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A New Sapeornithid Bird from China and Its Implication for Early Avian Evolution

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Abstract: Recent discoveries of basal birds have greatly improved our understanding of early bird evolution, yet the evolution of several important features such as cranial kinesis and arboreality remain debated. A new sapeornithid bird, *Shenshiornis primita* gen. et sp. nov., based on an articulated skeleton from the Early Cretaceous Jehol Group of western Liaoning, China, sheds new light on these issues. *Shenshiornis* possesses a skull as primitive as or even more primitive than that of *Archaeopteryx* and hind limbs modified for an improved arboreal capability. A cladistic analysis shows that: 1) presence of a diapsid skull is a plesiomorphy of the Aves and a kinetic skull evolved incrementally later in avian evolution; and 2) cursorial capability significantly weakens at the base of the Pygostylia due to a change in locomotor system.

Key words: basal bird, Cranial kinetism, locomotor systems, sapeornithid, *Shenshiornis primita*, Early Cretaceous, Liaoning

1 Introduction

The Late Jurassic *Archaeopteryx* has formed the core of our understanding of the earliest avian evolution (Chiappe, 1995) until recent discoveries of a number of basal birds (Zhou, 2004; Ji et al., 2002a,b; Forster et al., 1998). We report here a new sapeornithid bird from the Jehol Group, western Liaoning, China, which has a combination of both primitive and derived features and adds significant new information on the earliest avian evolution.

2 Material and Methods

The specimen was found from the lacustrine deposits of the Yuanjiawa Bed of the Lower Cretaceous Jiufotang Formation, Dapingfang Town, western Liaoning in 2005 by the expedition team of the Shenyang Normal University (Fig. 1) and is housed at Liaoning Paleontology Museum, Shenyang Normal University, Shenyang, Liaoning province (prefix LPM).

The data matrix (see supporting information (SI)) for phylogenetic analysis was based on a recently published dataset for basal bird phylogeny (Chiappe, 2002) and was analyzed using the NONA (ver. 2.0) software package (Goloboff, 1993), and formatting and character exploration were performed in WinClada (Nixon, 1999). The analysis protocol consisted of 1000 Tree Bisection and Regrafting tree searches followed by branch swapping. Settings included collapsing unsupported branches and counting all states in polymorphic coding. Other settings followed Chiappe (2002).

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3 Systematic Paleontology

Aves Linnaeus, 1758
Sapeornithiformes Zhou et Zhang, 2006
Sapeornithidae Zhou et Zhang, 2006
Shenshiornis gen. nov.

Etymology: *Shenshi*, the Chinese abbreviation for Shenyang Normal University; *ornis*, the Greek term for bird.

Diagnosis: as for only species (see below).

Type and only Species: *Shenshiornis primita* gen. et sp. nov.

Shenshiornis primita gen. et sp. nov.
(Figs. 2–4)

Etymology: the specific name is derived from the primitive nature of the animal.

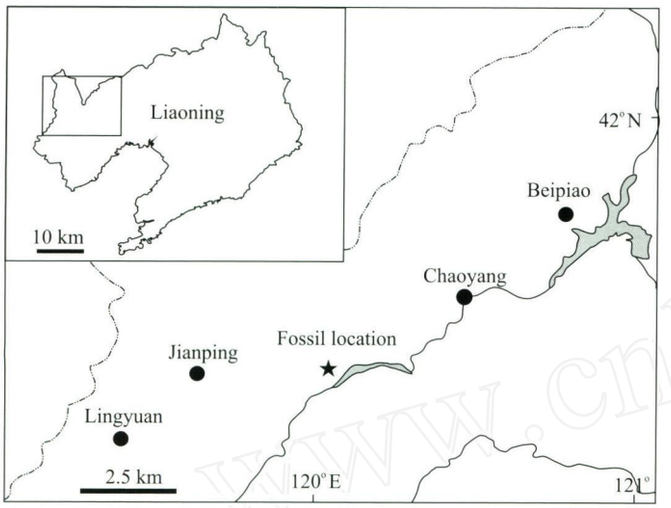

Fig. 1. Geographic position of Dapingfang fossil location in western Liaoning, China.

Holotype: LPM B00018 is an articulated skeleton missing the pectoral girdle and forelimb (Fig. 2).

Type locality and horizon: Dapingfang, Chaoyang, western Liaoning, China; Yuanjiawa Bed of the Lower Cretaceous Jiufotang Formation; lacustrine deposits. (Swisher et al., 1999).

Diagnosis: A small sapeornithid with a small pre-naris portion of the premaxilla; a long maxillary process of the premaxilla; premaxillary and maxillary teeth present but dentary teeth absent; and a prominent tuberosity at the posterior end of the ilium. Sub-triangular tooth crowns wider than the corresponding tooth root. Amphicoelous cervical vertebrae, with elongate postzygapophyseal processes of the middle and posterior cervicals reaching to the mid-length of the succeeding vertebra; seven sacral vertebrae; and more than 10 free caudal vertebrae. Pelvis with an anteriorly tapered preacetabular process of the ilium; short pubis about 95% of the femur. Foot with elongate metatarsal I and V about 30% and 40% of metatarsus length, respectively.

Description and comparison: The holotype of *Shenshiornis primita* has a skull of about 40 mm long and about 25 mm tall at the postorbital region (Fig. 3). Similar to non-avian theropods (Xu, 2002; Chatterjee, 1997) and some basal birds such as *Jeholornis* (Zhou and Zhang, 2002; Ji et al., 2002a, b) and other sapeornithids (Zhou and Zhang, 2003; Yuan, 2008; Provini et al., 2009), the snout is blunt in lateral view, which is caused by the short pre-orbital region (about half skull length) and the relatively tall premaxilla with a large premaxillary angle (about 70 degrees). As in most non-avian theropods, the premaxilla has a small pre-naris portion, a relatively short nasal process (extending only slightly posterior to the external naris), and a long maxillary process contacting the robust maxillary process of the nasal to exclude the maxilla from the external naris (Xu, 2002; Sereno, 1999). Similar to *Jeholornis* (Zhou and Zhang, 2002; Ji et al., 2002a, b) and to a lesser degree some dromaeosaurids (Barsbold and Osmólska, 1999; Xu and Wu, 2001), there is a muzzle-like area anterior to the orbit. The maxilla has a relatively small ascending process, which contributes only to the anterior border of the antorbital cavity. The large nasal is slightly longer than the frontal and forms the dorsal margin of the antorbital cavity, which is significantly smaller than the orbit. The jugal has a strap-like suborbital ramus and a robust ascending process contacting the postorbital to form a complete postorbital bar. The quadratojugal is a slender, rod-like element, forming the ventral border of a large lower temporal fenestra.

The mandible is about 40 mm long, robust and subequal in depth for the whole length, as in *Jeholornis* and confuciusornithids (Chiappe, et al., 1999). The mandibular symphysial facet is flat and relatively small. The dorsoventrally deep dentary is slightly upturned anteriorly, has sub-parallel dorsal and ventral margins, and is bifurcated posteriorly. The lateral surface is covered by two rows of 6-8 foramina, the ventral row of which is less distinct.

The dentition is represented by four premaxillary teeth and three maxillary teeth per side. They become smaller in size posteriorly along the tooth row, ranging in the height of the tooth crown from about 2 mm to 1 mm. Unlike some basal birds where the posterior premaxillary teeth are positioned anterior to the external naris (Xu, 2002), those in *Shenshiornis primita* are located under the external naris as in non-avian theropods (Fig. 3). In lateral view, the tooth crowns are wider than the corresponding root, are sub-triangular in outline and posteriorly inclined, about as wide as tall, are labially bulbous at the base, and have not any ornament, carinae, and serrations (Fig. 4a); the cross-section of the tooth crowns seems to be sub-round.

The cervical centra are about twice as long as tall and the cervical neural spines are low. The postzygapophyses of the middle and posterior cervical vertebrae are long and robust, reaching to the mid-length of the succeeding vertebra (Fig. 4b). The dorsal vertebrae lack large pneumatic openings on the lateral surfaces of the centra, although deep lateral depressions are present. Probably 22 presacral vertebrae are present. They have either amphicoelous or amphiplatyan centra. There appears to be seven vertebrae incompletely fused at the sacral region.

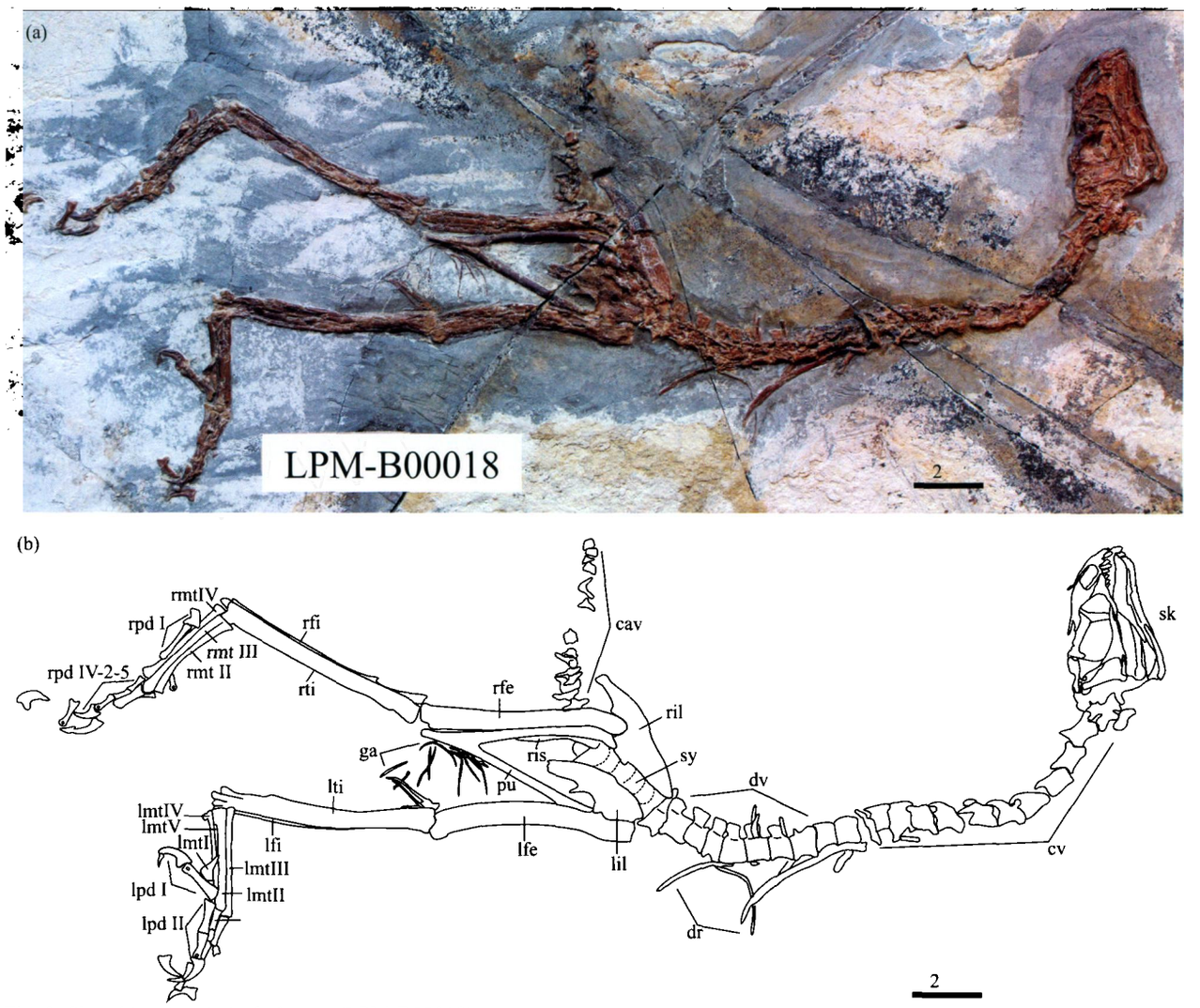

Fig. 2. *Shenshiornis primita* holotype (LPM-B00018).
(a) photograph and (b) line-drawing. Abbreviations: cav, caudal vertebra; cv, cervical vertebra; dr, dorsal rib; dv, dorsal vertebra; ga, gastralia; lfe, left femur; lfi, left fibula; lil, left ilium; lpdI-II, left pedal digit I-II; lti, left tibiotarsus; lmtI-V, left metatarsus I-V; pu, pubis; rfe, right femur; rfi, right fibula; ril, right ilium; ris, right ischium; rpdI, right pedal digit I; rpdIV2-5, second through firth phalanges of the right pedal digit IV; rmtII-IV, right metatarsus II-IV; rti, right tibiotarsus; sk, skull; sy, synsacrum. Scale bar = 20 mm.

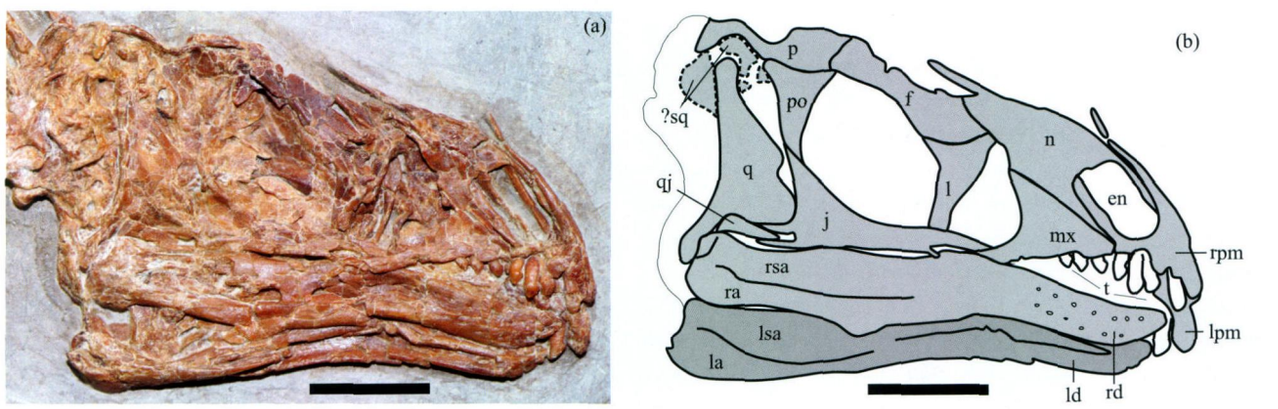

Fig. 3. Skull of *Shenshiornis primita* holotype (LPM-B00018) in right lateral view.
(a) close-up photograph and (b) line-drawing. Abbreviations: en, external nares; f, frontal; j, jugal; l, lacrimal; la, left angular; ld, left dentary; lsa, left surangular; mx, maxilla; n, nasal; p, parietal; po, postorbital; q, quadrate; qj, quadratojugal; ra, right angular; rd, right dentary; rpm, right premaxilla; rsa, right surangular; sq, squamosal; t, tooth. Scale bar = 10 mm.

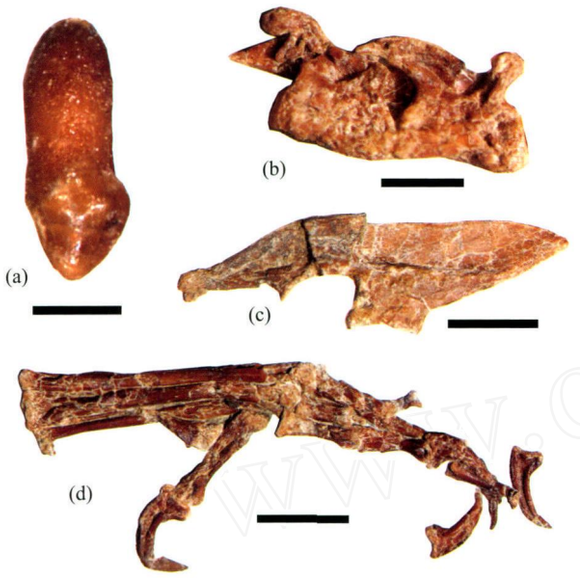

Fig. 4. *Shenshiornis primita* holotype: close-up photos of several skeletal elements of LPM-B00018.
(a) a premaxillary tooth in labial view; (b) two middle cervicals in right lateral view; (c) right ilium in lateral view; (d) left pes in mediocranial view. Scale bar = 1 mm for (a), 5 mm for (b), and 10 mm for (c) and (d).

Shenshiornis primita is distinguishable from *Didactylornis jii* (Yuan, 2008) and *Sapeornis angustis* (Provini,, 2009) in having seven sacral vertebrae, the latter two taxa having six sacral vertebrae. More than ten free caudal vertebrae are present, but whether a pygostyle is present or not is uncertain.

The ilium at 44 mm is much shorter than the femur (about two-thirds femoral length), as in basal deinonychosaurs and basal birds (Xu, 2002). Also as in other basal birds, *Shenshiornis primita* has a much longer and deeper preacetabular process relative to the posterior one (about 1.7 times), and a much wider and deeper pubic peduncle relative to the ischial peduncle. However, the preacetabular process of the ilium is shallow and anteriorly tapered (Fig. 4c) rather than deep and lobe-shaped as in other birds (Chiappe, 1996). A prominent tuberosity is present at the posterior end of the ilium (Fig. 4c), a feature also seen in *Sapeornis chaoyangensis* (Zhou and Zhang, 2003). The pubis at about 57 mm is slightly shorter than the femur. It has a rod-like shaft and a short pubic symphysis (about one-third of the pubic length) and lacks a pubic foot. The ischium is about half of the pubic length.

The hind limb is not cursorial in design. The tibiotarsus at about 65 mm and the metatarsus at about 32 mm are about 105% and 50% the femoral length, respectively, proportionally considerably shorter than those of small non-avian coelurosaurs and most birds (Gatesy, 1991; Christiansen and Bonde, 2002). The fibula reaches to the calcaneum and its distal end is slightly expanded. The pes shows many features seen in arboreal birds (Bock and Miller, 1959; Zhou and Farlow, 2001; Hopson, 2001): the reversed first pedal digit is long and robust, with a strongly expanded distal end of metatarsal I comparable in size to that of other metatarsals; a phalanx I-1 longer than other non-ungual pedal phalanges; and a I-2 considerably larger than other unguals; the penultimate phalanges are as long as or longer than the more proximal phalanges; all unguals are strongly curved and proportionally large relative to non-ungual phalanges (Fig. 4d).

4 Discussion

The specimen LPM B00018 is probably sub-adult based on the following fusion features: neurocentral sutures on all presacral vertebrae are closed; the sacrals are fused although the sutures are visible; the cervical ribs are not fused to the corresponding centra; and the absence of the fusion of the proximal ends of the metatarsals.

Our phylogenetic analysis (See SI) posits *Shenshiornis primita* as the sister taxon of *Sapeornis chaoyangensis*, forming a monophyletic Sapeornithidae (Zhou and Zhang, 2006) at the base of the Pygostylia (Fig. 5). *Shenshiornis*

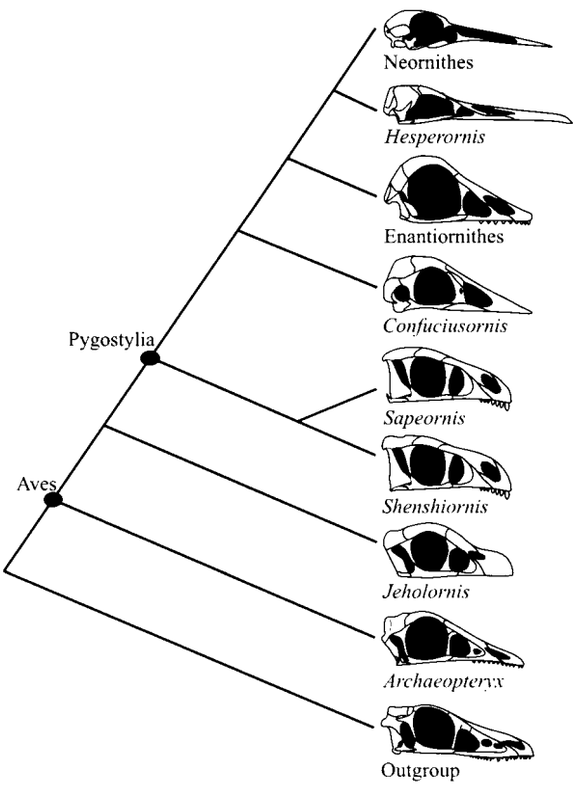

Fig. 5. A simplified tree from SI Fig. 1 showing the systematic position of *Shenshiornis primita* and the evolution of a streamlined and kinetic skull in the Aves.

primita and *Sapeornis chaoyangensis* share numerous derived similarities, such as the unusual dentition (premaxillary and maxillary teeth present but dentary teeth absent) and a prominent rugosity on the lateral surface of the posterior extremity of the ilium (Zhou and Zhang, 2003).

As the basalmost pygostylians, sapeornithids display a combination of primitive cranial and relatively derived postcranial characters bearing on the early avian evolution. Derived birds possess a streamlined and kinetic skull in contrast to a blunt and akinetic skull as in non-avian theropods (Chatterjee, 1997). Previously only confuciusornithids among the Aves have been confirmed to possess a diapsid skull, but it is not known whether it is primitive for Aves or represents a secondary modification for confuciusornithids. This is mainly because the distribution of this character in basal birds is not clear. As in *Confuciusornis* (Chiappe et al., 1999; Hou et al., 1999) and non-avian theropods (Chatterjee, 1997), sapeornithids retain a postorbital bar and an intertemporal bar, suggesting that the diapsid condition has a wide distribution among basal Aves (Peters and Ji, 1998). Cranial kinetism in modern birds mainly resulted from three cranial modifications: the loss of the quadratojugal-squamosal contact, the loss of the postorbital bar, and the disappearance of the ectopterygoid. It is generally accepted that basal paravians including basal birds have the ectopterygoid bone but lack the quadratojugal-squamosal contact, but whether the postorbital bar is lost or not is debated (Xu, 2002; Chiappe et al., 1999; Hou et al., 1999; Chiappe et al., 1998). The proposed evidence for the loss of the postorbital bar includes a postorbital bone not seen in many basal paravians including *Archaeopteryx* specimens as well as the postorbital process of the jugal being small and located considerably posteriorly (Chiappe et al., 1999). However, absence of a postorbital bone in these specimens could be a preservational artifact as the postorbital bone is loosely connected to the skull in maniraptoran dinosaurs and is very likely to be lost during the preservational process. This inference is supported by a recently discovered basal troodontid specimen from the earliest Late Jurassic Tiaojishan Formation of Liaoning, China (Hu et al., 2009) in which a postorbital bone is found to have a long and slender descending process contacting the small and posteriorly located ascending process of the jugal, although in all other known specimens the postorbital bone is not preserved. This suggests that the presence of a postorbital bar might characterize all basal birds, though a lack of squamosal-quadratojugal connection, a feature seen in basal birds and some non-avian theropods (Xu, 2002; Chiappe et al., 1998; Xu and Norell, 2004), indicates an initial development of a kinetic skull in early paravian evolution. Interestingly, sapeornithids have a relatively blunt snout, a feature similar to non-avian theropods and *Jeholornis*; sapeornithids and *Jeholornis* also have a muzzle-like area anterior to the orbit, making an even less streamlined skull (Fig. 5). Character optimization shows that basal birds retain the primitive non-avian theropod skull design and a streamlined and kinetic skull evolved later in avian evolution. *Hesperornis* is the most basal bird which can be confirmed to possess a modern type of skull kinesis (prokinesis) (Bühler et al., 1988) and shows an extremely streamlined skull (Fig. 5).

Contrary to the primitive cranial morphology, the postcranial skeleton is relatively derived in sapeornithids. The extremely elongate forelimb suggests that sapeornithids have a powerful flight capability (Zhou and Zhang, 2003), and the highly modified pes indicates an improved arboreal capability. There are debates about whether some basal birds are predominantly arboreal because these birds have a combination of characters indicating both an arboreal and ground lifestyle (Xu, 2002). As one of the major characters used to infer an arboreal life style, a fully reversed hallux was recently suggested to be absent in basalmost birds such as *Archaeopteryx* (Mayr et al., 2005) and *Jeholornis* (Zhou and Zhang, 2006). Character optimization shows that a fully reversed hallux, a long pedal digit I, proportionally long penultimate pedal phalanges, and a number of other skeletal modifications including a pygostyle occur at the base of the Pygostylia, suggesting a significant change in locomotor system and lifestyle from more basal birds (Xu, 2002; Xu et al., 2000). Interestingly, an unusual shortening of the tibiotarsus relative to the femur also occurs at the base of the Pygostylia, which is not consistent with an evolutionary trend of the tibiotarsus-elongation relative to the femur in theropod evolution (Gatesy, 1991; Christiansen and Bonde, 2002). Previous statistic analyses (Christiansen and Bonde, 2002; Jones et al., 2000) show that birds, especially derived birds, have a more elongated tibiotarsus relative to the femur than theropods, suggesting that the tibia-elongation-evolutionary trend continues into the Aves from theropods. However, recent discoveries of some basal birds show clearly that the tibiotarsus of these specimens (Zhou and Zhang, 2003; Chiappe et al., 1999; Zhang et al., 2000) is proportionally significantly shorter than that of small non-avian coelurosaurs, basalmost birds, and also of more derived birds (Christiansen and Bonde, 2002). The significant shortening of the tibiotarsus in these basal birds indicates a reduced cursorial capability, which we interpret as either due to a substantial improvement of flight capability or shifting to arboreal lifestyle at the base of the Pygostylia. The presumed

strong flight capability (Zhou and Zhang, 2003) and still-elongated tibiotarsus in *Jeholornis* appear to be against the former interpretation and thus the shortening of the tibiotarsus, co-evolving with a number of pedal features related to arboreality, is more likely to be an adaptation to an arboreal lifestyle.

5 Conclusions

Shenshiornis primita gen. et sp. nov. from the Lower Cretaceous Jiufotang Formation of Liaoning is a basal bird that differs from all other birds except for sapeornithids. The skull is different from other known sapeornithids in the following features: sub-triangular tooth crowns wider than the corresponding tooth root; amphicoelous cervical vertebrae, with elongate postzygapophyseal processes of the middle and posterior cervicals reaching to the mid-length of the succeeding vertebra; more than 10 free caudal vertebrae; an anteriorly tapered preacetabular process of the ilium; a short pubis about 95% of the femur; and long metatarsals I and V about 30% and 40% of the metatarsus length, respectively. The new taxon is distinguishable from *Didactylornis jii* and *Sapeornis angustis* in having seven sacral vertebrae rather than six).

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Supporting Information

1 Cladistic analysis

Character list: Characters are derived from a recently published dataset for basal bird phylogeny (Chiappe, 2002) and characters 170-179 are newly added.

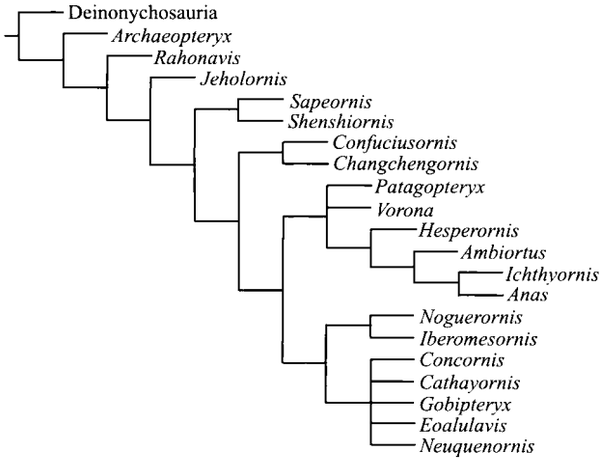
1	Rostral portion of the premaxillae in adults: unfused (0); fused (1)
2	Maxillary process of the premaxilla: restricted to its rostral portion (0); subequal or longer than the facial contribution of the maxilla (1).
3	Frontal process of the premaxilla: short (0); relatively long, approaching the rostral border of the antorbital fenestra (1); very long, extending caudally near the level of lacrimals (2).
4	Premaxillary teeth: present (0); absent (1).
5	Maxilla: toothed (0); toothless (1) (modified)
6	C audal margin of naris: farther rostral than the rostral border of the antorbital fossa (0); nearly reaching or overlapping the rostral border of the antorbital fossa (1).
7	Dorsal ramus of the maxillary nasal process: present (0); absent (1)
8	Cup-shaped caudal maxillary sinus: absent (0); present (1).
9	Rostral margin of the jugal: away from the caudal margin of the osseous external naris (0), or very close to the caudal margin of the osseous external naris (1).
10	Jugal process of palatine: present (0); absent (1).
11	Ectopterygoid: present (0); absent (1).
12	Squamosal incorporated into the braincase, forming a zygomatic process: absent (0); present (1).
13	Postorbital: present (0); absent (1).
14	Postorbital-jugal contact: present (0); absent (1).
15	Quadratojugal: sutured to the quadrate (0); joined through a ligamentary articulation (1).
16	Quadratojugal-squamosal contact: present (0); absent (1).
17	Lateral, round cotyla on the mandibular process of the quadrate (quadratojugal articulation): absent (0); present (1).
18	Quadrate orbital process (pterygoid ramus): broad (0); sharp and pointed (1).
19	Quadrate pneumaticity: absent (0); present (1).
20	Quadrate: articulating only with the squamosal (0); articulating with both prootic and squamosal (1).
21	Quadrate distal end: with two transversely aligned condyles (0); with a triangular, condylar pattern, usually composed of three distinct condyles (1).
22	Caudal tympanic recess: opens on the rostral margin of the paraoccipital process (0); opens into the columellar recess (1).
23	Basicranial fontanelle on the ventral surface of the basisphenoid (basisphenoid recess): present (0); absent (1).
24	Deeply notched rostral end of the mandibular symphysis: absent (0); present (1).
25	Coronoid bone: present (0); absent (1).
26	Articular pneumaticity: absent (0); present (1).
27	Dentary tooth implantation: teeth in individual sockets (0); teeth in a communal groove (1).
28	Teeth: serrated crowns (0); unserrated crowns (1).
29	Atlantal hemiarches: unfused (0); fused, forming a single arch (1).
30	One or more pneumatic foramina piercing the centra of midcranial cervicals, caudal to the level of the parapophysis-diapophysis: present (0); sbsent (1).
31	Cranial cervical vertebrae heterocoelous: absent (0); present (1).
32	Promin ent carotid processes in the intermediate cervicals: absent (0); present (1).
33	Postaxial cervical epipophyses: prominent, projecting farther back from the postzygapophysis (0); weak, not projecting farther back from the postzygapophysis, or absent (1).
34	Prominent (50% or more the height of the centrum's cranial articular surface) ventral processes of the cervicothoracic vertebrae: absent (0); present (1).
35	Cervicothoracic vertebrae with parapophyses located at the same level as the prezygapophyses: absent (0); present (1).
36	Thoracic vertebral count: 13-14 (0); 11-12 (1); fewer than 11 (2).
37	Wide vertebral foramen in the midcaudal thoracic vertebrae, vertebral foramen/articular cranial surface ratio (vertical diameter) larger than 0.40: absent (0); present (1).
38	Hyposphene-hypantrum accessory intervertebral articulations in the thoracic vertebrae: present (0);absent(1).
39	Lateral side of the thoracic centra: weakly or not excavated (0); deeply excavated by a groove (1); excavated by a broad fossa (2).
40	Parapophyses: located in the cranial part of the centra of the thoracic vertebrae (0); located in the central part of the thoracic vertebrae (1).
41	Synsacrum: formed by fewer than eight vertebrae (0); eight or more vertebrae (1).
42	Synsacrum procoelous: absent (0); present (1).
43	Caudal portion of the synsacrum forming a prominent ventral keel: absent (0); present (1).
44	Convex caudal articular surface of the synsacrum: absent (0); present (1).
45	Caudal vertebra prezygapophyses: present (0); absent(1).
46	Distal caudal vertebra prezygapophyses: elongate, exceeding the length of the centrum by more than 25%(0); shorter (1).
47	Procoelous caudals: absent (0); present (1).
48	First caudal with a ventrally sharp centrum: absent (0); present (1).
49	Proximal haemal arches: elongate, at least three times longer than wider (0); shorter (1); absent (2).
50	Pygostyle: absent or rudimentary (fewer than three elements) (0); present (1).
51	Pygostyle: longer than of equal to the combined length of the free caudals (0); shorter (1).
52	Caudal vertebral count: more than 35 (0); fewer than 25-26 (1); fewer than 15 (2).
53	Ossified uncinate processes: absent (0); present (1).
54	Coracoid and scapula: articulate through a wide, sutured articulation (0); articulate through more localized facets (1).
55	Scapula: articulated at the shoulder (proximal) end of the coracoid (0); well below it (1).
56	Humeral articular facets of the coracoid and the scapula: placed in the same plane (0); forming a sharp angle (1).
57	Procoracoid process on coracoid: absent (0); presen (1).
58	Coracoid shape: short (0); elongated with trapezoidal profile (1); strutlike (2).
59	Distinctly convex lateral margin of coracoid: absent (0); present (1).
60	Bicipital tubercle (=acrocoracoidal process): present (0); or absent (1).

61 Supracoracoidal nerve foramen of coracoid: centrally located (0); displaced toward (often as an incisure or even without passing through) the medial margin of the coracoid (1).
62 Supracoracoidal nerve foramen opening into an elongate furrow medially and separated from the medial margin of the coracoid by a thick, bony bar: absent (0); present (1).
63 Broad, deep fossa on the dorsal surface of the coracoid: absent (0); present (1).
64 Sternocoracoidal process on the sternal half of the coracoid: absent (0); present (1).
65 Scapular caudal end: blunt and usually expanded (0); tapered to a sharp point (1).
66 Scapular shaft: straight (0); sagittally curved (1).
67 Prominent acromion in the scapula: absent (0); present (1).
68 Dorsal and ventral margins of the furcula: subequal in width (0); ventral margin distinctly wider than the dorsal margin (1).
69 Furcula: boomerang-shaped, with interclavicular angle of approximately 90°(0); U-shaped, with an interclavicular angle of less than 70°(1).
70 Hypocleideum: absent or poorly developed (0); well developed (1).
71 Sternum: subquadrangular to transversely rectangular (0); longitudinally rectangular (1).
72 Distinctly carinate sternum, more prominent than a faint ridge: absent (0); present (1).
73 Sternal carina: near to, or projecting rostrally from, the cranial border of the sternum (0); not reaching the cranial border of the sternum (1).
74 Lateral process of the sternum: absent (0); present (1).
75 Prominent distal expansion in the lateral process of the sternum: absent (0); present (1).
76 Medial process of the sternum: absent (0); present (1).
77 Rostral margin of the sternum broad and parabolic: absent (0); present (1).
78 Wide V-shaped caudal end of the sternum: absent (0); present (1).
79 Costal facets of the sternum: absent (0); present (1)
80 Proximal and distal humeral ends: twisted (0); expanded nearly in the same plane (1).
81 Humeral head: concave cranially and convex caudally (0); globe-shaped, craniocaudally convex (1).
82 Proximal margin of the humeral head concave in its central portion, rising ventrally and dorsally: absent (0); present (1).
83 Ventral tubercle of the humerus: projected ventrally (0); projected proximally (1); projected caudally, separated from the humeral head by a deep capital incision (2).
84 Humerus with distinct transverse ligamental groove: absent (0); present (1).
85 Pneumatic fossa in the caudoventral corner of the proximal end of the humerus: absent or rudimentary (0); well developed (1).
86 Prominent, subquadrangular (i.e., subequal length and width)deltopectoral crest of the humerus: absent (0); present (1).
87 Prominent bicipital crest of the humerus, cranioventrally projectin: absent (0); present (1).
88 Ventral face of the humeral bicipital crest with a small fossa for muscular attachment: absent (0); present (1)
89 Humeral distal condyles: mainly located on distal aspect (0); on cranial aspect (1).
90 Humerus: with two distal condyles (0); a single condyle (1).
91 Well-developed brachial depression on the cranial face of the distal end of the humerus: absent (0); present (1).
92 Well-developed olecranon fossa on the caudal face of the distal end of the humerus: absent (0); present (1).
93 Distal end of the humerus very compressed craniocaudally: absent (0); present (1).
94 Ulna: shorter than humerus (0); nearly equivalent to or longer than humerus (1).
95 Ulnar shaft: considerably thicker than the radial shaft, radial-shaft/ulnar-shaft ratio larger than 0.70 (0); smaller than 0.70 (1).
96 Olecranon process of ulna: relatively small (0); hypertrophied, nearly one-third the length of the ulna (1); one-half the length of the ulna (2).
97 Proximal end of the ulna with a well-defined area for the insertion of M. brachialis anticus: absent (0); present (1).
98 Semilunate ridge on the dorsal condyle of the ulna: absent (0); present (1).
99 Shaft of radius with a long longitudinal groove on its ventrocaudal surface: absent (0); present (1).
100 U-shaped to heart-shaped ulnare (scapholunar): absent (0); present (1).
101 Semilunate carpal and proximal ends of metacarpals: unfused (0); semilunate fused to the alular (Ⅰ) metacarpal (1); semilunate fused to the major (Ⅱ) and minor (Ⅲ) metacarpals (2); fusion of semilunate and all metacarpals (3).
102 Distal end of metacarpals: unfused (0); partially or completely fused (1).
103 Intermetacarpal space: absent or very narrow (0); at least as wide as the maximum width of minor metacarpal (III) shaft (1).
104 Extensor process on alular metacarpal (I): absent or rudimentary (0); well developed (1).
105 Minor metacarpal (III) projecting distally more than the major metacarpal (II): absent (0); present (1).
106 Round-shaped alular metacarpal (I): absent (0); present (1).
107 Alular metacarpal (I) large, massive, depressed, and quadrangular: absent (0); present (1).
108 Alular digit (I): long, exceeding the distal end of the major metacarpal (0); short, not surpassing this metacarpal (1).
109 Alular digit (I) large, robust, and dorsoventrally compressed: absent (0); present (1).
110 Prominent ventral projection of the proximolateral margin of the proximal phalanx of the alular digit (I): absent (0); present (1).
111 Ungual phalanx of major digit (II): present (0); absent (1).
112 Ungual phalanx of major digit (II) much smaller than the unguals of the alular (I) and minor (III) digits: absent (0); present (1).
113 Proximal phalanx of the minor digit (III) much shorter than the remaining nonungual phalanges of this digit: absent (0); present (1).
114 Ungual phalanx of minor digit (III): present (0); absent (1).
115 Proximal phalanx of major digit (II): of normal shape (0); flat and craniocaudally expanded (1).
116 Intermediate phalanx of major digit (II): longer than proximal phalanx (0); shorter than of equivalent to proximal phalanx (1).
117 Alular ungula phalanx with two ventroproximal foramina: absent (0); present (1).
118 Pelvic elements: unfused (0); fused or partially fused (1).
119 Preacetabular process of ilium twice as long as postacetabular process: absent (0); present (1).
120 Small acetabulum, acetabulum/ilium length ratio equal to or smaller than 0.11: absent (0); present (1).
121 Postacetabular process shallow and pointed, less than 50% of the depth of the preacetabular wing at the acetabulum: sbsent (0); present (1).
122 Orientation of proximal portion of pubis: cranially to subvertically oriented (0); retroverted, separated from the main synsacral axis by an angle ranging between 65°and 45°(1); more or less parallel to the ilium and ischium (2).
123 Prominent antitrochanter: caudally directed (0); caudodorsally directed (1).
124 Iliac brevis fossa: present (0); absent (1).
125 Pubic pedicel: cranioventrally projected (0); ventrally or caudoventrally projected (1).
126 Supracetabular crest on ilium: well developed (0); absent or rudimentary (1).
127 Supracetabular crest: extending throughout the acetabulum (0); extending only over the cranial half of the acetabulum (1).
128 Ischium with a proximodorsal process approaching, or abuttin, the ventral margin of the ilium: absent (0); present (1).
129 Ischiadic terminal processes forming a symphysis: present (0); absent (1).
130 Ischium: two-thirds or less the length of the pubis (0); more than two-thirds the length of the pubis (1).

131	Obturator process of ischium: prominent (0); reduced or absent (1).
132	Pubic apron: one-third or more the length of the pubis (0); shorter (1); absent (absence of symphysis) (2).
133	Pubic shaft laterally compressed throughout its length: absent (0); present (1).
134	Pubic foot: present (0); absent (1).
135	Laterally compressed and kidney-shaped proximal end of pubis: absent (0); present (1).
136	Femur with distinct fossa for the capital ligament: absent (0); present (1).
137	Femoral neck: present (0); absent (1).
138	Femoral anterior trochanter: separated from the greater trochanter (0); fused to it, forming a trochanteric crest (1).
139	Femoral posterior trochanter: absent to moderately developed (0); hypertrophied (1).
140	Conical and strongly distally projected lateral condyle of femur: absent (0); present (1).
141	Femur with prominent patellar groove: absent (0); present (1).
142	Femoral popliteal fossa distally bounded by a complete transverse ridge: absent (0); present (1).
143	Tibiofibular crest in the lateral condyle of femur: absent (0); poorly developed (1); prominent (2).
144	Fossa for the femoral origin of M. tibialis cranialis: absent (0); present (1).
145	Caudal projection of the lateral border of the distal end of the femur: absent (0); present (1).
146	Tibia, calcaneum, and astragalus: unfused or poorly co-ossified (sutures still visible) (0); complete fusion of tibia, calcaneum, and astragalus (1).
147	Cranial cnemial crest on tibiotarsus: absent (0); present (1).
148	Round proximal articular surface of tibiotarsus: absent (0); present (1).
149	Medial border of medial articular facet strongly projects proximally: absent (0); present (1).
150	Extensor canal on tibiotarsus: absent (0); present (1).
151	Wide and bulbous medial condyle of the tibiotarsus: absent (0); present (1).
152	Narrow, deep intercondylar sulcus on tibiotarsus that proximally undercuts the condyles: absent (0); present (1).
153	Proximal end of the fibula: prominently excavated by a medial fossa (0); nearly flat (1).
154	Fibula: tubercle for M. iliofibularis craniolaterally directed (0); laterally directed (1); caudolaterally or caudally directed (2).
155	Fibula: reaching the proximal tarsals (0); greatly reduced distally, without reaching these elements (1).
156	Metatarsals II–IV completely (or nearly completely) fused to each other: absent (0); present (1).
157	Distal tarsals: free (0); completely fused to the metatarsals (1).
158	Metatarsal V: present (0); absent (1).
159	Proximal end of metatarsal III: in the same plane as metatarsals II and IV (0); reduced, not reaching the tarsals (arctometatarsalian condition) (1); plantarly displaced with respect to metatarsals II and IV (2).
160	Well-developed tarsometatarsal intercondylar eminence: absent (0); present (1).
161	Tarsometatarsal vascular distal foramen completely enclosed by metatarsals III and IV: absent (0); present (1).
162	Trochlea of metatarsal II broader than the trochlea of metatarsal III: absent (0); present (1).
163	Completely reversed hallux (arch of ungula phalanx of digit I opposing the arch of the unguals of digits II-IV): absent (0); present (1).
164	Metatarsal IV significantly thinner than metatarsals II and III: absent (0); present (1).
165	Plantar surface of tarsometatarsus excavated: absent (0); present (1)
166	Tubercle on the dorsal face of metatarsal II: absent (0); present (1).
167	Hypotarsus: absent (0); present (1).
168	Feathers: absent (0); present (1).
169	Alula: absent (0); present (1).

Newly added characters:

170	Prenarial snout, length: shorter (0), or longer (1), than maximum snout height (Sereno, 1999).
171	Premaxilla, maxillary process: long, forming the whole ventral border of the external naris (0) short, maxilla contributing to the ventral border of the external naris (1).
172	Dentary, robustness: slender, dentary length to dentary depth ratio more than 5 (0), robust, dentary length to dentary depth ratio less than 5 (1).
173	Dentary, dentition: present (0) or absent (1).
174	Premaxillary teeth, location: under the external naris (0) or anterior to the naris (1).
175	Premaxillary teeth, size: subequal to or smaller than (0) or larger than (1) maxillary teeth.
176	Ilium, prominent tuberocity on the lateral surface of the posterior end: absent (0) or present (1).
177	Tibiotarsus, length: long, more than 120% of the femoral length (0) or short, less than 120% (1)
178	Pedal phalanx I-1, length: shorter than (0) or longer than (1) other proximal pedal phalanges
179	Pedal phalanx I-2, length: shorter than (0) or longer than (1) other pedal unguals



SI Fig. 1.

The analysis resulted in 10 equally most parsimonious trees (Tree length= 292; CI = 0.47; RI=0.69). The strict consensus tree shows that *Shenshiornis primita* is a sister-taxon with *Sapeornis chaoyangensis* at the base of the Pygostylia. Clade diagnoses for select clades (both slow and fast character optimization): Aves: none; Pygostylia: 50.1, 61.1, 100.1, 116.1, 119.0, and 163.1. Clade diagnoses for select clades (fast character optimization): Aves: 3, 6, 10.1, 15.1, 20.1, 25.1, 28.1, 32.1, 33.1, 37.1, 46.1, 52.1, 74.1, 119.1, 121.1, 124.1, 128.1, 129.1, 137.1, 153.1, 154.1, and 171.1; Pygostylia: 17.1, 19.1, 50.1, 54.0, 61.1, 79.1, 84.1, 100.1, 114.1, 116.1, 119.0, 123.1, 142.1, 146.1, 163.1, 177.1, 178.1, and 179.1. Clade diagnoses for select clades (slow character optimization): Aves: 3.1, 10.1, 15.1, 25.1, 28.1, 46.1, 52.1, 119.1, and 128.1; Pygostylia: 6.1, 34.1, 50.1, 61.1, 69.1, 100.1, 116.1, 119.0, 131.1, and 163.1.

2 Matrix

	10	20	30	40	50	60
Deinonychosauria	0000000000	00000[01]0010	0[01][01]000[01]000	000[01]000000	00000000[01]0	?0100000100
Archaeopteryx	0010010001	000111000?	01??1?0100	0?1000??00	00?0010?10	-100000100
Jeholornis	????101?0?	0??0??0?0?	0??0?0?1?0	0??????00	?0?0000?10	01?1110111?
Sapeornis chaoyangensis	00100?1?0?	???011????	???0??-1??	1?01?0??00	0???0????1	02000001-0
Shenshiornis primita	0010011?0?	??00?1?0??	???0???1?0	0?01?0??0?	0?????????	??????????
Rahonavis	??????????	??????????	??????????	????0?1020	010?010010	-??1??????
Confuciusornis	102111000?	0000111??1	0??1?0--??	0?11?01120	0100010??1	0110000200
Changchengornis	1??1110???	??????????	0??1?0--??	????????2?	0?0001???1	01?00?0200
Noguerornis	??????????	??????????	??????????	??????????	?0????????	??????????
Iberomesornis	??????????	??????????	??????????	???101??00	0000010011	010????200
Concornis	??????????	??????????	??????????	????????11	??0???001?	??01110210
Gobipteryx	1021111101	0??????0??	0??010--??	??????????	?1??010??1	???11?02?0
Cathayornis	1010010???	???????0??	??????01??	????????11	1??0??0??1	?101??0210
Eoalulavis	??????????	??????????	????????0?	??1107???2?	??????????	??01110210
Neuquenornis	??????????	??????????	??????????	????????11	??????????	???11?0210
Ambiortus	??????????	??????????	????????0?	11????????	??????????	???1111200
Patagopteryx	??????????	?1??111011	1?1??0??11	1111011100	11011-10??	??01110200
Vorona	??????????	??????????	??????????	??????????	??????????	??????????
Hesperornis	1121011111	1111111101	1100101171	1101021120	100?1-0020	021100120-
Ichthyornis	1?210?????	?111111111	?????10111	1111021120	1?00010?21	1??1111200
Anas	1121111111	1111111111	011011--10	1111021100	10001-0021	1211111200
	70	80	90	100	110	120
Deinonychosauria	000000[01]000	00?0?00000	0000000000	0000000000	0000000000	0000000000
Archaeopteryx	0000001000	?0-??????0	?000000000	00?0000000	0000000000	0000000010
Jeholornis	00??101?00	0??1--?000	??0001???0	0?01100000	2100000000	0000000010
Sapeornis chaoyangensis	10?0101000	?????????0	1???010?10	0?0110?001	200000000-	0001010000
Shenshiornis primita	?????????	??????????	??????????	??????????	??????????	???????000
Rahonavis	????001???	??????????	??????????	????10100?	??????????	???????010
Confuciusornis	1000000000	10-1000110	0001010?10	0000101?01	2000000000	01100001?0
Changchengornis	1000?00000	10-????1?0	?0???1????	???010??0?	?000000000	0110010???
Noguerornis	?????????1	??????????	00????0???	???10???0?	3?00110?0?	??????????
Iberomesornis	1??010??11	??????????	00?0?00??0	0??110????	??????????	???????1??
Concornis	1110?0?111	1111111?0	0121?01110	0?1110????	??0???010?	0???01????
Gobipteryx	??10??11?1	?????????0	??????????	0??11?111?	?00?1?????	????0?????
Cathayornis	1110101?11	1111111?0	012?101110	01?110?111	3000110100	0?01010?00
Eoalulavis	1110111111	10-0—0000	1121001110	0111101?1?	?01?1?010?	0?0?010???
Neuquenornis	1110?01110	11011????1	??2?1?????	11111??11?	3000110???	??????????
Ambiortus	10???11010	?11???????	10?10000??	????1????1	3??0?10???	0???11-???
Patagopteryx	1000111???	??????1??1	00???00010	0000100?0?	?11???0??0	0???00?100
Vorona	??????????	??????????	??????????	??????????	??????????	??????????
Hesperornis	0000010000	10-0-0101-	10--0000--	000-------	----------	-------101
Ichthyornis	10011100??	110???1??1	1021000110	110110110?	3111000100	1--?11?1?1
Anas	1001111010	1101001011	1021100010	1100101101	3111000100	1--111-101
	130	140	150	160	170	
Deinonychosauria	0[01]0011?000	0000000000	0000000000	0000[01]000[01]0	00000[01]0??[01]	000[01]00000
Archaeopteryx	10-?11-1?0	00000?1000	0?0?000?00	00??000000	0000000101	100100000
Jeholornis	010?1??111	?100????00	?0??000??0	00??111000	0000?001??	?11--0000
Sapeornis chaoyangensis	01-?1??1?0	1100??????	???2??1????	00??011000	0010?00??0	010011111
Shenshiornis primita	01??100???	?10???????	?????0????	????000?0?	?010?????0	010011111
Rahonavis	100111-110	0000?01100	0010000000	00?2100?00	00?00101??	?????0000
Confuciusornis	?11111-110	1101?101?0	??1??1??00	10?1101000	0010110101	111--0100
Changchengornis	??????????	?10??????0	?????1????	????10100?	??100?01?1	111--0111
Noguerornis	???????10?	??????????	??????????	??????????	???????1??	???????11
Iberomesornis	???????1?1	1?0??????0	0????0010?	?????00?00	0?10??????	?????0011
Concornis	???????111	010??00???	0???110107	1????01?00	0111???1??	?????001?
Gobipteryx	????1?????	?1?1??????	??????0100	1?1?101100	?1?1010??1	101--????
Cathayornis	11??11-1?1	1??0??0110	011?01??00	111?10??00	????1?0??1	1011000??
Eoalulavis	??????????	???????11?	??????????	??????????	???????11?	?????????
Neuquenornis	??????????	???????11?	0????1?????	?????0??0?	0111??????	?????????
Ambiortus	??????????	??????????	??????????	??????????	???????1??	?????????
Patagopteryx	010011-011	12010?0??0	012?010000	1111111100	1000101???	?????0000

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