Connor *et al.* 2009). However, even these departures remained within the mesorostrine morphospace with the rostrum of *Longipteryx* representing the upper known limit, contributing to 65% of the skull length (O'Connor & Chiappe 2011). All Jehol enantiornithines with rostral elongation are inferred to form a clade, the Longipterygidae (O'Connor *et al.* 2009). Although once considered the most diverse recognized Early Cretaceous enantiornithine

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clade, in some recent analyses the group has collapsed into two clades, the Longipterygidae *Boluochia* + *Longipteryx* and the Longirostravidae *Rapaxavis* + *Shanweiniao* + *Longirostravis* (O'Connor *et al.* 2009; S. Zhou *et al.* 2014).

The Early Cretaceous record of the Ornithuromorpha, the derived avian lineage that includes living birds, has steadily grown over the last decade due nearly entirely to discoveries of largely complete specimens from the Jehol Group in north-eastern China (S. Zhou *et al.* 2013b; S. Zhou *et al.* 2014; M. Wang *et al.* 2015). At the last time rostral proportions were investigated in the Enantiornithes, the sister group to the Ornithuromorpha and the first major avian radiation, no ornithuromorph preserved rostral proportions similar to those observed in the longipterygids; *Yanornis* had the most elongate rostrum, contributing approximately 57% of the skull length. However, new discoveries have expanded the range of known rostral proportions in the Ornithuromorpha, and the recently described taxon *Xinghaiornis lini* has the longest recognized Early Cretaceous avian rostrum, forming approximately 67% of the total skull length (X.-R. Wang *et al.* 2013). Here we describe another specimen with relatively elongate rostral proportions representing a new species, *Dingavis longimaxilla* gen. et sp. nov. We compare the structure of the rostrum in the new specimen to that of *Xinghaiornis* and longipterygid enantiornithines, and discuss the bearing of this discovery on our current understanding of rostral evolution in early birds.

Systematic palaeontology

Class **Aves** Linnaeus, 1758
Pygostylia Chiappe, 2002
Ornithothoraces Chiappe, 1995
Ornithuromorpha Chiappe 2001

Definition. The first ancestor of Neornithes that is not also an ancestor of the Enantiornithes, and all of its descendants.

Remarks. We use the formerly node-based taxon Ornithuromorpha (Chiappe 2001, 2002) to refer to Neornithes and all taxa that are more closely related to it than to the Enantiornithes (O'Connor *et al.* 2015). We are thus providing this taxon with a stem-based definition. Although the proposed definition does not strictly equate with the published node-based definition, it does provide a formal definition for the current widespread usage of this term in most recent literature (Bell *et al.* 2010; O'Connor *et al.* 2010; S. Zhou *et al.* 2013a; M. Wang *et al.* 2015). We feel that node-based definitions are premature at this time given the fluctuating morphology of basal bird phylogenies and the rapid rate of discovery of new material. For example, the avian status of *Archaeopteryx* is now

debated, with growing evidence this taxon may be more closely related to troodontids (Xu *et al.* 2011). Furthermore, it is recognized that the next youngest avifauna, the Jehol, represents a relatively derived fauna with the earliest known ornithuromorphs being already derived members of a specialized clade of Early Cretaceous waders, the Hongshanornithidae (M. Wang *et al.* 2015). Therefore, any node-based definition at this time would be expected to change, especially if any fossils are found that fill the temporal gap between *Archaeopteryx* and the Jehol avifauna. We support the use of stem-based definitions until we achieve greater phylogenetic clarity.

Genus ***Dingavis*** gen. nov.

Type species. *Dingavis longimaxilla* sp. nov.

Etymology. The genus name is in honour of the late distinguished Chinese geologist Wenjiang Ding, often considered the 'father of Chinese geology', who brought Amadeus William Grabau to Beijing University in 1920. Professor Ding was the first person to teach palaeontology in China and he also served as the chief editor of *Palaeontologia Sinica*, one of the earliest Chinese journals to receive international recognition.

Diagnosis. See diagnosis of type and only species below.

Dingavis longimaxilla sp. nov.
(Figs 1−3)

Diagnosis. A large basal ornithuromorph with the following unique combination of characters: rostrum forms 63−65% of total skull length; jugal process of lacrimal caudolaterally excavated; both upper and lower jaws edentulous; length of carpometacarpus + major digit exceeds humeral length by 25%; short alular metacarpal (13.7% of major metacarpal); tarsometatarsus with small but sharp medial and lateral plantar crests, plantar surface not excavated; metatarsal II much shorter than metatarsal IV; metatarsal II and IV trochlea plantarly displaced; and metatarsal II trochlea strongly angled craniomedially.

Holotype. Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V20284, a nearly complete adult individual preserved in dorsal view with gastroliths and trace impressions of integument around the neck.

Etymology. The species name refers to the elongate maxilla that distinguishes this taxon from all other Jehol ornithuromorphs.

Occurrence. Sihedang, Liaoning Province, north-eastern China; Lower Cretaceous, Yixian Formation, Jehol Group.

Description. We conducted X-ray analysis of the slab to extract additional morphological information

Figure 1. *Dingavis longimaxilla* gen. et sp. nov., holotype, IVPP V20284, full slab photograph. Scale bar = 20 mm.

(Supplemental Figs 1, 2). Although the specimen is articulated and appears fairly complete (Figs 1, 2), the bone is poorly preserved in most places, obscuring morphological details.

Skull. The skull is exposed primarily in left lateral view. The rostrum forms 63−65% of the skull length. This is greater than the proportion observed in any other Jehol ornithuromorph with the exception of *Xinghaiornis* (Tables 1, 2). The premaxillary corpus is preserved in lateral view. As far as can be discerned, the premaxilla is edentulous. As in enantiornithines with the most elongate rostra, the premaxillary corpus is low (length is roughly three to four times the height) and the dorsal and ventral margins are nearly parallel. The left maxillary process is not preserved. A crack separates the frontal processes, which are preserved in dorsal view. Rostrally, a suture is present between the left and right processes. They become unfused along their distal halves. Although the processes do not reach the frontals, the distalmost extremity of both

processes is not preserved. The right premaxillary corpus is visible in ventral view in articulation with the elongate right maxilla. The rostral ends of the premaxillae appear to be unfused (Fig. 3). The maxilla also appears to be toothless, although small teeth cannot be ruled out due to the poor preservation. The premaxilla-maxilla contact is level with the rostral preserved ends of the frontal processes. Consistent with the interpretation that this is not a crack, the premaxilla articulates laterally with the maxilla. Caudally, the right maxilla is poorly preserved; the blunt caudal end is approximately level with the lacrimal. Distal and ventral to the caudal end of the maxilla is a slightly curved rod-like bone that is probably one of the jugal bones. The left lacrimal is preserved in articulation with the frontal. The craniodorsal process is weakly angled rostroventrally and the caudodorsal process is angled caudodorsally, as in other basal birds (e.g. *Jeholornis*, *Sapeornis*, *Pengornis*). The ventral process is laterally excavated so that the cross section of this process is L-shaped. This morphology is also observed in some
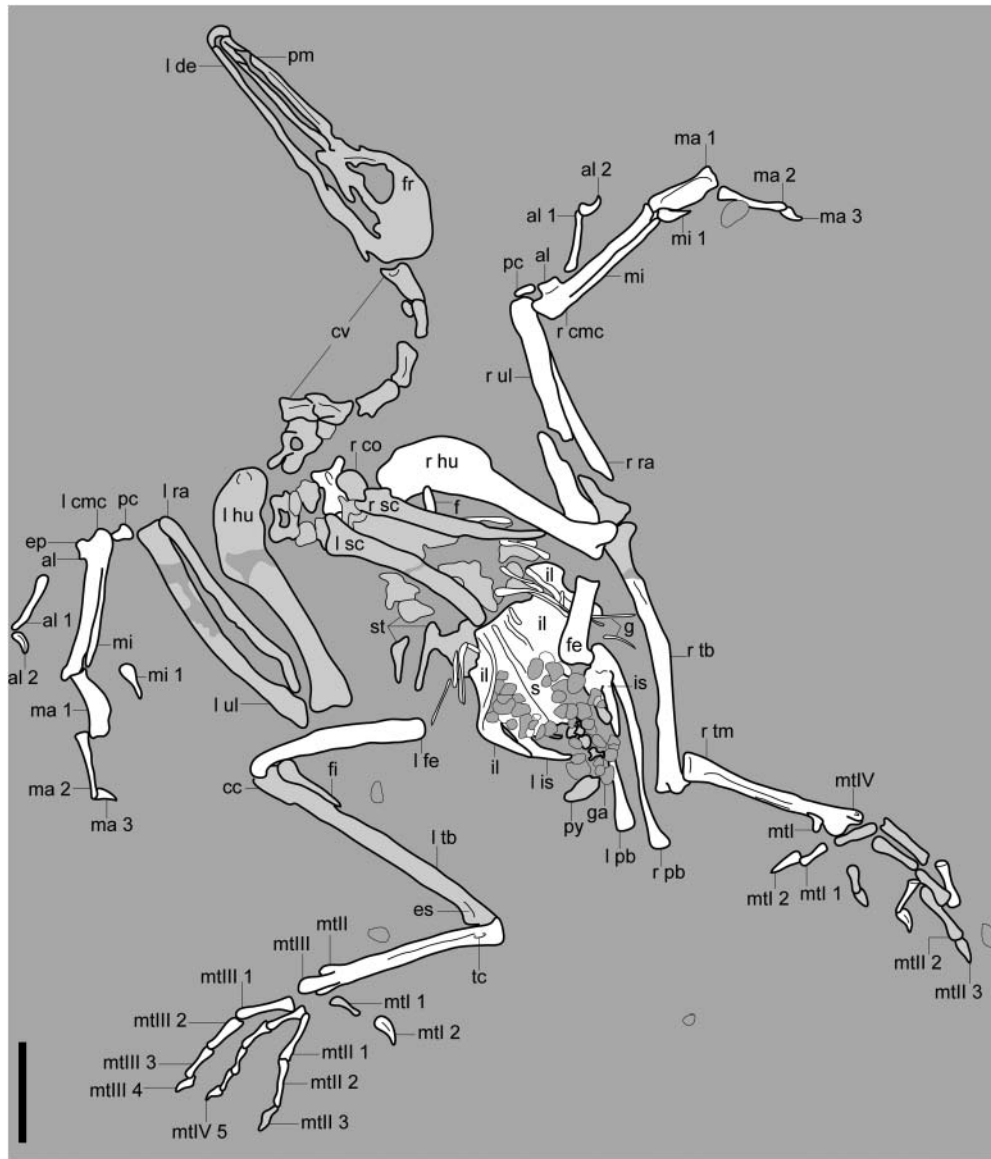
Figure 2. *Dingavis longimaxilla* gen. et sp. nov., holotype, IVPP V20284, interpretative drawing. Anatomical abbreviations: 1−5, phalanges one through five; ca, caudal vertebrae; cc, cnemial crest; cmc, carpometacarpus; co, coracoid; cv, cervical vertebrae; de, dentary; ep, extensor process; es, extensor sulcus; f, furcula; fe, femur; fi, fibula; fr, frontal; g, gastralia; ga, gastroliths; ha, hallux; hs, horny sheath; hu, humerus; il, ilium; is, ischium; ma, major digit; mi, minor metacarpal; mtI−IV, metatarsals I−IV; p, phalanx; pb, pubes; pc, proximal carpal; pm, premaxilla; py, pygostyle; ra, radius; s, synsacrum; sc, scapula; st, sternal fragments; tc, attachment of the m. tibialis cranialis; tb, tibiotarsus; th, thoracic vertebrae; tm, tarsometatarsus; ul, ulna; l and r represent left and right side, respectively. Scale bar = 20 mm.

enantiornithines (e.g. *Parabohaiornis*, *Pengornis*). The frontals are petal-shaped and strongly domed as in other Early Cretaceous birds. Preserved in the orbit, two bones form an expanded articulation (Fig. 3); we suggest this is the right pterygoid-quadrate articulation.

The mandible is slightly displaced rostral to the cranium so that the mandibular symphysis is located proximal to the rostral end of the premaxillae (Fig. 3). The left dentary appears to be preserved primarily in lateral view. The mandibular symphysis appears to be fully fused and

U-shaped, probably incorporating a predentary bone (Z.-H. Zhou & Martin 2011). The width of the mandibular symphysis suggests a very wide lower bill, similar to some living birds such as ducks, but also observed in *Epidendrosaurus*. The bone forming the rostral margin is heavily recrystallized, and we cannot rule out the possibility that the preserved morphology is exaggerated by taphonomic processes. Breaks in the bone separate the remaining left dentary from the mandibular symphysis. The dentary is long and straight, contributing to more
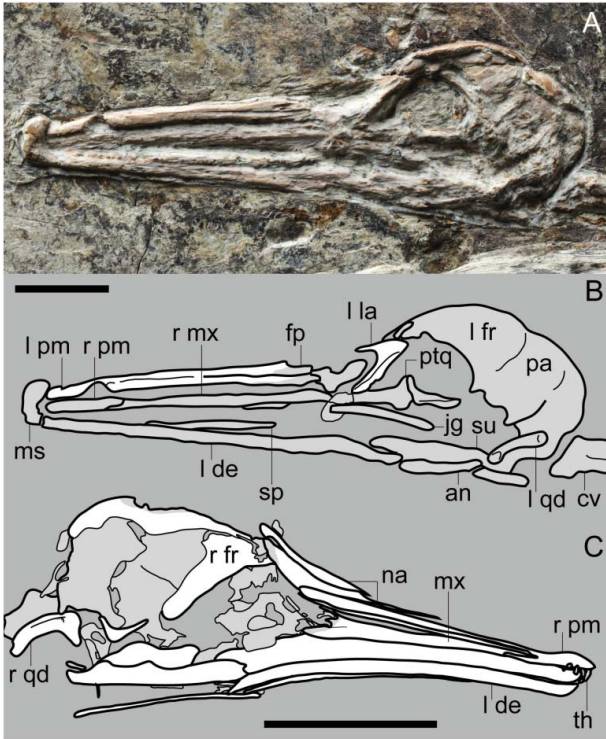
Figure 3. Maxillary elongation in Early Cretaceous ornithothoracines. **A, B,** *Dingavis longimaxilla* gen. et sp. nov., holotype, IVPP V20284; **A,** photograph; **B,** interpretative drawing. **C,** interpretative drawing of the skull of *Rapaxavis* (Enantiornithes) for comparison (modified from O'Connor *et al.* 2011). Anatomical abbreviations: an, angular; cv, cervical vertebrae; de, dentary; fp, frontal process; fr, frontal; jg, jugal; la, lacrimal; ms, mandibular symphysis; mx, maxilla; na, nasal; pa, parietal; pm, premaxilla; ptq, pterygoid − quadrate articulation?; qd, quadrate; sp, splenial; su, surangular; th, teeth; l and r represent left and right side, respectively. Scale bars = 10 mm.

than two-thirds the length of the mandible. Caudally the dentary is unforked, forming a caudoventrally sloping articulation with the surangular. The poorly preserved left angular is visible unfused to the surangular. The mandibular bones are usually preserved completely unfused in other basal ornithuromorphs. Two condylar structures preserved near the left mandibular joint are interpreted as the mandibular and otic processes of the left quadrate. A fragment of the left splenial is visible between the two dentaries in dorsal view; its preserved portion ends well caudal to the mandibular symphysis. Both the upper and lower jaws appear to be edentulous. Although patchy dark mineralization between the left dentary and splenial superficially resembles teeth, this mineralization is observed throughout the specimen.

Axial skeleton. At least eight cervical vertebrae are preserved in near articulation (Figs 1, 2). Some poorly preserved fragments underlying the proximal vertebra may represent the axis; the atlas is either not preserved or is

Table 1. Select measurements of the holotype of *Dingavis longimaxilla* gen. et sp. nov. (IVPP V20284) in mm. Parentheses indicate incomplete measurements.

	Right	Left
Skull length		58.64
Synsacrum	28.2	
Pygostyle	7.8	
Humerus	48.9	(51)
Ulna	(44.9)	(52)
Carpometacarpus	30.4	29.9
Alular metacarpal	4.1	(3.6)
Alular digit phalanx 1	12.4	12.5
Alular digit phalanx 2	4.9	5
Major digit phalanx 1	14	13.2
Major digit phalanx 2	13.2	13.2
Major digit phalanx 3	3.9	4
Minor digit phalanx 1	6.6	7.9
Scapula	38.4	(36.4)
Pubis	42.7	−
Femur	(16)	36.1
Tibiotarsus	55.6	55.4
Tarsometatarsus	37.9	40.6

overlain by the skull but could not be identified in the X-rays due to low resolution (Supplemental Figs 1, 2). The vertebrae are elongate, with their length more than twice exceeding their dorsoventral height in lateral view. The articular surfaces appear to be heterocoelic. A low neural spine can be observed in a vertebra caudal in the series. The thoracic vertebrae are mostly obscured by other elements. The synsacrum is fully fused with the neural spines, forming a spinal crest along the dorsal surface. Unfortunately, it is so well consolidated that in the absence of

Table 2. Comparative rostral lengths of Early Cretaceous Jehol ornithothoracines (referable to Ornithuromorpha unless otherwise specified). Measurements were taken from the holotype specimens with the exception of *Yanornis martini*, and all specimens were studied first hand with the exception of *Xinghaiornis lini* and *Gansus zheni*. Parentheses indicate estimated measurements.

	Skull length	Rostral length	Rostral % of skull
Dingavis	58.64	37	63
Yanornis martini STM9-51	57	32.7	57
Iteravis	(43−46)	26	57
Gansus zheni	46.3	26.5	57
Xinghaiornis lini	69.6	46.9	68
Longipteryx (Enantiornithes)	55	(35.6)	65
Longirostravis (Enantiornithes)	(33)	(25)	−
Rapaxavis (Enantiornithes)	31	18	59

preserved transverse processes it is impossible to estimate the number of fused vertebrae. However, the synsacrum is proportionately long, as in other ornithuromorphs. The caudal series is incompletely preserved; the pygostyle is preserved in lateral view revealing a slightly upturned, triangular profile, characteristic of early ornithuromorphs.

Thoracic girdle. Both scapulae are preserved; the left is in dorsolateral view and the right is dorsomedially exposed (Figs 1, 2). A well-developed acromion was clearly present, but its morphology cannot be clearly determined (acromion small in *Xinghaiornis*). It appears to be straight. The scapular blade is strongly curved and tapered as in other ornithuromorphs. The omal end of the right coracoid is visible near the proximal end of the right scapula. A fragment identified as the omal end of the right clavicular ramus is visible between the right scapula and humerus. It is delicate and tapered. Partially underlying the left ilium is a fragment we identify as the caudal part of the sternum including the left intermediate trabecula (Fig. 2). A more robust fragment preserved lateral to this piece may be part of the left lateral trabecula. Fragments ventral to the left scapula are probably also part of the sternum. Many rib fragments and several isolated gastralia are preserved ventral to these fragments, proximal to the left ilium.

Thoracic limb. Both humeri are in caudal view. The humeral shaft is twisted, clearly visible in the right element, which is well preserved compared to most other elements. The proximal articular surface is strongly convex proximocaudally. The capital incision is wide and very shallow. The region of the ventral tubercle lacks any signs of pneumaticity (excavated in some enantiornithines, pneumatopore in some Late Cretaceous enantiornithines and living birds). The deltopectoral crest is slightly less than shaft width (slightly greater than shaft width in *Xinghaiornis*) and extends for more than one-third the length of the humerus. Proximally, it is not continuous with the humeral head but separated by a slight concavity. This crest steadily decreases in width distally but ends rather abruptly. Distally, the olecranon fossa is well developed but whether muscle grooves were developed cannot be determined due to abrasion. The left ulna and radius are poorly preserved and the two elements overlap on the right. The ulna is proximally bowed as in other Early Cretaceous birds; it has a blunt olecranon process. The straight radius is fairly robust, being more than half the thickness of the ulna.

A single free carpal is preserved on the left, and two on the right; these preserve no anatomical information. The hand (carpometacarpus + major digit) is 25% longer than the humerus; in other Early Cretaceous ornithuromorphs the hand is typically subequal to the humerus (e.g. *Hongshanornis*, *Schizooura*, *Xinghaiornis*, *Yanornis*) or shorter (e.g. *Iteravis*, *Gansus*, *Piscivoravis*, *Zhongjianornis*). The humerus is approximately 10% shorter than the

hand in *Yixianornis*. Proximally the major and minor metacarpals are fully fused to the distal carpals. The major metacarpal is straight with an even thickness; the cranial margin is weakly concave. The minor metacarpal is slightly less than half (44%) the thickness of the major metacarpal. The minor metacarpal is completely straight (as in *Yixianornis*, *Gansus* and others), whereas it is distinctly bowed in some taxa (e.g. *Piscivoravis*). Distally, the minor metacarpal ends short of the major metacarpal. The distal ends of these two metacarpals are unfused. The alular metacarpal does not appear to be fully fused to the major metacarpal (fused on the left, slightly separated on the right). This element is also proportionately short, being only 13.7% of the total length of the carpometacarpus, whereas it is typically 20% or greater in other early ornithuromorphs (O'Connor & Sullivan 2014). Clearest on the left, the alular metacarpal has a moderate extensor process, also present in some Early Cretaceous ornithuromorphs (e.g. *Gansus*, *Hongshanornis*) but absent in others (e.g. *Archaeorhynchus*, *Piscivoravis*, *Schizooura*). As a consequence of the extensor process, the proximal margin of the carpal is concave, as in some basal ornithuromorphs and most living birds. The alular digit is composed of two phalanges; the first is slightly bowed, less than half the length of the carpometacarpus and roughly the same thickness as the minor metacarpal. The second phalanx is a weakly recurved ungual. The proximal two phalanges of the major digit are nearly equal in length, but the caudal margin of the first phalanx forms a dorsoventrally compressed keel-like expansion as in other ornithuromorphs. The caudal expansion is absent at the proximal end of the phalanx but rapidly expands, reaching maximum thickness by the proximal third and maintaining this thickness distally (expanded proximally in *Xinghaiornis*). The absence of this expansion proximally accommodates the phalanx of the minor digit, preserved in articulation on the right. A similar morphology is observed in *Iteravis*. The distal ungual phalanx is small and nearly straight. The minor digit preserves a single wedge-shaped phalanx that appears to include the second phalanx fused to it distally (preserved free in *Piscivoravis*) so that the distal end tapers sharply (e.g. *Iteravis*, *Hongshanornis*).

Pelvic girdle. The pelvic girdle is fairly complete but preserved largely in dorsal view with the elements dorsoventrally stacked over one and other obscuring some features (Figs 1, 2). In dorsal view the cranioventral margin of the ilium forms nearly a 90° angle that separates the convex rostral margin from the deeply concave lateral margin, as in many other Jehol ornithuromorphs (e.g. *Archaeorhynchus*, *Piscivoravis*, *Schizooura*, *Xinghaiornis*). Rostrally the preacetabular wing of the ilium is concave and appears to have been very wide, although this is exaggerated by compression. The postacetabular wing of the ilium is medially curved and tapered caudally. The

left ischium is preserved ventral and medial to the left ilium. A fragment of the distal end of the right is also preserved. The left ischium is medially curved so that it is laterally convex and medially concave. Medial curvature is observed in other ornithuromorphs preserved in partial dorsal view (e.g. *Piscivoravis*, *Schizooura*). It appears to have a low dorsal process located mid-corpus, as in most other ornithuromorphs (a distinct, pointed process appears to be unique to *Xinghaiornis*). The ventral surface is concave and the distal half is tapered. The pubes are preserved only slightly disarticulated, visible in the X-ray (Supplemental Fig. 1). The medially and dorsally curved pubes are distally unfused but would have contacted in vivo, as evidenced from the change in texture visible on the medial surface of the distal left pubis. The distal ends are expanded relative to the shaft, as in *Iteravis*, although they do not form a distinct boot like that present in some enantiornithines (e.g. *Pengornis*, *Longipteryx*).

Pelvic limb. The femur is short and straight, slightly shorter than the tarsometatarsus (femur much longer than tarsometatarsus in *Xinghaiornis*) and approximately 65% the length of the tibiotarsus (Table 1). The lateral surface of the left femur is smooth proximally, indicating the absence of a posterior trochanter, present in enantiornithine birds (Chiappe & Walker 2002). A weak fibular condyle appears to be present distally. The tibiotarsus bears a proximocranially projecting cnemial crest and a short fibular crest. Distally, in cranial view, a well-developed extensor sulcus is visible on the left. On the right in caudal view the tibial cartilaginous trochlea is well developed but is distally limited in its extension up the cranial surface, similar to other basal ornithuromorphs (e.g. *Piscivoravis*). The fibula is short, fat and rapidly tapered distally.

The left tarsometatarsus is preserved in dorsal view, whereas the right is in plantar view. The tarsometatarsus is fully fused, although the presence of shallow grooves allows identification of the individual metatarsals; these grooves may represent a rudimentary flexor sulcus. Metatarsal III is the longest, followed by metatarsal IV; metatarsal II ends short of the metatarsal IV trochlea. A fairly robust tubercle for the m. tibialis cranialis is present on the dorsomedial surface of metatarsal III, just below the proximal articular surface where this metatarsal is plantarly displaced, as in other ornithuromorphs. This tubercle is well developed in enantiornithines whereas it is typically more delicate in ornithuromorphs (e.g. *Apsaravis*, *Hongshanornis*) or not developed at all (e.g. *Piscivoravis*); the tubercle in *Dingavis* is well developed compared to other ornithuromorphs. As in other basal ornithuromorphs, no hypotarsus is present. Very low but distinct medial and lateral plantar crests are present, as in *Gansus* (Y.-M. Wang *et al.* 2015), but the plantar surface is not deeply excavated as in *Xinghaiornis*. The metatarsal III trochlea is the widest. The trochlea of metatarsals II and

IV are preserved plantarly displaced relative to metatarsal III. A vascular foramen is present between metatarsals III and IV, visible on the left. The trochlea of metatarsal II appears to be strongly angled, similar to *Piscivoravis*. The lateral condyle of the metatarsal IV trochlea, excavated by a deep collateral pit, projects farther plantarly than the medial condyle, also observed in *Apsaravis*. The right metatarsal I is preserved nearly in articulation (Figs 1, 2). It is short (12% of metatarsal II) and articulates with the plantar surface of metatarsal II so that the hallux was fully reversed. It is also slightly twisted so that the surface between the two articulations is concave. The shaft is sharply tapered proximally; the trochlea is mediolaterally wide. The pedal phalangeal formula is 2-3-4-5-x. The two phalanges of the first digit are subequal in length. The pedal phalanges in the other digits decrease in length distally. The proximal phalanx of the third digit is the longest and most robust in the foot. The total length of the third digit is less than that of the tarsometatarsus, as in *Changmaornis* (longer in *Gansus*) (Y.-M. Wang *et al.* 2013). The pedal unguals are all small, subequal, with very little curvature. This foot morphology strongly resembles that of *Changmaornis* from the Xiagou Formation (Y.-M. Wang *et al.* 2013, 2015).

Gastroliths. Approximately 40 gastroliths are visible in the region of the pelvic girdle. Additional stones are scattered about the slab. These stones are fairly large (2−4 mm), smooth and moderately polished. We interpret these as gizzard stones underlying the pelvic region. The delicate overlying bone is crushed and broken, revealing the underlying stones. These gastroliths are similar in size, morphology and mineralogy to those preserved in specimens of *Iteravis* and *Gansus* (S. Zhou *et al.* 2014; Y.-M. Wang *et al.* 2015) but are more numerous in IVPP V20284, potentially indicating slight dietary differences. Alternatively, the gastroliths in specimens of *Iteravis* and *Gansus* may represent incomplete aggregates.

Phylogenetic analysis

In order to confirm our morphological inferences, we placed IVPP V2084 in an expanded version of the O'Connor & Zhou (2013) Mesozoic bird matrix (see Supplemental material). The data set has been modified to include only *Jeholornis* (other taxa considered junior synonyms of this taxon) and exclude the probable scansoriopterygid *Zhongornis*. Recently described ornithuromorphs were also included (*Archaeornithura*, *Iteravis*, *Schizooura*). Although very little information is available we also added *Xinghaiornis*, the first analysis to include this important taxon (X.-R. Wang *et al.* 2013). The modified matrix consists of 61 taxa, 30 of which are considered ornithuromorphs. We analysed the data using the TNT software
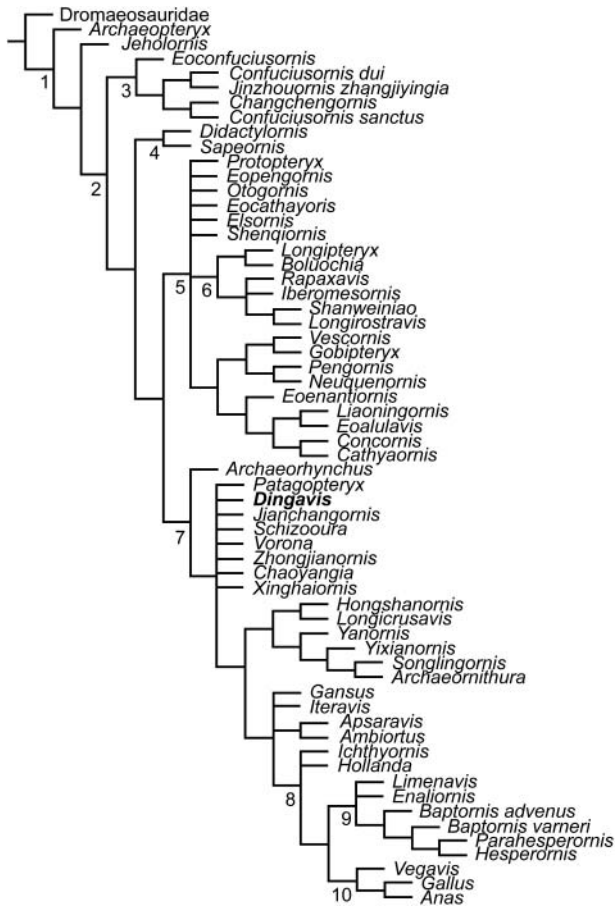
Figure 4. Hypothetical phylogenetic relationships of Mesozoic birds (trees = 860, length = 889 steps). Nodes: 1, Aves; 2, Pygostylia; 3, Confuciusornithiformes; 4, Sapeornithiformes; 5, Enantiornithes; 6, Longipterygidae; 7, Ornithuromorpha; 8, Ornithurae; 9, Hesperornithiformes; 10, Neornithes.

(Goloboff *et al.* 2008). We conducted a heuristic search using tree bisection reconnection (TBR), retaining the single shortest tree out of every 1000 replications. This produced three most parsimonious trees with a length of 889 steps. A second round of TBR produced a total of 860 most parsimonious trees of the same length. In the strict consensus tree (Fig. 4), *Dingavis* is part of a basal polytomy of taxa more derived than *Archaeorhynchus*, which includes *Patagopteryx*, *Jianchangornis*, *Zhongjianornis*, *Schizooura*, *Xinghaiornis*, *Vorona* and *Chaoyangia*. This tree is only weakly supported, with a consistency index of 0.374 and a retention index of 0.651. Bremer support values are also very low indicating that the current topology would largely collapse in trees a single step longer.

Discussion

The new specimen IVPP V20284 can be assigned to the Ornithuromorpha on the basis of the curved scapula,

plough-shaped pygostyle, globose humeral head, caudally expanded first phalanx of the major digit, proximally projecting cnemial crest on the tibiotarsus and well-fused tarsometatarsus. IVPP V20284 can be distinguished from other known taxa by its elongate rostrum and maxilla, hand that is 25% longer than the humerus and proportionately short alular metacarpal; thus, we erect the new taxon *Dingavis longimaxilla* gen. et sp. nov. Previously, all bird specimens from the newly discovered Sihedang locality appeared to be referable to a single taxon, *Iteravis huchzermeyeri* (S. Zhou *et al.* 2014). However, as discoveries continued, additional ornithuromorph diversity has surfaced (Liu *et al.* 2014). These authors described three new specimens they assigned to a new species of *Gansus*, *G. zheni*. Although we do not consider these specimens to be referable to *Gansus*, previously only known from the Xiagou Formation (You *et al.* 2006), we also recognize minor differences that suggest they are not referable to *Iteravis huchzermeyeri*. The discovery of the edentulous *Dingavis* provides evidence of greater trophic diversity in the Sihedang avifauna. Furthermore, similarities in preservation (bones somewhat three dimensional, colour of the fossilized bone and similar lithology of the slab) suggest that the holotype of *Xinghaiornis lini* may also be from Sihedang rather than the Sihetun locality, as reported (Z.-H. Zhou pers. comm.). A study of the histology in the holotype of *Iteravis huchzermeyeri* has suggested the three-dimensional preservation of Sihedang specimens is taphonomic, not due to the presence of medullary bone (O'Connor *et al.* 2015). This increased taxonomic diversity (potentially as many as four ornithuromorph species) further weakens hypotheses that the Sihedang locality may represent a breeding site of *Iteravis* (S. Zhou *et al.* 2014).

Rostralization in Early Cretaceous birds

In Aves, the plesiomorphic skull is characterized by small premaxillae and mesorostrine proportions. In neornithines, the premaxilla is expanded and forms a majority of the rostrum in all taxa, whereas the maxilla is greatly reduced. Expansion of the premaxilla is a derived feature within Aves that evolved outside Neornithes, present in Late Cretaceous ornithurine *Hesperornis* (Marsh 1880). Varying degrees of premaxillary expansion also evolved in parallel in the Early Cretaceous Confuciusornithiformes and in at least one lineage of enantiornithines, present in the Late Cretaceous *Gobipteryx* (Elzanowski 1977; Chiappe *et al.* 2001).

In contrast, rostral elongation in *Dingavis* and the Early Cretaceous longipterygid enantiornithines was achieved primarily by lengthening the maxilla (e.g. *Rapaxavis*, *Longipteryx*, *Longirostravis*) (Fig. 3C) − an extinct morphotype within Aves. Notably, the premaxillary corpus is also somewhat elongated in these taxa relative to the

plesiomorphic condition (O'Connor & Chiappe 2011). The upper limit in rostral elongation in both lineages is approximately equal (*Longipteryx* 65%; *Dingavis* 63−65%). This could be merely coincidence or it may suggest that there are structural limitations to elongating the rostrum through the maxilla that do not permit truly longirostrine proportions (>70% skull length). This may ultimately have led this structural organization to be abandoned during avian evolution. Notably, if limitations existed in the construction of the avian skull, no such structural limitations are present in the Pterosauria. This clade includes taxa with rostral elongation achieved through both the premaxilla (e.g. *Pteranodon*, *Tropeognathus*) and maxilla (e.g. *Gnathosaurus*, *Zhenyuanopterus*) (Witton 2013) and also reached extremes of rostralization even greater than observed in Aves (Marugán-Lobón & Buscalioni 2003). We suggest this may be due to differences in the articulation between the premaxilla and the maxilla in pterosaurs (extensive contact between the bones) and birds (short articulation between fairly delicate processes), the former affording greater structural stability.

The longest rostrum in an Early Cretaceous bird is observed in *Xinghaiornis* (X.-R. Wang *et al.* 2013). This taxon shows yet another skull configuration in which the premaxilla and maxilla contribute equally to the facial margin. In Xinghaiornis both the premaxilla and the maxilla are elongated but the premaxilla significantly more so than the maxilla, which plesiomorphically is much more elongate than the premaxilla. Although *Xinghaiornis* is not truly longirostrine in proportions, the presence of premaxillary elongation probably allowed this lineage to achieve a greater degree of rostralization than any other in the Early Cretaceous. *Xinghaiornis* and *Dingavis* are both from the Yixian Formation, probably both from the Sihedang locality, and both fall in the polytomy of basal ornithuromorphs only more derived than *Archaeorhynchus* (Fig. 4). Differences in the rostral configuration of these two sympatric taxa highlight the diversity of skull configurations present in early birds as they diversified into new niches and evolved rostral modifications to suit a variety of trophic habitats. Although parallel diversity evolved in the Neornithes, this was achieved primarily through modifications to the premaxilla, whereas basal birds show a greater diversity of configurations but within a more limited morphospace. *Dingavis*, *Xinghaiornis* and the longipterygids thus represent early avian experiments in skull rostralization.

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Supplemental data

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