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A primitive confuciusornithid bird from China and its implications for early avian flight

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Confuciusornithids, lived from 120—125 million years ago, form a basal bird group and include the oldest birds with horny beaks. Here we describe *Eoconfuciusornis zhengi*, gen. et sp. nov. from the Early Cretaceous Dabeigou Formation (131 Ma) in Fengning, Hebei Province, northern China. It represents a new and, more primitive than other known, member of this group and extends the lifespan of this family to 11 Ma, the longest of any known Early Cretaceous avian lineages. Furthermore, *Eoconfuciusornis* and its relatives present many osteological transformations, such as the size increase of the deltopectoral crest of the humerus and the keel of the sternum, apparently an adaptation toward improved flight in the evolution of the Confuciusornithidae.

Birds, Early Cretaceous, confuciusornithids, flight

1 Introduction

In quantity, confuciusornithid birds exceed all other avian groups in the Jehol Biota[1]. Phylogenetically, they are more derived only than *Archaeopteryx*, *Jeholornis*, *Sapeornis*, and *Rahonavis*, but are more basal than the two major Mesozoic avian lineages: Enantiornithes and Ornithurae[2−4].

In osteology, confuciusornithids are mainly different from other birds in the following features: both upper and lower jaws are toothless, and the mandibular symphysis is forked; the deltopectoral crest of the humerus is prominent; the alular metacarpal is not fused with metacarpals II and III complex; the first phalanx of manual digit III (minor digit) is much shorter than other non-ungual phalanges; the ungual of manual digit II (major digit) is significantly shorter than those of other manual digits, and the caudal end of the sternum is "V" shaped[5].

The first confuciusornithid bird, *Confuciusornis sanctus*, was found from the Early Cretaceous Yixian Formation in western Liaoning Province[6,7]. In 1999 and 2000, two other genera referable to the Confuciusornithidae, *Changchengornis*[8] and *Jinzhouornis*[9], were established respectively. They are all from the Yixian Formation. In 2006, a new specimen (IVPP V13313) from the Jiufotang Formation was referred to *Confuciusornis sanctus*[10], representing the first report of a confuciusornithid from this formation.

Deposits of both the Jiufotang Formation and Yixian Formation are distributed mainly in Liaoning Province, and their ages are about 120 Ma and 125 Ma, respectively[11,12]. Most of the Jehol Biota animals come from these two formations[1,4,13,14].

Eoconfuciusornis zhengi was discovered from the Dabeigou Formation at Sichakou in Fengning, Hebei Province (Figure 1). Mesozoic lacustrine deposits from this locality comprise the Huajiying Formation and the underlying Dabeigou Formation. The former is roughly comparable to the Yixian Formation in Liaoning Pro-

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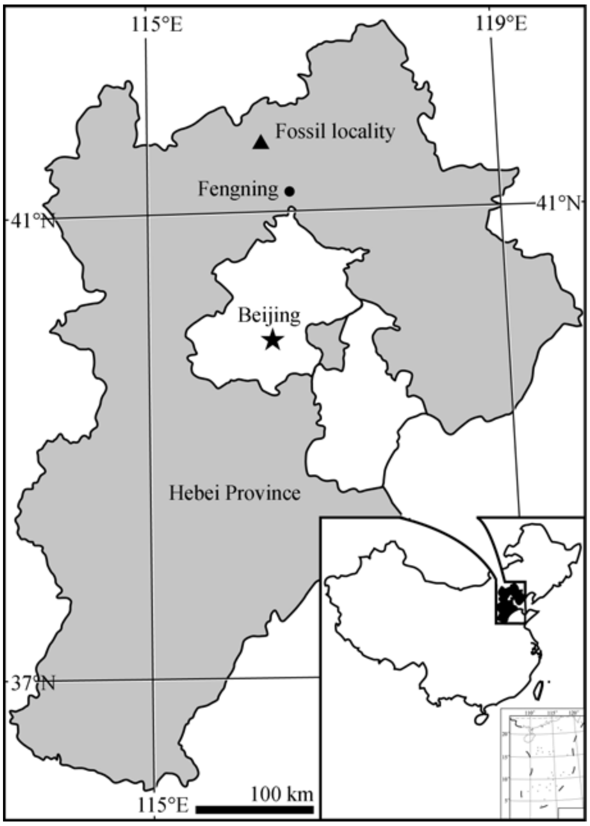

Figure 1 Map of Hebei Province in North China showing the locality of *Eoconfuciusornis zhengi*, Sichakou, Fengning County.

vince whereas the latter is slightly older[15], and SHRIMP U-Pb and $^{40}Ar/^{39}Ar$ [16,17] dating indicated that the age of the Dabeigou Formation is about 131 Ma. The newly discovered avian is a middle-sized confuciusornithid, similar to that of an extant rook[18]. In contrast to the extremely abundant vertebrate fossils found from the Yixian and Jiufotang formations, so far only four vertebrate taxa have been reported from the Dabeigou Formation, including two birds, *Eoconfuciusornis zhengi*, and *Protopteryx fengningensis*[19], and two acipenseriform fish *Peipiaosteus fengningensis* and *Yanosteus longidorsalis*[15,20].

2 Material and methods

The specimen is housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. The phylogenetic relationships between the new bird, *Eoconfuciusornis zhengi*, and other major primitive birds was analyzed with PAUP 4.0 beta 10[21]; the data matrix comprise 169 osteological and integumental characters for 25 bird and dinosaur taxa (24×169 taxon matrix is from ref. [3], see S1 and S2).

3 Description of specimen

3.1 Taxonomy

Aves Linnaeus 1758
Confuciusornithiformes Hou et al. 1995
Confuciusornithidae Hou et al. 1995
Eoconfuciusornis zhengi gen. et sp. nov.

3.2 Etymology

The genus name "*Eoconfuciusornis*" is derived from the Greek prefix "eo" (dawn), and "confuciusornis", indicating that some features of this new bird are more primitive than other confuciusornithid birds; the species name "*zhengi*" is dedicated to the distinguished Chinese ornithologist ZHENG Guangmei.

3.3 Holotype

Institute of Vertebrate Paleontology and Paleoanthropology Collection IVPP V11977; a nearly complete specimen including skull, mandible, postcranial elements and feather impressions, preserved on the main and/or counterpart slabs (Figures 2—5).

3.4 Locality and horizon

Sichakou, Fengning County, Hebei Province, China; Dabeigou Formation, Early Cretaceous, the lowest fossil horizen of the Jehol Biota, about 131 Ma ago[17].

3.5 Diagnosis

The new taxon is distinguishable from other known confuciusornithids by a combination of the following features: lateral depressions in thoracic vertebrae undeveloped; scapula without prominent acromion and glenoid facet; coracoid short, with relatively wide sternal facet; deltopectoral crest of humerus not prominent; proximal end of humerus no more than twice the width of distal end and lacking a fenestra; astragalus pierced by foramina; tarsometatarsus slightly longer than half of the length of tibia.

3.6 Description

(1) Skull and mandible. Most skull elements are exposed in left lateral to ventral views; while mandible elements are usually exposed in ventral view. They are either articulated naturally, or disarticulated but preserved closely together. Like those of other confuciusornithids, the rostral region of the skull and mandible is pointed, robust and toothless. Both the neurovascular foramina and grooves located on the rostral region of the upper and the lower jaws indicate that the beak is cov-

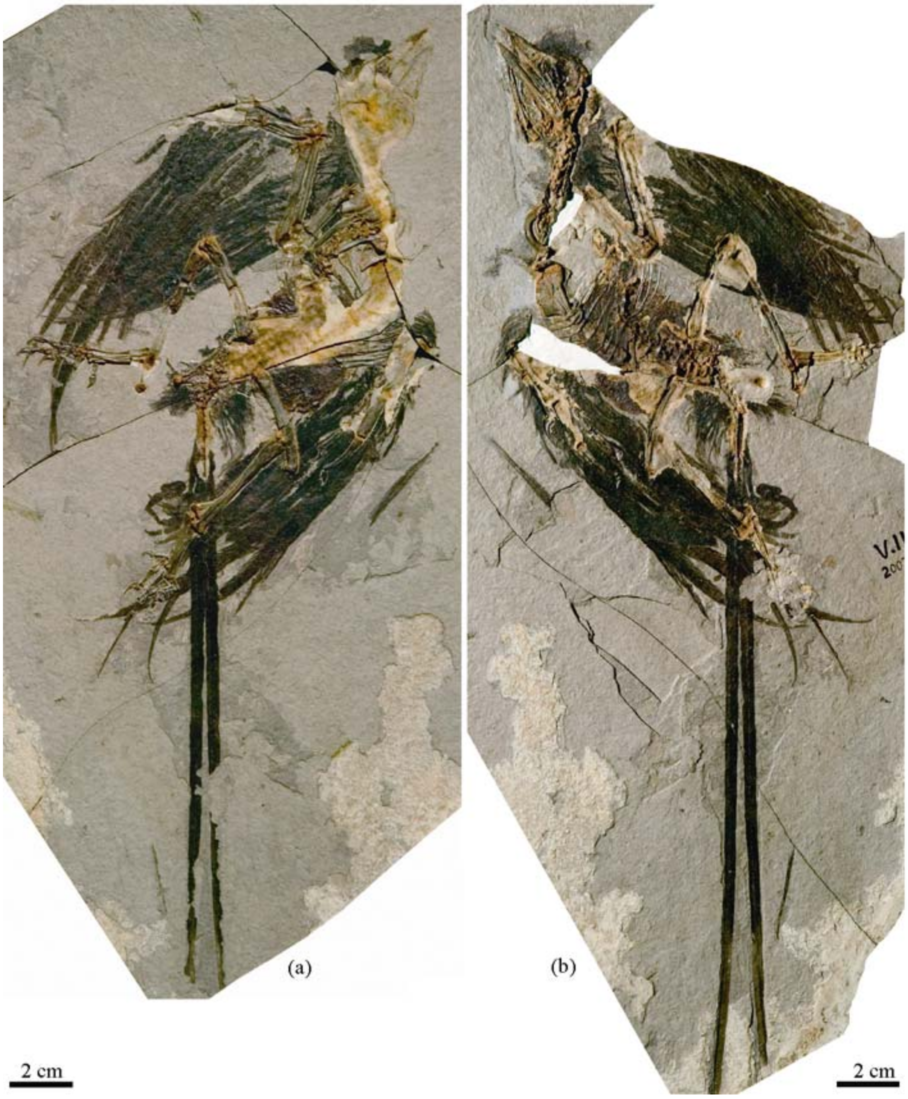

Figure 2 *Eoconfuciusornis zhengi*, skeleton and feather impression in counterslab (a) and mainslab (b).

ered with rhamphotheca[5−7,22] and what is more, it is proved by the beak impression at the rostral ends of both upper and lower jaws, which is very difficult to be observed in other specimens (Figures 2—5).

In lateral view, the premaxilla is asymmetrically "V"-shaped, a rostrally tapering body with a long dorsal ramus (frontal process) and a short ventral one (maxillary process). At the body, left and right premaxillae are fused, although the rostralmost part is slightly apart, forming a small notch. The long frontal process is straight and robust, reaching the dorsal middle-margin of the orbit; the maxillary process is not as robust as the frontal process, tapering gradually, and appears to end at the narrowest region of the premaxilla-maxilla complex.

The maxilla is triradiate, possessing three processes in lateral view. The premaxillary process appears rostrally, meeting with the premaxilla at the narrowest region of the premaxilla-maxilla complex; the boundary between these two processes is not clear. Dorsally there is a long ascending process, reaching the level of the frontal process of premaxilla. However, it is very difficult to identify whether this process is an intact nasal process, or just the frontal margin of the foramen of nasal process, as in *Confuciusornis*[5]. The jugal process is the most robust; caudally it meets or fuses with the jugal bar; it is very difficult to identify the suture or other boundary between these two elements.

At the caudal end of the frontal process of the premaxilla is a small ossification, which is interpreted as the nasal based on its location, morphology, and com-

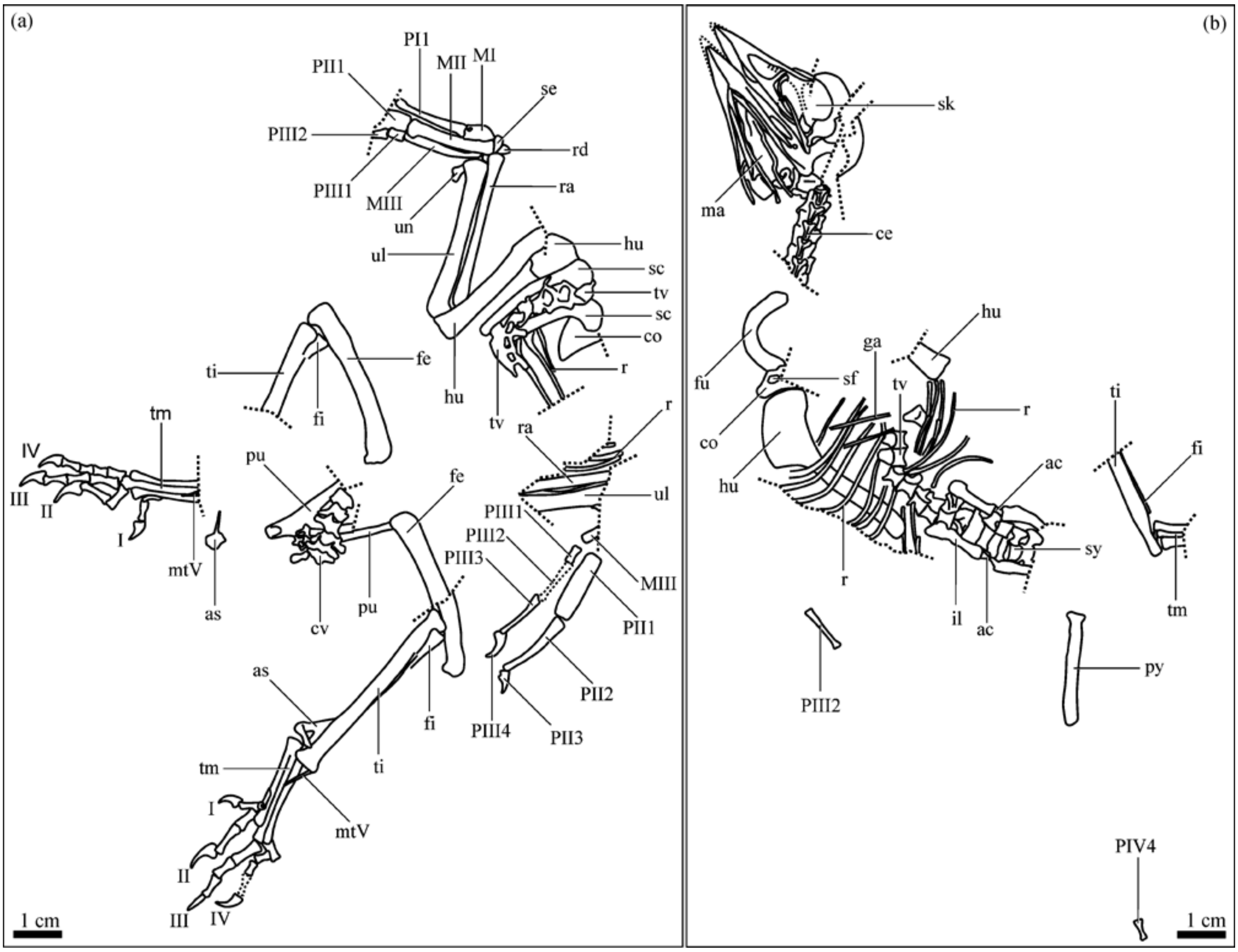

Figure 3 *Eoconfuciusornis zhengi*, skeleton on the counter slab (a) and main slab (b). ac, acetabulum; as, astragalus; ce, cervical vertebrae; co, coracoid; cv, caudal vertebrae; fe, femur; fi, fibula; fu, furcula; py, pygostyle; ga, gastralia; hu, humerus; I—IV, pedal digits I—IV; il, ilium; ma, mandible; MI, alular metacarpal; MII, major metacarpal; MIII, minor metacarpal; MtV, metatarsal V; PI1-2, 1st and 2nd phalanx of alular digit; PII1-3, 1st to 3rd phalanx of major digit; PIII1-4, 1st to 4th phalanx of minor digit; PIV4, 4th phalanx of pedal digit IV; pu, pubis; py, pygostyle; r, rib; ra, radius; rd, radiale; sc, scapula; se, semilunate carpal; sf, supracoracoid nerve foramen; sk, skull; sy, synsacrum; ti, tibia; tm, tarsometatarsus; tv, thoracic vertebrae; ul, ulna; un, ulnare.

parison with *Confuciusornis sanctus*[5]. This element is partly overlapped by the frontal process of premaxilla; the exposed part is subrectanglar. Its rostral end reaches the level of the dorsal process of the maxilla, while its caudal end abuts the frontal.

The external naris is nearly oval in shape and far from the skull's rostral tip as in *Confuciusornis sanctus*[5]. The formation of naris is involved with different parts of the premaxilla, maxilla, and presumed nasal. The ventral margin of the frontal process of the premaxilla forms the dorsal and part of the rostral boundary; the dorsal margin of the maxillary process of the premaxilla forms the ventral and part of the rostral boundary. The caudal naris is demarcated by the rostral margin of the ascending process of the maxilla. In lateral view it is very difficult to identify whether or not the presumed nasal contributed to the formation of nares although it should be involved as in other birds or dinosaurs[23].

The frontal is expanded and inflated, and its bony wall is thin and fragile as in other confuciusornithids or other primitive and extant birds[5,24,25]. The wall is crashed and lots of gaps or breaks are easily observed. Rostrally the frontal is connected with the frontal process of the premaxilla; caudally it connects with the parietal, although the suture is not easy to identify. In fact these two elements may have fused together as do those of other confuciusornithids and more derived birds.

Compared with the frontal, the parietal is more expanded and inflated. Its bony wall is also thin and full of gaps.

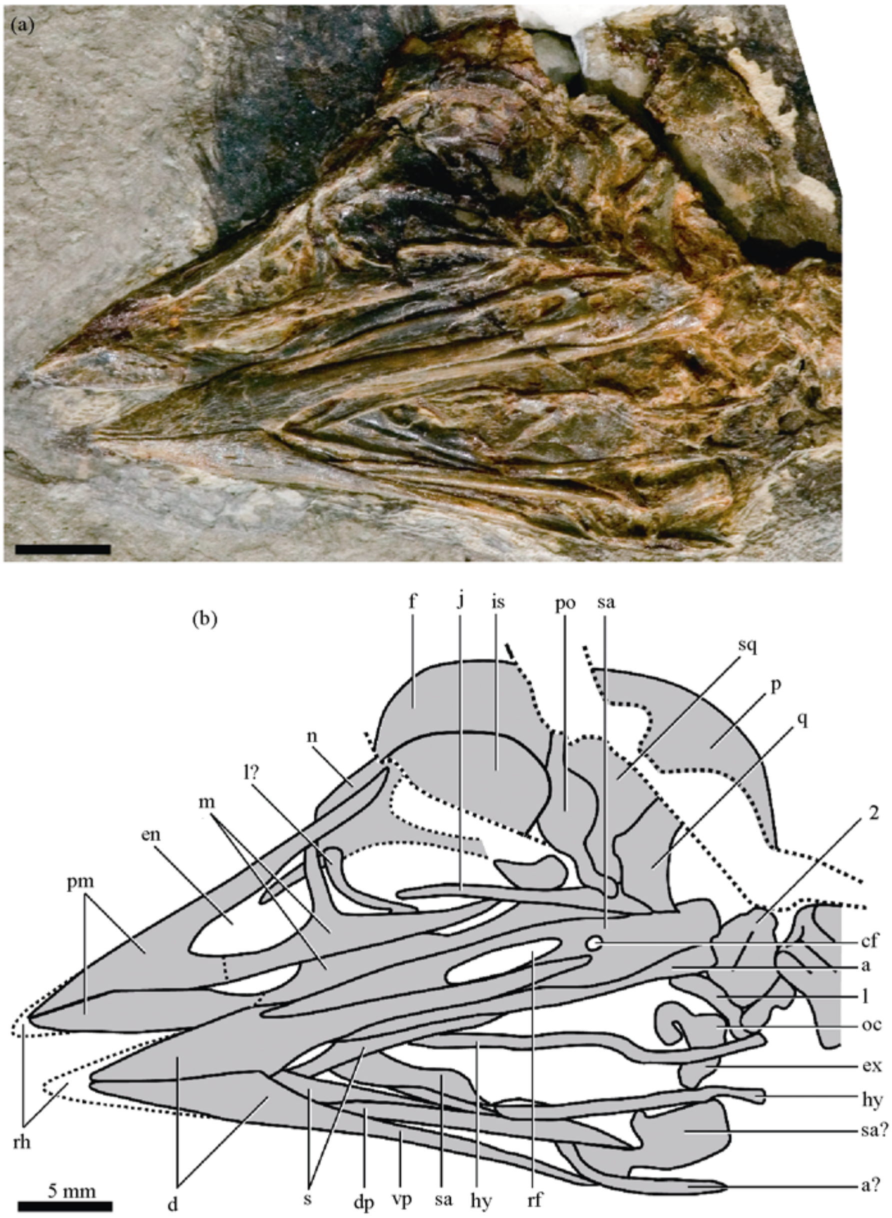

Figure 4 Skull and mandible of *Eoconfuciusornis zhengi*. 1, Atlas; 2, axis; cf, caudal mandibular fenestra; d, dentary; dp, dorsal process of dentary; en, external nares; ex, exoccipital; f, frontal; hy, hyoid; is, interorbital septum; j, jugal; l, lacrimal; m, maxilla; n, nasal; oc, occipital condyle; p, parietal; pm, premaxilla; po, postorbital; pt, pterygoid; q, quadrate; rf, rostral mandibular fenestra; rh, rhamphotheca impression; s, splenial; sa, surangular; sq, squamosal; vp, ventral process of dentary.

Ventral to the frontal, the postorbital is obliquely located on the caudal margin of the orbit. There appear to be only two processes in the postorbital, the frontal and the jugal, rather different from other confuciusornithids. The frontal process tightly abuts the frontal. The jugal process, which is smaller than the frontal, overlaps the jugal. Between these two processes the body is expanded.

Caudal to the postorbital is fragment, tentatively interpreted as part of the squamosal based mainly on its position. It is impossible to identify whether the supratemporal and infratemporal fossa exist or not for the postorbital-squamosal bar cannot be identified, which is present usually in some other confuciusornithid specimens[5−7].

From its rostral end, with a faint suture with the maxilla, the jugal becomes gradually narrow; its caudal part is overlapped by the quadratojugal.

The quadratojugal is long and slender. Its rostral end reaches the boundary between the maxilla and the jugal;

Figure 5 Close-up photos of *Eoconfuciusornis zhengi*. (a) Scapulae and scapular part of right coracoid in dorsal view; (b) furcula and sternal part of right coracoid in ventral view; (c) right humerus; (d), (e) some proximal elements of left hand and distal elements of right hand; (f) right ankle. as, astragalus; co, coracoid; fo, foramen in the astragalus; fu, furcula; h, humerus; PI1, 1st phalanx of alular digit; PII1-3, 1st to 3rd phalanx of major digit; PIII1-4, 1st to 4th phalanx of minor digit; MI, alular metacarpal; MII, major metacarpal; MIII; minor metacarpal; r, ribs; ra, radius; rd, radiale; s, sternum; sc， scapula; se, semilunate carpal; sf, supracoracoid nerve foramen; ti, tibia; tv, thoracic vertebra; ul, ulna; un, ulnare.

its caudal end is connected with the quadrate; from caudally to rostrally the quadratojugal tapers off evenly.

Dorsal to the quadratojugal is a small and stout ossification, which is partly overlapped by the quadratojugal. By the position and its stout morphology it is tentatively interpreted as the pterygoid.

The orbit margin is composed of the lacrimal, premaxilla, jugal, quadratojugal, postorbital and frontal. The caudal margin of the lacrimal forms the rostral boundary of the orbit. The dorsal boundary is formed by the ventral margin of the frontal process of the premaxilla; the caudal boundary is formed by the rostral margin of the postorbital; and the ventral boundary is formed by the dorsal margin of the quadratojugal and the jugal respectively. There are other elements that should contribute to the formation of the orbit, such as the assumed nasal, and the palpebral if it is present as in other confuciusornithids[5]. The sclerotic plates are not preserved, and yet these are commonly found in other birds[25].

Overlapped by the left hyoidal branch, the occipital condyle is dislocated to the caudal region of mandible. There is a low concave notch on the caudoventral end of the occipital condyle, which is comparable to the medial condylar incisura of modern birds[26]. From the lateral side of the occipital condyle two ridge-like ossifications are interpreted as part of the exoccipital.

The mandible is tapering, stout and toothless. It is compressed dorsoventrally; however, some of its elements are exposed in lateral view, and some in medial view. In ventral view, both the straight dorsal margins of the dentary and surangular, and their rostralmost pointed end form the mandible as a subtriangular projection.

Two dentary rami are not completely fused. There is a clear suture throughout their rostral one third, rostrally forming a small notch at their tips. Caudal to the stout body the dentary bifurcates into two asymmetric processes. The dorsal one appears remarkably shorter than the ventral. The ventral process is robust and long, forming about two thirds of the total length of the dentary. Its caudalmost end reaches the caudal fenestra of the surangular.

The surangular forms the main caudal region of the mandible. Its dorsal margin is straight throughout, and so is the dorsal margin of the dentary. The ventral margin of the angular forms the caudal two-thirds of the ventral border of the mandible. Laterally the angular was partly overlapped by the dentary. The caudalmost surangular and angular appear totally fused with the articular. In the caudal region there is a round foramen comparable to the caudal mandibular fenestra of some modern birds, and the surangular foramen of non-avian theropods as previously suggested[5]. The rostral mandibular fenestra is remarkably larger than the caudal fenestra, and it is a long opening which is intermediate between oval and rhombic in shape.

There are two enantiomorphous ossifications overlapped by the dentary and angular. From their position and morphology, they are assumed as the splenials, which appear partly comparable in morphology to those of *Archaeopteryx* and *Vescornis*[27,28].

In the left mandibular ramus, the articular appears totally fused with the caudal ends of the angular and surangular; in the right mandible ramus, however, there is a long and slender structure, which should be interpreted as the caudal end of the angular from its morphology and position. If this interpretation is correct, the articular is not completely fused with the angular.

Two hyoidal branches are preserved roughly along the middle longitudinal line of mandibles. Rostrally they are overlapped by the splenial; caudally they are beyond the level of the articular.

(2) Vertebral column. From the atlas to the pygostyle most of the vertebral elements of *Eoconfuciusornis* are articulated, while other elements are either connected closely/loosely, or fused completely.

Seven cervical vertebrae are preserved including the atlas and axis; but with vertebral impressions and the space between the last preserved cervical vertebra and the first assumed thoracic vertebra, the total number of cervical vertebrae appears to be nine. Caudal to the occipital condyle and rostral to the axis is a band-like ossification, identified as the atlas (Figure 4). Its morphology and position is comparable to that of *Vescornis*[28]. Compared with the atlas, the axis is stout and strong (Figure 4). There is no sign of ventral process on the axis, which is usually present in enantiornithine and modern birds[26]. The caudal articular process of the axis is strong and round in ventral view.

The other five preserved cervical vertebrae share similar morphology (Figures 2 and 3). They are roughly subquadrate in ventral view; the longitudinal length is slightly greater than the transverse width. The ventral process is robust or blunt, which is different from the modern bird's lamella-like ventral process. The craniocaudal length of the ventral process is about half the longitudinal length of the cervical vertebra (LoV); it is larger than those of modern birds in which the length of the ventral process is usually no more than one third of the LoV. Another feature of the ventral process which is different from that of modern birds is that the caudal end of the ventral process reaches the caudalmost extent of the vertebral body. This feature, i.e., the robust, blunt, and long ventral process, is similar to that of primitive birds such as other confuciusornithids and some enantiornithine birds[5,25]. In ventral view the prezygapophysis is a robust projection with an expanded rostralmost end. Caudally it is continued with the ventral process, forming a "Y"-shaped structure. Cervical vertebrae 3 to 7 possess ribs that are tightly connected to the lateral side of the vertebrae, while they appear not fused with the diapophyses or parapophyses. These ribs are long and connected rostrocaudally with each other throughout the cervical series. Because all preserved cervical vertebrae are connected together, *Eoconfuciusornis* does not show the central articulation type, i.e., heterocoelic or non-heterocoelic.

The number of thoracic vertebrae is estimated to be between 12 and 14; the anterior six or seven are crashed and/or disarticulated; the posterior six or seven are tightly connected with the synsacrum, making it very difficult to identify the exact number. Generally the cranial series is exposed in dorsal aspect on the counter slab. The dorsal processes are compressed sometimes, showing their lateral sides. These dorsal processes are high and narrow (in lateral view), and roughly subquadrate in shape, but possess slightly expanded dorsal extreme ends. The assumed second thoracic vertebra is shorter than the cervical vertebrae; its dorsal process appears slimmer than those of the middle ones; its caudal-oblique costal process is long, reaching the level of its caudalmost end (Figures 2, 3, 5(a) and (c)).

The posterior six or seven thoracic vertebrae (preserved on the main slab) are counted from a disarticulated one with strong vertebral body, 1), to the last vertebra with a pair of ribs, or 2), and then to the next one whose caudal end reaches the level of the ilium. All the above-mentioned vertebrae are ventrolaterally exposed, in contrast to the ventrally exposed sacrals. The vertebral centrum is sandglass-shaped, its body is narrow in the middle region, and is expanded at both cranial and caudal ends. The anterior articular surface is slightly concave. The ventral surface of the vertebral body is smooth. There is a slight and narrow longitudinal concavity on the lateral side of the vertebral body, which is comparable, in position, with lateral excavations of the thoracic centra of *Confuciusornis*. These concavities are varied in size, but even the largest concavity is relatively far smaller than that of *Confuciusornis sanctus*[5]. In lateral view the dorsal processes are wide, almost equal to those of vertebrae. This is different from those of the cervical vertebrae, which are no more than half of the vertebral length. Another difference between these two dorsal processes is that the dorsal margin of the dorsal process is arc-like in lateral view, contrasting to the subquadrate shape of the cervical vertebra. Craniocaudally the transverse processes and other projections become more elongate or developed gradually (Figures 2, 3, 5(a) and (c))

The exact number of vertebrae in the synsacrum is not easy to count, because of 1) poor preservation, 2) the absence of obvious distinguishing features to identify them either from thoracic vertebrae rostrally or from caudal vertebrae posteriorly, and 3) the disarticulation of some synsacral vertebrae. Only three medial synsacral vertebrae are tightly fused. Anterior to the fused synsacral vertebrae are two vertebrae with long transverse processes which contact the medial surface of the preacetabular wings of the ilia; while posteriorly there are two vertebrae with long and expanded transverse processes contacting the medial surface of the postacetabular wings of the ilia. All seven vertebrae are interpreted as synsacral vertebrae. The ventrolateral sides of the first two synsacral vertebrae are smooth and without excavation. The centrum of the synsacral vertebra is sandglass-shaped. The middle of the vertebral centrum is laterally and ventrally obviously thinner than those of the two expanded ends. Both the rostral and caudal articular facets are slightly concave. Synsacral vertebrae 3 to 5 are tightly fused together. They possess long and strong transverse processes. In ventral view the ventral facet of the third synsacral vertebra is smooth, while the fourth and fifth possess shallow longitudinal grooves. The distal ends of transverse processes of the sixth and seventh are extremely expanded, broadly connected with the ilia (Figures 2 and 3).

Six closely connected free caudal vertebrae are preserved between the synsacrum and the pygostyle. Their centra are relatively short compared to those of the thoracic or synsacral vertebrae, possessing concave cranial articular facets. In ventral view the ventral faces of the vertebral bodies are not as smooth as those of the synsacral vertebrae. The transverse processes are not expanded at their ends, and become gradually shorter from the first to the last. There are also two isolated caudals which are far from the above-mentioned closely connected caudal series. The pygostyle is about the same as the tarsometatarsus in length. Anteriorly it bears an expanded proximal end connected to the free caudal series (Figures 2 and 3).

(3) Thoracic girdle. In caudal view the furcula is boomerang-shaped with a long and shallow concavity along its longitudinal middle line. The ascending region is slightly wider than the middle one in caudal view, while the former is more rostrocaudally compressed than the latter. There is no sign of a hypocleideum or slightly caudal swelling as in *Confuciusornis sanctus*, or a distinct tubercle as in *Changchengornis hengdaoziensis*[5,8]. At the ascending extreme end an oval area near the medial margin possesses a rough surface, contacting the smooth neighboring area. It can be interpreted as the articular facet for the scapula. The lateral area of the dorsalmost end of the right clavicular ramus is tightly connected with the right coracoid (Figures 2, 3 and 5(b)).

The right scapula is exposed with its lateral side visible, while the left scapula shows its medial side. In lateral view the cranial region of the scapula possesses a large lateral swelling which may be comparable with the articular facet, the glenoid process or tuberosity of more derived birds for articulating with the coracoid or humerus. Its dorsolateral projecting tuberosity is extremely developed. The acromion, usually distinctly preserved in more derived birds, is not prominent in *Eoconfuciusornis*. The cranial extremity is spherical both in lateral and medial views. There appears to be no distinctive neck of the scapula both in lateral and medial views. At the middle of the shaft the cross section of the scapula appears oval, not as round as in some modern birds. In the shaft region the medial surface appears more convex than the lateral. The distal region of the scapula is not expanded as in some more advanced birds, but thins out mediolaterally and gradually posteriorly (Figures 2, 3 and 5(a)).

Only the right coracoid is preserved; its scapular part is preserved on the main slab in ventral view and its sternal part on the counter slab in dorsal view. The medial side of the scapular extremity, comparable to the clavicular articular facet of more derived birds, is tightly articulated to the articular facet of the furcula. The endmost part of the shoulder extremity is located near the lateral side, contrasting to the medial side of more derived birds. In ventral view the endmost margin of the scapular region is obliquely straight to the lateral side. In cross section, almost half of the lateral region of the coracoid is curved ventrally, at least from the scapular limit to the longitudinal midpoint of the coracoid. In this part, in cross section the medial and lateral regions nearly form a right angle. Another distinctive feature of the coracoid is that the shoulder extremity is pierced dorsoventrally by a large foramen for supracoracoidal nerve. This foramen is elliptical, and its long axis is roughly parallel to the longitudinal axis of the coracoid; its width is no more than one third the diameter of the coracoid at the same level. The sternal part of the coracoid has a concave lateral margin and convex sternal articulation. Its lateral region appears thinner than the medial region (Figures 2, 3, 5(a) and (b)).

(4) Sternum, ribs and gastralia. The sternum appears not completely ossified as in *Confuciusornis* or some other primitive birds. Its shape is recognized mainly by the dark red color presumably left by the sternum bone, which distinguishes the sternum from the surrounding skeleton elements, integuments, and matrix, although in the caudal region the sternum appears a little ossified as a thin lamina-like structure. The sternum is roughly subquadratic in shape. Its longitudinal axis is slightly longer than the tibia, while it is narrower in transverse width (Figures 2, 5(a), 5(c) and 6(b)).

Thoracic ribs and gastralia are interwoven together. However, the thoracic ribs are usually longer than the presumed gastralia, and some of them are attached to the thoracic vertebrae. In the rostral part of the sternum there are some interlaced elements that are interpreted as the gastralia. These elements are shorter and thinner than the thoracic ribs. The sternal ribs and uncinate processes which are usually present in primitive birds are not recognizable in *Eoconfuciusornis* (Figures 2, 3 and 5(c)).

(5) Thoracic limb. The thoracic limb elements are preserved in both the main and counter slabs (Figures 2 and 3).

The right humerus is exposed in cranial view. The inflated proximal region is more than one third of the total length. The humeral head is slightly expanded with a coarse surface. The ventral corner is not as developed as that of other confuciusornithids[5,10], but it continues to a prominent crest with coarse cranial surface, comparable to the bicipital crest of modern birds. The deltopectoral crest is large, but smaller than that of other confuciusornithids, lacking a prominent angle of the deltopectoral crest. It is very difficult to find a ridge on the cranial margin of the crest, which is present in other confuciusornithids[5]. On the other hand, in *Eoconfuciusornis*, the ventral margin of the humeral proximal extremity is straight, in contrast to the curved ventral margin of other confuciusornithids[5]. The humeral body is straight to slightly curved dorsally in the distal region. Its cranial surface and adjacent distal extremity region are overlapped by the sternum and ribs, making it difficult to identify its detailed morphology. However, a prominent cranially swelling at the caudalmost end suggests the presence of both dorsal and ventral condyles (Figures 2, 3, 5(c) and 6(f)).

The left humerus was broken and folded before being embedded, and was preserved in the counter slab. Its proximal extremity is exposed in caudal view; its shaft portion is exposed in cranial view. The distal extremity is turned and is exposed in caudal view because it is preserved on the main slab. Caudally the humeral head is more developed than in cranial view. It has a prominent expanded cranialmost end. Caudal to the inflated humeral head the proximal extremity surface is longitudinally convex, without other distinctive structures such as the tuberosity, fossa or foramen, which are usually preserved in more advanced birds. Similar to the right humerus, the cranial surface of the left humerus is straight and compressed, with a long and fine crack along its longitudinal midline, suggesting that the shaft should be cylindrical in cross section before it became embedded in the rock. The caudal surface of the humeral distal extremity has a straight distalmost end, nearly perpendicular to the longitudinal axis of the humerus, but the ventral corner (near the comparable ventral epicondyle of modern birds) of the distal end appears more acute than the dorsal corner (near the comparable dorsal epicondyle). The sulcus or process which is commonly present in modern birds is not found on the caudal surface of the humeral distal extremity. The distinct humeral foramen of *Confuciusornis* is not present in *Eoconfuciusornis* (Figures 2, 3 and 6(f)).

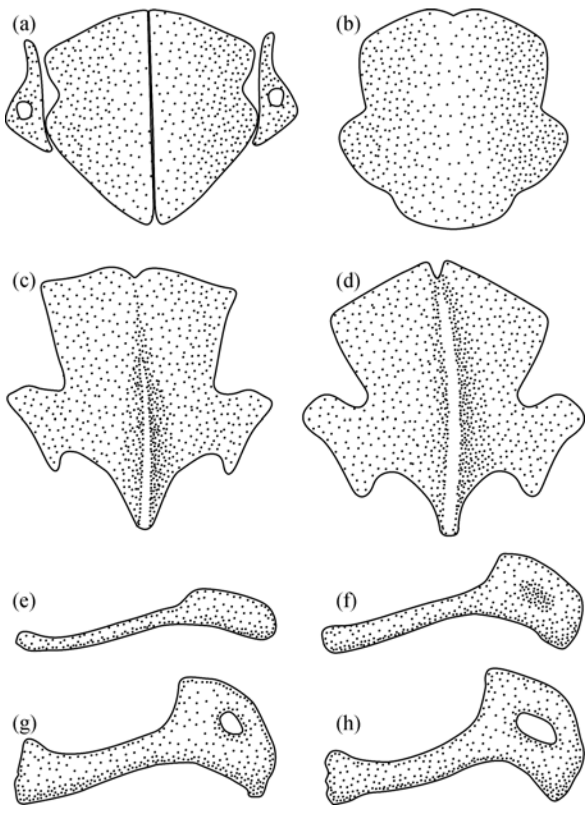

Figure 6 Two flight-related trends showing the progressive morphological transitions among early primitive birds. (a)—(d) Unfused sternal plates (a) → fused sternum (b) → gradually elongate carina ((c),(d)). (a) *Jeholornis*, IVPP V13274; (b) *Eoconfuciusornis*; (c) *Confuciusornis*, IVPP V10928; (d) *Confuciusornis*, IVPP V13313; not to scale. (e)—(h) proximal diameters of humerus are gradually increased. (e) *Archaeopteryx*, Berlin specimen, 145 Ma; (f) *Eoconfuciusornis*, 131 Ma; (g) *Confuciusornis*, IVPP V13156, 125 Ma; (h) *Confuciusornis*, IVPP V13313, 120 Ma. Not to scale.

The ulna and radius are straight throughout their length and lack a prominent interosseous space between them. The line-shaped cracks, throughout the midshaft surface, indicate that both the ulna and radius possessed round or oval cross sections before burial, and are laterally compressed. The midshaft of the ulna is slightly thinner in diameter than the proximal or distal regions of the same bone. The distal extremity of the ulna is inflated, especially toward the ventral side, which may correspond to the dorsal condyle of more derived birds. The midshaft width of the radius is about three quarters that of the ulna. The inflated distal extremity of the radius is relatively larger than that of the ulna. (Figures 2, 3 and 5(d)).

Between the ulna+radius and carpus+metacarpals there are two isolated ossifications: the robust one located at the distal end of the radius is interpreted as the radiale, while the small one near the distal end of the ulna is interpreted as the ulnare. The presumed radiale appears tightly connected with the carpus which abuts the proximal ends of the alular and major metacarpals (Figures 2, 3 and 5(d)).

Apart from the radiale and ulnare, another carpal bone, identified as the semilunate, is closely connected with the proximal ends of the alular and major metacarpals. The semilunate is also closely connected with the radiale and just as big (Figures 2, 3 and 5(d)).

In caudal view the ventral margin of the alular metacarpal is closely connected to the dorsal surface of the major metacarpal with obvious boundary. Its proximal end is oval-shaped with a small tuberosity near its ventral corner. The dorsal margin is slightly convex in the proximal two-thirds and becomes slightly concave in the distal third. The ventral margin appears more complex: the proximal third is conspicuously convex, followed by a short and obvious concavity, and then a long slight convexity. The distal end is mainly concave centrally and expanded distally to articulate with the alular phalanx. As in the pedal digit this articulation bears two trochlea-like structures, divided by a longitudinal groove. Cranial to the above-mentioned lateral trochlea-like structure is a distinctive depression comparable to the collateral ligamental fovea of the pedal digits (Figures 2, 3 and 5(d)).

The major metacarpal is the longest and strongest among three metacarpals. It is more than three times the length of the alular metacarpal. However, the latter is slightly wider than the former in diameter. The proximal extremity of the major metacarpal is slightly inflated with a round to straight proximalmost articulation for the semilunate carpal. The shaft is somewhat dorsally curved; its dorsal margin is slightly concave while its ventral margin is slightly convex. The caudal surface was compressed postmortem, forming a longitudinal fine crack. The distal extremity is expanded dorsoventrally, and especially the ventral corner is overly expanded to an obvious ventral process, occupying about one quarter of the whole distal diameter, and overlapping the minor metacarpal for half its area. The minor metacarpal is shorter and slimmer in length and diameter respectively than those of the major metacarpal. Its proximal end does not reach the level of the major metacarpal, while its distal end shares the same level with the major metacarpal. At midshaft, the diameter of the minor metacarpal is about one third or quarter of the major one. Both proximal and distal ends of the minor metacarpal are closely connected to the major metacarpal, forming a less obvious intermetacarpal space. The minor metacarpal is dorsally curved. The proximal one third appears more dorsoventrally compressed and then turned to be more craniocaudally compressed in the distal two thirds. The proximal end is sharply tapering, forming a subtriangular articular facet. Along the midline the distal half bears longitudinal cracks due to postmortem compression. The distal extremity of the minor metacarpal is not expanded, simply bearing a round articular facet at its distalmost end (Figures 2, 3, 5(d) and (e)).

Eoconfuciusornis shares a similar manual phalangeal formula with *Archaeopteryx* and other confuciusornithids, 2-3-4, in contrast to more advanced birds in which some phalanges are lost. All the preserved manual elements of *Eoconfuciusornis* are naturally articulated together (Figures 2, 3, 5(d) and (e)).

The alular digit bears two phalanges. The proximal one is long and slender. It is about 90% of the major metacarpal in length. Both the proximal and the distal extremities are expanded, but the proximal end is significantly larger than the distal. From proximal to distal, the proximal alular phalanx is straight to slightly curved dorsally and becomes gradually thinner in diameter. In cross section this phalanx is round. The proximal articular facet is flat to slightly round; the distal articular facet is more complex, possessing an obvious collateral ligamental fovea at the lateral side. The ungual phalanx is about half of the proximal one in length. Its proximalmost end is a curved articular cotyla in lateral view. The flexor tubercle is developed. The curved phalangeal sulcus is wide and long, almost running through the whole phalangeal length. Its width is tapering gradually from proximal to distal and about one third of the whole width proximally. Like those of other manual or pedal ungual phalanges, the remnant of horny sheath of the phalanx is hardly preserved (Figures 2, 3, 5(d) and (e)).

The major manual digit possesses three phalanges. The proximal phalanx is the most robust among all manual phalanges. It is craniocaudally compressed; its diameter is overwhelmingly larger than those of other phalanges both in cranial and caudal view. Its length, however, is merely 90% that of the proximal phalanx of the alular digit. This proximal phalanx is subrectangular although both its dorsal and ventral margins are slightly convex, while it is slightly concave in its proximal one quarter on the ventral margin. Both proximal and distal extremities of the proximal phalanx are slightly inflated caudally. The proximal articular facet is round to slightly flat, while the distal articular facet is concave in caudal view, corresponding with the convex proximal articular facet of the intermediate phalanx. The intermediate phalanx is slightly longer than the proximal one, and obviously curved ventrally in caudal view. Its proximal extremity is conspicuously larger and more expanded than the distal one. From proximal to distal ends the diameter becomes gradually smaller. Like the proximal phalanx of the alular digit, the intermediate phalanx is round in cross section. The ungual phalanx of the major digit is the most undeveloped among the three ungual phalanges. It is only about two-thirds of the length of the minor digit, while both of them share similar width at their proximal ends. Its flexor tubercle and ungual lateral sulcus are smaller and shallower than those of alular and minor ones, suggesting it is a degenerative ossification, for both its flexor which is connected to the flexor tubercle, and lateral sulcus which carries nerves and vessels are undeveloped (Figures 2, 3, 5(d) and (e)).

The minor digit contains four phalanges. The proximal phalanx is the shortest among all manual phalanges; it is only about one third the length of the first intermediate phalanx. However the proximal phalanx appears more robust than the intermediate phalanges. The proximal and distal articular facets of the proximal phalanx appear slightly concave and convex respectively.

Two intermediate phalanges are more slender than the others. The first intermediate phalanx is slightly shorter than the second. Gradually both of them appear tapering from the proximal to the distal ends. Their extremity ends are slightly expanded, while their articular facets are not as clear as those of other phalanges. The first intermediate phalanx is straight in caudal view while the second is ventrally curved, but the latter is not as curved as the intermediate one of the major digit. The ungual phalanx of the minor digit is intermediate in size between the alular and major ungual digits. It possesses a similar flexor tubercle in shape and a lateral sulcus in size with the alular ungual phalanx (Figures 2, 3, 5(d) and (e)).

(6) Pelvic girdle. In ventral view the preacetabular wing of the ilium is narrow with a round cranial end; the medial margin of the preacetabular wing is thick and strong, contracting the thin and slim lateral margin. The medial surface of the ilium tightly abuts the series of transverse processes of the synsacrum. In ventral view the dorsal-inner surface of the acetabulum is thinner than the connection area for the pubis and ischium. The ischium appears ventrally exposed. Its acetabular region is more robust than the following caudal part. The distal parts of the pubes are preserved on the counter slab in cranial view. They are totally fused distally to a symphysis, and at the distalmost end form an expanded pubic foot-like structure that is perpendicular to the pubic shaft. There is a thin and shallow groove on the medial line of the symphysis (Figures 2 and 3).

(7) Pelvic limb. The femur is similar to the ulna in length and diameter, but the former is slightly curved craniocaudally in lateral view. At its proximal extremity, the trochanter is not as developed as in more derived birds; it is a small expanded ridge. The femoral head appears undeveloped, lacking any sign of a femoral neck. The shaft is slightly caudally curved, and is thinner than both proximal and distal regions. Except for some cracks due to postmortem compression, it is very difficult to find any sign of an iliotrochanter impression, or intermuscular lines on the surface of the femoral shaft, which are usually present in extant birds. At the distal extremity the lateral epicondyle is expanded laterally. Both lateral and medial supracondyle crests are developed, which are long and caudally expanded. Between them is a long and deep groove. Both lateral and medial condyles are caudally developed, while the medial one appears more caudally prominent than the lateral one. The patellar articular facet between the two condyles is obviously present (Figures 2 and 3).

The tibia is straight, about one fifth longer than the femur. The proximal extremity is inflated laterally and caudally. The expanded lateral margin of the proximal articulation is extended to a significant fibular crest laterally. In caudal view there is an obvious groove dividing the proximal articulation into two facets, which is respectively comparable to the lateral and medial articular facets of extant birds. The lateral facet is slightly wider than the medial in caudal view, while the medial facet projects more caudally. The groove between these two facets should be comparable with the interarticular area of modern birds. From the proximal end distally, the shaft of the tibia becomes gradually thinner to the midshaft and then thicker when approaching the distal extremity in caudal view. At the distal extremity, in caudal view, the distalmost region is obviously expanded laterally and medially, while the caudal margin is flat. The articulation is flat to slightly convex in caudal view. In lateral view the distal extremity is craniocaudally compressed (Figures 2, 3 and 5(f)).

The proximal tarsus, the astragalus, is neither fused to the distal tibia as in some primitive and extant birds, nor tightly connected to the tibia. As in some dinosaurs and primitive birds, the astragalus possesses a long tapering ascending process[29,30]. Different from those of dinosaurs and primitive birds[29,31], however, the tarsal possesses an opening near the distal end in caudal view (Figures 2, 3 and 5(f)). This opening appears comparable to the upper opening of the extensor canal for the tendon of the M. extensor digitorum longus in modern birds[26].

The fibula is slender and long, and its distal end appears to reach the level of the ascending process of the astragalus. The proximal extremity is inflated with a flat to slightly round proximal articular facet. From proximal to distal, the shaft of the fibula gradually tapers in diameter, and its cross section also changes from oval to round. The proximal three-quarters of the fibula are located on the lateral side of the tibia and the distal one-quarter is turned to the cranial side (Figures 2 and 3).

The metatarsals are slightly shorter than half the length of the tibia. The left proximal first third of the metatarsals is preserved on the main slab in plantar view; while the distal two-thirds is preserved on the counter slab in dorsal view. In plantar view, the right metatarsals

II-IV are totally fused in their proximal region; while, in dorsal view, the left metatarsals II-IV appear not totally fused, but tightly connected. Among metatarsals II to IV, metatarsal II is the shortest which is about 83% of metatarsal III, the longest one. Metatarsal IV appears slightly shorter than metatarsal III, while obviously longer than metatarsal II. The proximal end of metatarsal II is obviously expanded medially. Dorsally, the proximal ends of metatarsals II-IV are slightly expanded; while in plantar view the proximal ends of metatarsals II and III are also slightly expanded. The shaft of metatarsal II is straight throughout its full length, only medially curved or inflated at its distal extremity. Its distal articular facet projects medially instead of distally, forming an angle of approximately 30 degrees to the shaft longitudinal midline of metatarsal II. Centrally, its distal extremity is slightly concave in plantar view. The width of this trochlea is similar to that of metatarsal III, and appears slightly greater than metatarsal IV. The shaft of metatarsal III is straight to slightly medially curved, while its distalmost articular facet is slightly medially curved. Apparently, compared with metatarsal III, the shaft of metatarsal IV is laterally curved in its distal half (Figures 2, 3 and 5(f)).

Metatarsal I is "J"-shaped in dorsal or plantar view. Distally it is attached to the medial side of metatarsal II. The length of the former is less than one quarter of the latter. From distally to proximally, metatarsal I becomes gradually mediolaterally compressed and tapering, ending with an oblique tip. The distal articular facet is ball-shaped which articulates to the proximal phalanx of digit I (Figures 2 and 3).

Metatarsal V is delicate and thin, from proximally to distally it tapers gradually. Both left and right metatarsals V are longer than metatarsal I, and at least 30% of metatarsal II in length, although their exact size is not confirmed, as the proximal region is overlapped by the tibia and other metatarsals (Figures 2, 3 and 5(f)).

Like those of other known Early Cretaceous birds, the foot of *Eoconfuciusornis* is anisodactyl, with the usual phalangeal formula of 2-3-4-5. Digit I is the shortest toe, which is less than half the length of digit III, the longest of all toes and only slightly shorter than the tarsometatarsus. Digits II and IV are of similar length, longer than digit I but shorter than digit III. The non-ungual phalanges share similar morphological features such as the developed flexor tubercles, the articular trochleae, collateral ligamental foveae, and shallow longitudinal ventral depressions, etc. The ungual phalanges bear similar flexor tuberosities and vascular sulci. The variation of these phalanges focuses on their longitudinal and transverse size. The proximal phalanx of digit III and the preungual phalanx of digit II are in the same length, and are longer than other non-ungual toes. However the former appears slightly more robust than the latter. Two intermediate phalanges of digit IV are smaller than other nonungual phalanges. They are only about half of the longest toe in length (Figures 2 and 3).

The ungual phalanx of digit II is the longest, which is nearly 1.5 times the length of digit I, the shortest toe. The ungual phalanges of digits III and IV are roughly equal in length, which are about 85% the length of digit II. However, in proportion to its length, the ungual phalanx of digit I appears more robust than other ungual phalanges for its transverse size is relatively greater than others (Figures 2 and 3).

In digit I, the proximal phalanx is thin, roughly same as the ungual phalanx in length. In digit II, the proximal phalanx is more than 75% the length of the distal one, while it appears more robust than the latter. The distal phalanx appears equal to the ungual phalanx in length. In digit III, the proximal phalanx is about 120% that of the intermediate and the distal phalanges in length, and appears more robust than the latter two in width. The latter two phalanges are roughly equal in length and width. They are slightly shorter than the ungual phalanx. In digit IV, the proximal phalanx is slightly longer than the first intermediate one, which is slightly longer than the second intermediate one, while either proximal or intermediate ones are shorter than the distal phalanx which is slightly shorter than its attached ungual phalanx (Figures 2 and 3).

(8) Plumage. The plumage is obvious, for most of the feathers are black to deep brown, while the bones and matrix appear brown or grey. Like other Jehol Biota birds or dinosaurs, the feathers of *Eoconfuciusornis* were preserved as carbonizations or impressions (Figures 2)[25,31−33].

Both shafted feathers and non-shafted feathers[32] are preserved in *Eoconfuciusornis*; the former includes the flight and covert feathers which are attached to the forelimbs, two elongate tail feathers, and several isolated covert feathers near the skeleton; the latter only includes the down feather which is scattered near the skull, neck and free caudal vertebrae (Figures 2, 4(a) and 5). There are also some feathers that are very difficult to identify as shafted or non-shafted feathers, such as the ones near the vertebral column.

4 Discussion

Eoconfuciusornis is obviously a confuciusornithid, based on the following characters: both upper and lower jaws are toothless; the rostral end of mandibular symphysis is forked; the alular metacarpal is subquadrangular, and not fused to the other metacarpals; the major digital claw is significantly smaller than other two; the proximal phalanx of the minor manual digit is much shorter than other non-ungual phalanges. Phylogenetically, *Eoconfuciusornis* represents the most basal member of the Family Confuciusornithidae (Figure 7).

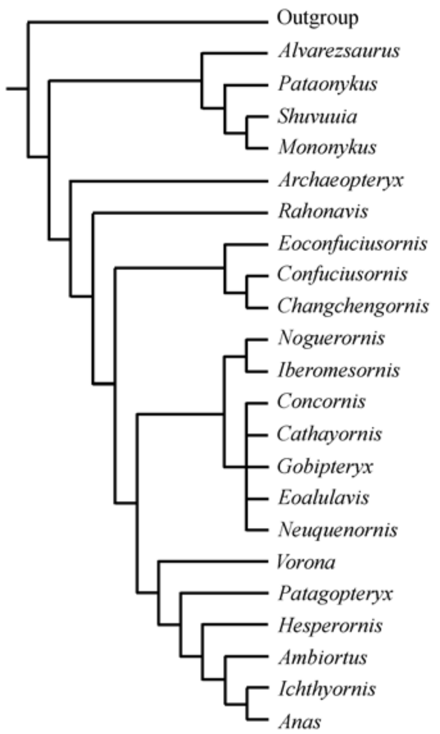

Figure 7 Cladogram showing relationships between *Eoconfuciusornis* and other major groups of birds. This strict consensus result is from 14 most parsimonious trees. (see Appendixes 1 and 2; tree length = 308; consistency index = 0.5942; retention index = 0.7664)

On the other hand, *Eoconfuciusornis* lacks apomorphies of derived confuciusornithids, such as: the thoracic centra lacks a prominent lateral groove; the proximal end of the scapula lacks a prominent acromion and glenoid facet; the coracoid is relatively short with 1) a foramen seemingly comparable to the supracoracoidal nerve opening of some dinosaurs, and 2) a wide sternal facet; generally the coracoid is more like that of *Archaeopteryx* than other confuciusornithids; the pubic foot is well developed, while other confuciusornithids entirely lack this structure; the deltopectoral crest of the humerus is not as prominent as in other confuciusornithids; and the astragalus possesses an elongate ascending process.

There are some features suggesting that the type specimen of *Eoconfuciusornis* is not a fully adult individual. For instance, the tarsometatarsus is not completely fused at the proximal end, the proximal tarsus is not fused with the tibia, and some articular surfaces of long bones are slightly coarser than those of the midshaft. Based on some morphological and integumentary aspects, however, the type specimen of *Eoconfuciusornis* is nearly an adult. *Eoconfuciusornis* is a middle-sized confuciusornithid, and is larger than some other known fully adult confuciusornithids, such as IVPP V 10928; *Eoconfuciusornis* bears a pair of extremely long central tail feathers, which is regarded as an indication of sexual dimorphism in *Confuciusornis*[34], which is only present in adult or very near adult individuals in modern birds[24].

It is interesting to note that the most primitive confuciusornithid (*Eoconfuciusornis*) comes from the Dabeigou Formation (131 Ma), which is older than Yixian Formation (125 Ma) which produced *Confuciusornis*, *Changchengornis* and *Jinzhouornis*. Since the youngest horizon that bears a confuciusornithid (*Confuciusornis*) is the Jiufotang Formation (120 Ma), therefore the Confuciusornithidae had a temporal span of about 11 Ma, the longest duration of any Early Cretaceous avian lineages, documenting a novel example of slow evolutionary rate in early avian evolution.

Corresponding with its greater age, *Eoconfuciusornis* exhibits many intermediate features in morphology between more basal birds and more advanced confuciusornithids. For example, in sternal anatomy, there is a clear trend from *Jeholornis*[29] to the confuciusornithids: 1) *Jeholornis* possesses a pair of flat sternal plates; 2) *Eoconfuciusornis* possesses an incompletely ossified sternum (but a brown outline of roughly rectangular shape on both slab and counter slab indicates that the sternum is more like that of other confuciusornithids (Figure 6); 3) the confuciusornithids from the Yixian Formation either developed a modest carina restricted to the caudal quarter of the sternum, as in some *Confuciusornis sanctus* (Figure 6), or not preserved, as in *Changchengornis hengdaoziensis*[5]; 4) the confuciusornithids from the Jiufotang Formation have a marked sternal carina, extending more than three-quarters of the length of the sternum (Figure 6). The depth of the carina is an indication of the size of the main flight muscles[2,24], and thus the confuciusornithids appear to show osteological evidence for increasing flight power throughout the 11 million years of their evolution (Figure 6).

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Appendix 1 Character list and character states used for the cladistic analysis

Skull and mandible

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 and dentary: toothed (0); toothless (1).
6. Caudal 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).

Vertebral column and ribs

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 parapophysisdiapophysis: present (0); absent (1).
31. Cranial cervical vertebrae heterocoelous: absent (0); present (1).
32. Prominent 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 centra 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 or 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).

Thoracic girdle and sternum

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); present (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).

Thoracic limb

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 projecting: 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 or equivalent to proximal phalanx (1).
117. Alular ungual phalanx with two ventroproximal foramina: absent (0); present (1).

Pelvic Girdle

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: absent (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 abutting, 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).

Pelvic limb

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 coossified (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 renpect 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 ungual 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).

Integument

168. Feathers: absent (0); present (1).
169. Alula: absent (0); present (1).

Appendix 2 Data matrix used for the cladistic analysis

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Allosauroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Troodontidae	0	0	0	0	0	0	0	0	0	?	0	0	0	0	?	?	?	0	1	0	0	1	1	0	?	?	1	0
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	0	1	0	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	?	0	1	?	?	1	?	0	1
Rahonavis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mononykus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	1
Shuvuuia	0	0	0	?	0	0	0	?	0	1	?	0	0	1	1	1	0	0	0	1	0	1	0	?	1	?	1	1
Alvarezsaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Patagonykus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Confuciusornis	1	0	2	1	1	1	0	0	0	?	0	0	0	0	1	1	1	?	?	1	0	?	?	1	?	0	n	n
Changchengornis	1	?	?	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	1	?	0	n	n
Eoconfuciusornis	1	?	2	1	1	1	0	?	0	?	?	?	0	0	?	?	?	?	?	?	?	?	?	1	?	0	n	n
Noguerornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Iberomesornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Patagopteryx	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1	1	0	1	1	1	?	1	?	?	0	?	?
Vorona	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Concornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cathayornis	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	1
Cobipteryx	1	0	2	1	1	1	1	1	0	1	0	?	?	?	?	?	?	0	?	?	0	?	?	0	1	0	n	n
Eoalulavis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neuquenornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ambiortus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hesperornis	1	1	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	0	1	1
Ichthyornis	1	?	2	1	0	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	?	?	?	?	?	1	0	1
Anas	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	n	n

Taxon	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Allosauroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	n	0	0	0	0	0
Troodontidae	?	0	0	0	0	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	n	?	1	0	0	0
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	n	0	1	0	0	0
Archaeopteryx	0	0	0	?	1	0	0	0	?	?	0	0	0	0	?	0	0	1	0	?	1	0	n	1	0	0	0	0
Rahonavis	?	?	?	?	?	?	0	?	1	0	2	0	0	1	0	?	0	1	0	0	1	0	n	?	?	1	?	?
Mononykus	?	1	0	1	1	1	1	?	1	1	0	0	?	1	1	1	?	?	1	1	?	?	n	?	?	0	0	0
Shuvuuia	0	0	0	1	1	1	1	?	1	1	0	0	0	1	1	1	0	1	1	1	0	0	n	?	?	0	0	0
Alvarezsaurus	0	?	?	?	1	?	0	?	?	?	0	0	0	0	0	?	0	1	1	1	0	?	n	?	?	0	0	0
Patagonykus	?	0	0	?	?	?	?	?	1	0	0	0	?	1	1	1	?	?	1	1	?	?	n	?	?	0	0	?
Confuciusornis	?	?	0	?	1	1	?	0	1	1	2	0	0	1	0	0	0	1	0	?	?	1	0	1	1	0	0	0
Changchengornis	?	?	?	?	?	?	?	?	?	?	2	?	0	?	0	0	0	1	?	?	?	1	0	1	?	0	0	?
Eoconfuciusornis	?	?	0	0	?	?	?	0	?	?	0	0	0	1	0	0	0	?	1	?	?	1	0	1	?	0	0	?
Noguerornis	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Iberomesornis	?	?	?	?	?	1	0	1	?	?	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	?	?	?
Patagopteryx	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	1	1	n	1	0	?	?	?	?	0	1	1	1
Vorona	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Concornis	?	?	?	?	?	?	?	?	?	?	1	1	?	?	0	?	?	?	0	0	1	?	?	?	0	1	1	1
Cathayornis	?	?	?	?	?	?	?	?	?	?	1	1	1	?	?	0	?	?	0	?	?	1	?	1	0	1	?	?
Cobipteryx	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	1	0	?	?	1	?	?	?	1	1	?
Eoalulavis	0	?	?	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1
Neuquenornis	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
Ambiortus	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Hesperornis	?	1	1	1	0	1	0	2	1	1	2	0	1	0	0	?	1	n	0	0	2	0	0	2	1	1	0	0
Ichthyornis	1	1	1	1	1	1	0	2	1	1	2	0	1	?	0	0	0	1	0	?	2	1	1	?	?	1	1	1
Anas	1	0	1	1	1	1	0	2	1	1	0	0	1	0	0	0	1	n	0	0	2	1	1	2	1	1	1	1

Taxon	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Allosauroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	n	?	?	?	?	?	0	0	0	0	0	0
Troodontidae	0	1	0	0	0	0	?	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Velociraptorinae	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	n	0	n	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	1	0	0	0	0	0	0	0	0	1	0	0	0	?	0	n	?	?	?	?	?	?	0	?	0	0	0
Rahonavis	?	?	?	?	?	?	?	?	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mononykus	0	0	0	1	0	0	0	0	0	0	0	?	?	?	1	1	0	0	n	0	0	0	0	1	0	0	1	0
Shuvuuia	0	0	0	1	0	0	0	0	0	0	0	?	?	?	1	1	0	0	n	0	0	0	0	1	0	0	1	0
Alvarezsaurus	0	?	?	?	0	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Patagonykus	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0
Confuciusornis	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0	n	1	0	0	0	1	1	0	0	0	0	1
Changchengornis	0	2	0	0	1	0	0	0	?	0	0	0	0	0	1	0	n	?	?	?	?	1	?	0	?	0	?	?
Eoconfuciusornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	n	?	?	?	?	?	?	0	?	0	0	0
Noguerornis	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0	0	?	?
Iberomesornis	?	2	0	0	1	?	?	0	1	0	?	?	1	1	?	?	?	?	?	?	?	?	?	?	0	0	?	0
Patagopteryx	0	2	0	0	1	0	0	0	1	1	1	?	?	?	?	?	?	?	?	?	1	?	?	1	0	0	?	?
Vorona	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Concornis	0	2	1	0	1	1	1	0	?	0	?	1	1	1	1	1	1	1	1	1	1	0	?	0	0	1	2	1
Cathayornis	0	2	1	0	1	1	1	0	1	0	1	?	1	1	1	1	1	1	1	1	1	0	?	0	0	1	2	?
Cobipteryx	0	2	?	0	?	?	1	0	?	?	1	1	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Eoalulavis	0	2	1	0	1	1	1	0	1	1	1	1	1	1	1	0	n	0	n	n	0	0	0	0	1	1	2	1
Neuquenornis	0	2	1	0	1	1	1	0	?	0	1	1	1	0	1	1	0	1	1	?	?	?	?	1	?	?	2	?
Ambiortus	1	2	0	0	1	0	?	?	?	1	1	0	1	0	?	1	1	?	?	?	?	?	?	?	1	0	?	1
Hesperornis	1	2	0	n	0	0	0	0	0	1	0	0	0	0	1	0	n	0	n	0	1	0	1	n	1	0	n	n
Ichthyornis	1	2	0	0	1	0	0	1	1	1	0	0	?	?	1	1	0	?	?	?	1	?	?	1	1	0	2	1
Anas	1	2	0	0	1	0	0	1	1	1	1	0	1	0	1	1	0	1	0	0	1	0	1	1	1	0	2	1

Taxon	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112
Allosauroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	n	0	0	0	0	0	0	0	0	0	0	0
Troodontidae	?	0	?	?	?	?	?	?	?	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rahonavis	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Mononykus	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	?	1	1	0	0	0	0	1	0	1	1	?	?
Shuvuuia	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	?	1	0	0	0	0	0	1	0	1	1	?	?
Alvarezsaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Patagonykus	0	?	0	0	1	1	0	0	1	?	0	1	?	0	?	?	1	?	?	0	?	0	1	0	1	1	?	?
Confuciusornis	0	1	0	?	1	0	0	0	0	0	1	0	1	?	0	1	2	0	0	0	0	0	0	0	0	0	0	1
Changchengornis	?	1	?	?	?	?	?	?	?	0	1	0	?	?	0	?	?	0	0	0	0	0	0	0	0	0	0	1
Eoconfuciusornis	0	0	0	0	?	0	?	?	0	0	1	0	?	?	0	?	0	0	0	0	0	0	0	0	0	0	0	1
Noguerornis	?	?	0	?	?	?	?	?	?	1	0	?	?	?	0	?	3	?	0	0	1	1	0	?	0	?	?	?
Iberomesornis	?	0	0	?	?	0	0	?	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Patagopteryx	?	0	0	0	1	0	0	0	0	0	1	0	0	?	0	?	?	1	1	?	?	?	0	?	?	0	0	?
Vorona	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Concornis	?	0	1	1	1	0	0	?	1	1	1	0	?	?	?	?	?	?	0	?	?	?	0	1	0	?	0	?
Cathayornis	1	0	1	1	1	0	0	1	?	1	1	0	?	1	1	1	3	0	0	0	1	1	0	1	0	0	0	?
Cobipteryx	?	?	?	?	?	?	0	?	?	1	1	?	1	1	1	?	?	0	0	?	1	?	?	?	?	?	?	?
Eoalulavis	0	0	1	1	1	0	0	1	1	1	1	0	1	?	1	?	?	0	1	?	1	?	0	1	0	?	0	?
Neuquenornis	1	?	?	?	?	?	1	1	1	1	1	?	?	1	1	?	3	0	0	0	1	1	0	?	?	?	?	?
Ambiortus	0	0	0	0	?	?	?	?	?	?	1	?	?	?	?	1	3	?	?	0	?	1	0	?	?	?	0	?
Hesperornis	0	0	0	0	n	n	0	0	0	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n
Ichthyornis	0	0	0	1	1	0	1	1	0	1	1	0	1	1	0	?	3	1	1	1	0	0	0	1	0	0	1	n
Anas	1	0	0	0	1	0	1	1	0	0	1	0	1	1	0	1	3	1	1	1	0	0	0	1	0	0	1	n

Taxon	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
Allosauroidea	0	0	0	0	0	0	0	0	0	0	n	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Troodontidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	n	0	0	0	0	0	?	?	?	?	0	0	0	0
Velociraptorinae	0	0	0	0	0	0	0	0	0	1	0	0	1	1	n	0	0	0	0	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	0	0	0	0	0	1	0	1	0	n	?	1	1	n	1	?	0	0	0	0	0	0	?	1	0	0	0
Rahonavis	?	?	?	?	?	0	1	0	1	0	0	1	1	1	n	1	1	0	0	0	0	0	?	0	1	1	0	0
Mononykus	?	?	?	?	1	1	?	?	?	1	0	?	0	0	1	?	?	?	?	?	?	?	1	0	0	1	?	1
Shuvuuia	?	?	?	?	1	?	0	0	0	1	0	0	0	0	1	0	1	1	1	2	1	1	1	?	0	?	?	?
Alvarezsaurus	?	?	?	?	0	?	0	0	0	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	0	?	0	?
Patagonykus	?	?	?	?	?	0	?	?	?	0	0	?	0	0	0	?	?	?	?	1	1	0	0	?	?	0	0	1
Confuciusornis	1	0	0	0	0	1	?	0	?	1	1	1	1	1	n	1	1	0	1	1	0	1	?	1	0	1	?	0
Changchengornis	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	0
Eoconfuciusornis	1	0	0	0	0	1	?	0	?	?	?	?	1	?	?	?	?	?	?	1	0	0	?	?	?	?	?	0
Noguerornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?
Iberomesornis	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	?	1	1	?	0	?	?	?	?	?	?	0
Patagopteryx	?	?	0	0	?	1	0	0	0	1	0	0	1	1	n	0	1	1	1	2	0	1	0	?	0	?	?	0
Vorona	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	0
Concornis	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	0	?	?	0	0	?	?	?
Cathayornis	0	1	0	1	0	?	0	0	1	1	?	?	1	1	n	1	?	1	1	?	?	0	?	?	0	1	1	0
Cobipteryx	?	?	0	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1	?	1	?	?	?	?	?	?
Eoalulavis	0	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
Neuquenornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
Ambiortus	?	?	1	1	n	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hesperornis	n	n	n	n	n	1	0	1	0	2	1	1	1	1	?	0	1	1	1	2	1	1	0	1	0	1	0	0
Ichthyornis	n	?	1	1	?	1	?	1	?	2	1	?	1	1	n	1	1	1	1	2	1	1	?	1	0	1	0	0
Anas	n	1	1	1	n	1	0	1	0	2	1	1	1	1	n	1	1	1	1	2	1	1	0	1	0	1	0	0

Taxon	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169
Allosauroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?
Troodontidae	0	?	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0	1	0	0	0	0	0	0	0	0	?	?
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?
Archaeopteryx	0	?	0	?	0	0	0	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Rahonavis	0	0	1	0	0	0	0	0	0	0	0	0	?	2	1	0	0	?	0	0	0	0	1	0	0	1	0	1	?
Mononykus	0	0	0	0	0	0	0	0	1	0	0	0	1	?	1	0	?	?	1	0	0	0	?	0	0	0	0	?	?
Shuvuuia	0	0	?	?	0	0	?	?	1	0	0	0	1	1	1	0	0	0	1	0	0	0	?	0	0	0	0	1	?
Alvarezsaurus	?	?	?	?	?	0	?	?	?	0	0	0	?	?	0	0	?	?	0	?	0	0	?	0	?	0	0	?	?
Patagonykus	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	?	0	0	?	?	?	?	?	?	0	?	?
Confuciusornis	?	?	1	?	?	1	?	?	0	0	1	0	?	1	1	0	1	0	0	0	0	0	1	0	1	1	0	1	0
Changchengornis	?	?	?	?	?	1	?	?	?	?	?	?	?	?	1	0	1	0	0	?	?	?	1	0	0	?	0	1	?
Eoconfuciusornis	?	?	?	?	?	0	?	0	0	0	0	0	?	?	?	0	?	0	0	0	0	0	1	0	0	?	0	1	0
Noguerornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
Iberomesornis	0	?	?	?	?	0	0	1	0	?	?	?	?	?	?	0	0	?	0	0	0	?	1	0	?	?	?	?	?
Patagopteryx	0	1	2	?	0	1	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	0	0	1	0	1	?	?
Vorona	0	1	1	?	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	0	?	0	1	0	0	?	?
Concornis	0	?	?	?	1	1	0	1	0	?	1	?	?	?	?	0	1	?	0	0	0	1	1	1	?	?	?	1	?
Cathayornis	0	1	1	?	0	1	?	?	0	0	1	1	1	?	1	0	?	?	0	0	?	?	?	?	1	?	0	?	?
Cobipteryx	?	?	?	?	?	?	0	1	0	0	1	?	1	?	1	0	1	1	0	0	?	1	?	1	0	1	0	?	?
Eoalulavis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
Neuquenornis	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	0	1	1	1	?	?	?	?	?
Ambiortus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
Hesperornis	1	1	2	1	0	1	1	0	0	1	0	0	1	2	1	1	1	1	2	1	1	0	0	0	0	0	0	?	?
Ichthyornis	1	1	2	?	0	1	1	0	0	1	0	0	?	2	1	1	1	1	2	1	1	0	?	0	0	0	1	?	?
Anas	1	1	2	1	0	1	1	0	0	1	0	0	1	2	1	1	1	1	2	1	1	0	1	0	0	0	1	1	1