

## **New Bird Remains from the Middle Eocene of Guangdong, China**

Authors: Wang, Min, Mayr, Gerald, Zhang, Jiangyong, and Zhou, Zhonghe

Source: *Acta Palaeontologica Polonica*, 57(3) : 519-526

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.0061>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# New bird remains from the Middle Eocene of Guangdong, China

MIN WANG, GERALD MAYR, JIANGYONG ZHANG, and ZHONGHE ZHOU



Wang, M., Mayr, G., Zhang, J., and Zhou, Z. 2012. New bird remains from the Middle Eocene of Guangdong, China. *Acta Palaeontologica Polonica* 57 (3): 519–526.

We describe a new avian taxon (*Sanshuiornis zhangii* gen. et sp. nov.) from Middle Eocene black oil shales in the Huayong Formation of Guangdong Province, south China. The specimen consists of a distal tibiotarsus and a complete foot with tarsometatarsus and pedal digits in articulation. A preliminary phylogenetic analysis does not resolve the affinities of the fossil, but the bones show resemblances to some “ciconiiform” birds. The peculiar hypotarsus morphology, which is block-like and exhibits four cristae, resembles that of the early Eocene *Rhynchaetites*, which is a stem group representative of the Threskiornithidae. The new Chinese fossil has, however, proportionally longer legs than *Rhynchaetites* and its phylogenetic affinities probably cannot be resolved without further material.

**Key words:** Aves, Ciconiiformes, Threskiornithidae, Middle Eocene, China.

Min Wang [wangmin\_nju@163.com], Jiangyong Zhang [zhangjiangyong@ivpp.ac.cn], and Zhonghe Zhou [zhonghe@yeah.net], Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, and Graduate University of Chinese Academy of Sciences, Beijing 100044, China;

Gerald Mayr [Gerald.Mayr@senckenberg.de], Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, 60325 Frankfurt am Main, Germany.

Received 2 June 2011, accepted 10 July 2011, available online 25 July 2011.

## Introduction

The fossil record of birds from the Paleogene of China is very scanty (Mayr 2009). To date, six genera and six species have been described. *Wanshuina lii* and *Songzia heidangkouensis*, which came from the Paleocene of Anhui and the early Eocene of Hubei respectively, were both referred to the Rallidae (Hou 1990, 1994). A very large species, *Zhongyuanus xichuanensis* from the early Eocene of Henan, was assigned to the anseriform family Gastornithidae (Hou 1980). *Eogrus aeola* from the middle Eocene of Inner Mongolia (Wetmore 1934) is a representative of the Eogruidae, which were widespread in the Paleogene of Asia (Kurochkin 1976; Clarke et al. 2005; Mayr 2009). *Eociconia sangequanensis* from the middle Eocene of Xinjiang (Hou 1989) was considered to belong to the Ciconiidae (storks). *Minggangia changgouensis* from the late Eocene of Henan (Hou 1982) was referred to the Threskiornithidae (ibises), while Stidham et al. (2005) suggested affinities to Rallidae (rails).

Here we describe a new fossil bird from the black oil shales of the Huayong Formation of the Sanshui Basin in Guangdong, south China (Fig. 1), which, based on morphological comparisons and the result of a phylogenetic analysis, shows closest affinities to some “ciconiiform” birds. The Paleogene strata in the Sanshui Basin are extensive, and numerous geological studies over the past years have made the Sanshui basin one of the best studied nonmarine Paleogene

strata and biotas from China (Hou et al. 2007). The deposits represent freshwater lacustrine environments, and abundant plants, invertebrates and some vertebrates have been recovered (Li et al. 2005; Hou et al. 2007). The age of the formation was regarded as either middle or late Eocene according to different authors (Zhang 1999; Hou et al. 2007), but it is most likely middle Eocene (Li et al. 2005; Meemann Chang, personal communication 2011).

## Material and methods

The avian material described in this paper is represented by a single incomplete specimen (IVPP V18116) that consists of a distal right tibiotarsus in articulation with a complete right foot, with tarsometatarsus and pedal phalanges in articulation.

The phylogenetic analysis is based on the data set of Mayr and Clarke (2003), with some erroneous scorings modified according to Mayr (2005, 2011) (see Appendix 1: 1). We added one new character to the data matrix, which is defined as: Character 149, second and third phalanx of the fourth toe, not as follows (0), strongly reduced and less than half the length of the fourth phalanx (1), as before but with the proximal phalanx strongly reduced to be nearly equal in length with the second and third phalanx (2). Twenty extant species were scored from materials in the collection of the In-

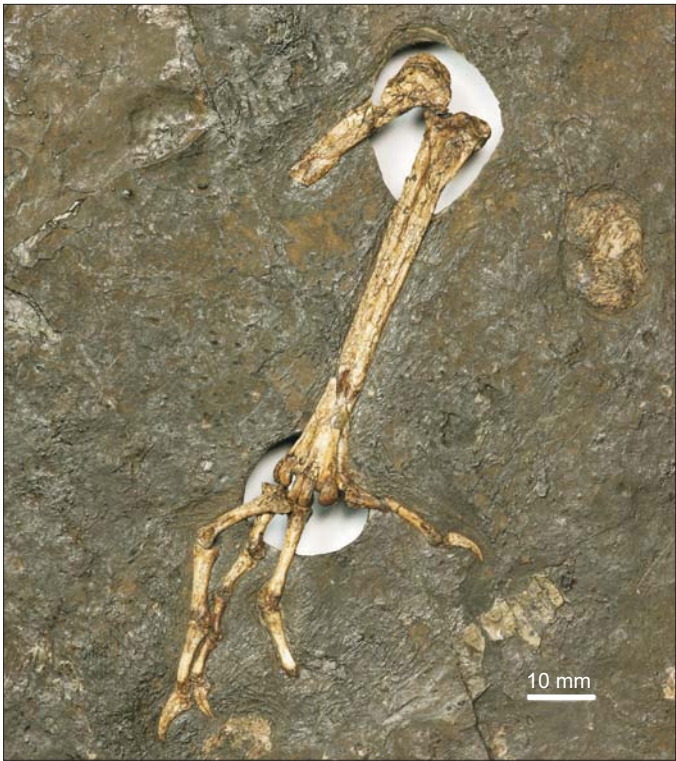


Fig. 1. Right leg of “ciconiiform” bird *Sanshuiornis zhangii* gen. et sp. nov. (IVPP V18116), from the Middle Eocene, Huayong Formation of Guangdong Province, south China.

stitute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science (IVPP) (Table 1), and the remaining taxa were scored from Mayr (2005) (see Appendix 1: 2, 3).

The phylogenetic analysis was carried out with Paup\* 4.0b10 (Swofford 2002), with three characters ordered (characters 55, 71, 91). We performed heuristic searches, with 1000 replicates of random stepwise addition (branch swapping: tree-bisection-reconnection), holding one tree at each step. Branches were collapsed to create polytomies if maximum branch lengths were zero. 500 bootstrap replicates were conducted with the same settings as in the primary search.

*Institutional abbreviation.*—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, China.

Systematic palaeontology

Aves Linnaeus, 1758  
cf. “Ciconiiformes” Bonaparte, 1984  
Genus *Sanshuiornis* nov.

*Type species:* *Sanshuiornis zhangii* sp. nov.; see below.  
*Etymology:* After Sanshui Basin where the holotype specimen was collected.  
*Diagnosis.*—As for the monotypic type species.

*Sanshuiornis zhangii* gen. et sp. nov.  
*Etymology:* The species name is dedicated to Xianqiu Zhang, a local geologist, who discovered the locality.  
*Holotype:* IVPP V18116, a distal right tibiotarsus in articulation with a complete right foot, with tarsometatarsus and pedal phalanges in articulation.  
*Type locality:* Foshan, Guangdong Province.  
*Type horizon:* Huayong Formation, Middle Eocene (Zhang 1999; Li et al. 2005; Meemann Chang, personal communication 2011)  
*Diagnosis.*—Medium-sized bird, which differs from all other known avian taxa in the block-like hypotarsus (Fig. 3), which exhibits four cristae and three well-delimited sulci.  
The new taxon differs from *Rhynchoaeites* in having the tarsometatarsus much longer, without marked tubercle on mid-section of proximal rim of medial parahypotarsal fossa, first phalanx of first pedal digit proportional longer, and four hypotarsal cristae more prominent. It differs from *Eociconia sangequanensis* in being proportionally much smaller, and

Table 1. List of the 20 scored taxa held in IVPP.

<i>Phasianus colchicus</i> (Galliformes: Phasianidae), V1864
<i>Chrysolophus pictus</i> (Galliformes: Phasianidae), V1866
<i>Aix galericulata</i> (Anatidae), V1869
<i>Podiceps cristatus</i> (Podicipedidae), V1899
<i>Nipponia nippon</i> (Threskiornithidae), V1376
<i>Syrhaptes paradoxus</i> (Pteroclididae), V529
<i>Tyto capensis</i> (Strigiformes), V1853
<i>Asio flammeus</i> (Strigiformes), V1890
<i>Strix leptogrammica</i> (Strigiformes), V1889
<i>Accipiter trivirgatus</i> (Accipitridae), V1879
<i>Buteo buteo</i> (Accipitridae), V1888
<i>Falco tinnunculus</i> (Falconiformes), V1800
<i>Centropus sinensis</i> (Cuculidae), V1887
<i>Gavia stellata</i> (Cuculidae), V1900
<i>Aptenodytes forsteri</i> (Spheniscidae), V1291
<i>Nycticorax nycticorax</i> (Ardeidae), V1861
<i>Ardeola bacchus</i> (Ardeidae), V1860
<i>Ardea cinerea</i> (Ardeidae), V1862
<i>Ciconia nigra</i> (Ciconiidae), V1543
<i>Puffinus leucomelas</i> (Procellariidae), V1734
<i>Otis tarda</i> (Otidae), V1711
<i>Otus bakkamoena</i> (Strigiformes), V1852
<i>Streptopelia orientalis</i> (Columbidae), V1883
<i>Streptopelia chinensis</i> (Columbidae), V1846
<i>Amaurornis phoenicurus</i> (Rallidae), V1894
<i>Gallinula chloropus</i> (Rallidae), V1893
<i>Grus japonensis</i> (Gruidae), V1029
<i>Melopsittacus undulatus</i> (Psittacidae), V1855
<i>Nymphicus hollandicus</i> (Psittacidae), V1895
<i>Psittacula alexandri</i> (Psittacidae), V1856
<i>Corvus frugilegus</i> (Passeriformes), V1903
<i>Lonchura punctulata</i> (Passeriformes), V1841
<i>Tarsiger cyanurus</i> (Passeriformes), V1808
<i>Phoenicurus aureus</i> (Passeriformes), V1810
<i>Corvus macrorhynchos</i> (Passeriformes), V1902
<i>Corvus monedula</i> (Passeriformes), V1904

Table 2. Measurement of *Sanshuiornis zhangii* gen. et sp. nov, from the middle Eocene Huayong Formation of Guangdong Province, south China, IVPP V18116.

Elements	Measurements (mm)
Tarsometatarsus length	64
Tarsometatarsus width (proximal end)	10
Tarsometatarsus width (middle shaft)	5
Metatarsal I length	11
Metatarsal II width (distal end)	3
Metatarsal III width (distal end)	3
Metatarsal IV width (distal end)	3
Pedal digit I-1 length	16
Pedal digit I-2 length	7
Pedal digit II-1 length	16
Pedal digit II-2 length	11
Pedal digit II-3 length	missing
Pedal digit III-1 length	15
Pedal digit III-2 length	12
Pedal digit III-3 length	10
Pedal digit III-4 length	8
Pedal digit IV-1 length	12
Pedal digit IV-2 length	7
Pedal digit IV-3 length	6
Pedal digit IV-4 length	6
Pedal digit IV-5 length	6

having trochlea metatarsi III in midline of tarsometatarsus. It is distinguished from Eogruidae in that the tarsometatarsus is much shorter, trochlea for second toe not reduced, and digit I well developed.

### Description

Anatomical terminology follows Baumel and Witmer (1993). The measurements (Table 2) represent the maximum length along the longitudinal axis; concerning the ungual phalanges, the distance between the extensor tubercle and the tip of the claw was measured; concerning the trochleae, the maximum width is measured.

**Tibiotarsus.**—The distal end of the right tibiotarsus is preserved in medial view and lacks a portion near the medial condyle. This bone resembles the tibiotarsus of extant *Threskiornis aethiopicus* (Threskiornithidae, African Sacred Ibis), in both medial and lateral views. The dorso-plantar width of the shaft near the proximal end of the medial condyle is similar to that of the Eocene ibis *Rhynchaetes messelensis* (SME-ME 3577, see Mayr 2009: fig. 7.8). In medial view, the lateral condyle extends a little further distally than the medial one, but it is shorter in the dorso-plantar direction. A prominent medial epicondyle is located on the upper border of the medial epicondylar depression. The distal rim of the medial condyle is flattened and bears a small notch. Clarke et al. (2005) listed this character as one of six unambiguously optimized synapomorphies supporting a (Psophiidae + Eogruidae + Gruidae) clade, but this character has a wider distribution, and occurs also in, e.g. Threskiornithidae, Podicipedidae, Phoenicopteridae, and some Ciconiidae (Mayr and Clarke 2003).

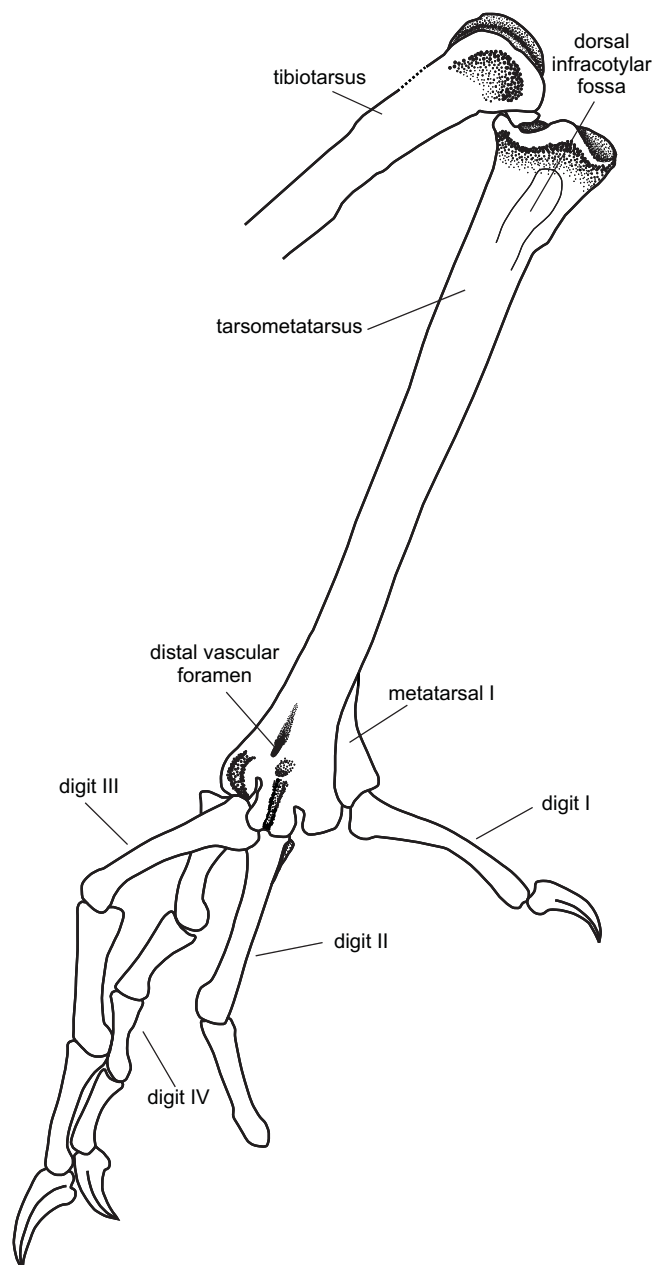


Fig. 2. Line drawing of “ciconiiform” bird *Sanshuiornis zhangii* gen. et sp. nov. (IVPP V18116), from the Middle Eocene Huayong Formation of Guangdong Province, south China.

On the reverse side of the slab, the lateral aspect of the lateral condyle is exposed, and some anatomical details are discernible. The lateral epicondylar depression is shallow and less developed compared with the corresponding depression of the medial condyle. The lateral epicondylar depression appears to be divided into two small depressions by a small crest. The distal rim of the lateral condyle has a subcircular outline, while the outline of the medial condyle is elliptical. A subcircular lateral condyle is also found in *Rhynchaetes messelensis* (Mayr 2009: fig. 7.8), *Minggangia changgouensis* (Hou 1982), some extant Threskiornithidae (Min Wang, personal observation), and *Ibidopsis hordwelliensis* (Harrison and Wal-





Fig. 3. Proximal end of tarsometatarsus of “ciconiiform” bird *Sanshuiornis zhangii* gen. et sp. nov. (IVPP V18116), from the Middle Eocene Huayong Formation of Guangdong Province, south China, in plantar view.

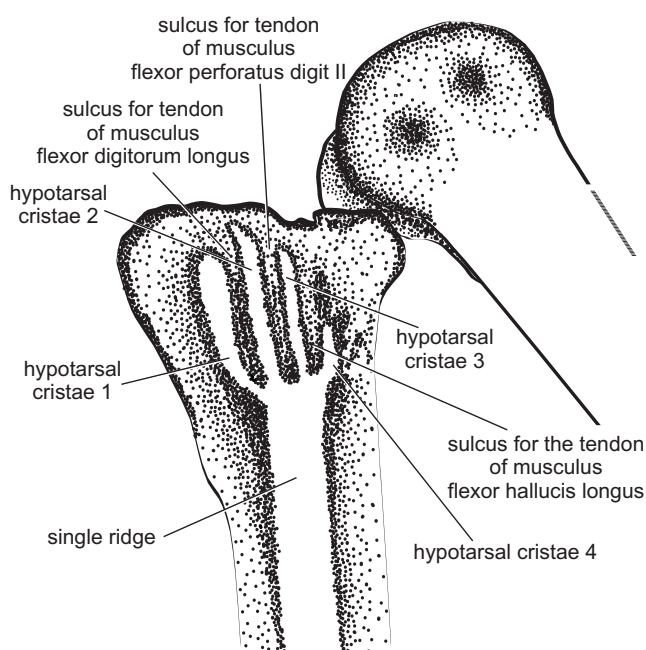


Fig. 4. Line drawing of the proximal end of the tarsometatarsus of “ciconiiform” bird *Sanshuiornis zhangii* gen. et sp. nov. (IVPP V18116), from the Middle Eocene Huayong Formation of Guangdong Province, south China, in plantar view. The single ridge is formed by convergence of the four hypotarsus cristae.

ker 1976: pl. 6E), but is absent in *Eogrus aeola* (Wetmore 1934: fig. 5) and extant Gruidae. Stidham et al. (2005) indicated that this primitive character would be consistent with a

transfer of *Minggania changgouensis* and *Ibidopsis hordwelliensis* to Rallidae (Harrison and Walker 1976), but the character clearly has a wider distribution (it is, for example, present in extant Threskiornithidae) and the rallid affinities of these two species are questionable (Mayr 2009). The medial and lateral condyles are separated by a shallow ovate depression, and the intercondylar sulcus is deeper than the trochlea for the tibial cartilage. Because the tibiotarsus is preserved in latero-medial view, the cranial aspect of the shaft is hardly exposed, and related anatomical features are uncertain. Clearly there is a sulcus between the medial and lateral condyles, presumably the extensor sulcus, but a supratendinal pons cannot be discerned.

**Tarsometatarsus.**—The tarsometatarsus is preserved in dorsal view, but on the reverse side of the slab, the plantar surfaces of the proximal and distal ends are exposed (Fig. 5). The shaft is almost straight. Its medio-lateral width narrows slowly from the proximal end to three quarters of the length of the shaft, where it is narrowest, and then expands to the distal end. The narrowest portion has a width of 5 mm, which is nearly half the width of the proximal end. The tarsometatarsus is nearly two times the length of that of *Rhynchaetites messelensis* and is proportionally more slender. In both taxa the bone is proportionally shorter than in extant Threskiornithidae. Compared with *Eogrus aeola* (Wetmore 1934), the tarsometatarsus of *Sanshuiornis zhangii* is much sturdier.

On the proximal end of the shaft, the intercotylar eminencia is low, medio-laterally broad, and directed slightly dorso-proximally. The medial side of the intercotylar eminencia slopes gently to the medial cotyla, while the lateral side slopes abruptly to the lateral cotyla. In dorsal view, the lateral cotyla is located a little more distally than the medial cotyla. The dorsal rim of the lateral cotyla is flattened medio-laterally, and is longer than the dorsal rim of the medial cotyla. The medial cotyla is somewhat curved medially away from the shaft. The dorsal rim of the medial cotyla is lower than the plantar one, and its lateral side abuts the relatively high intercotylar eminencia, so the medial cotylar facet projects dorso-proximally in dorsal view. The lateral cotyla appears not as deep as the medial one, and its facet runs in parallel to the shaft. The above morphologies are similar to those of *Rhynchaetites messelensis* and extant Threskiornithidae, but different from extant Ciconiidae or Gruidae, in which the intercotylar eminencia does not project abruptly.

The morphology of the hypotarsus resembles *Rhynchaetites messelensis* (see Mayr and Bertelli 2011: fig. 4) but still shows some clear differences. It lacks any bony canals, but is composed of four prominent cristae, which separate three sulci. If these four cristae are numbered from 1 to 4 starting medially, crista 1 is the widest. The remaining three cristae seem to be situated on the same platform, and diverge from a distal common basis. Cristae 2 and 3 have the same length and width. It is uncertain whether crista 4 is crushed or not, as the preserved section is extremely short. The sulcus between cristae 1 and 2 is markedly deep, and probably represents the



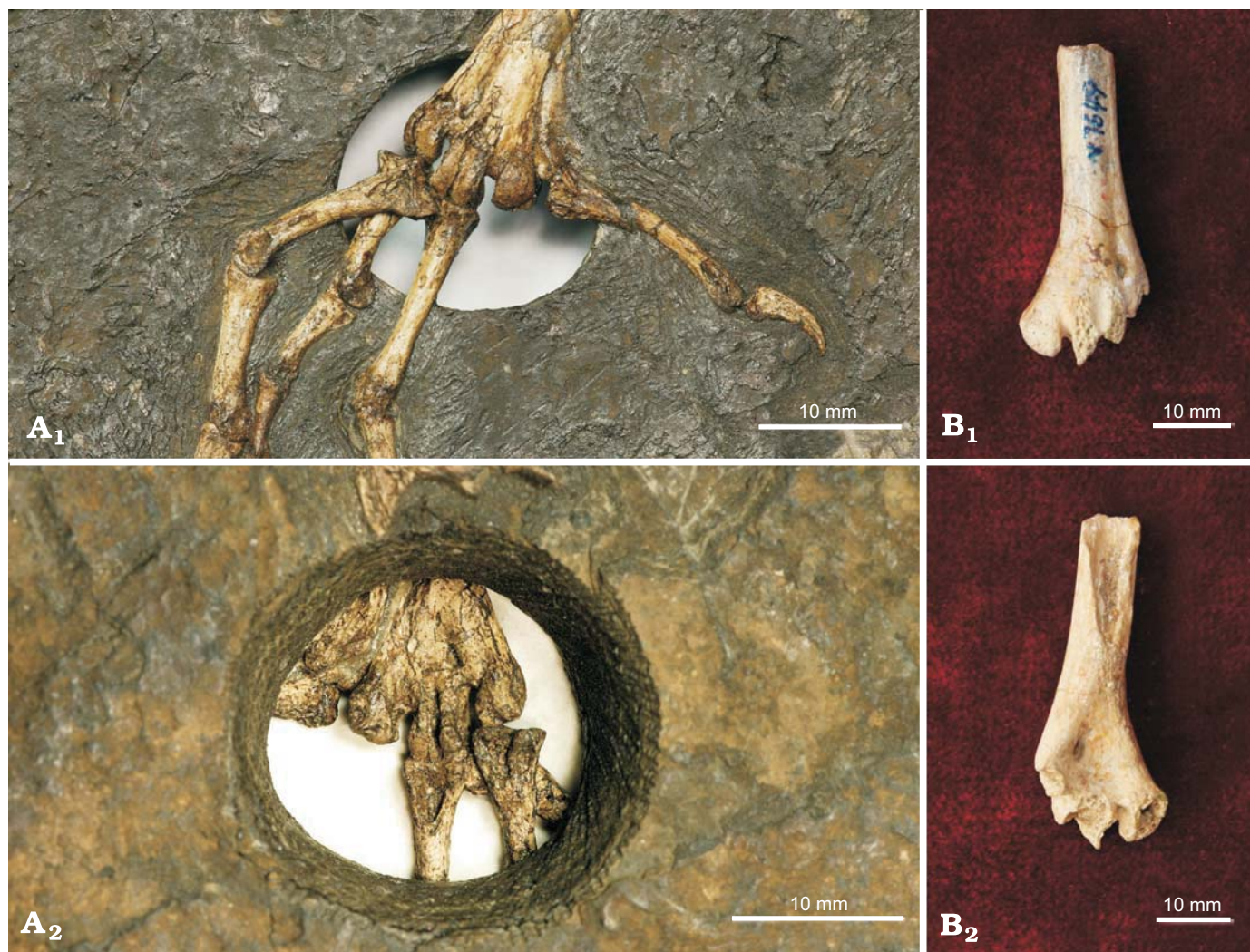


Fig. 5. Distal end of the tarsometatarsus. **A.** “Ciconiiform” bird *Sanshuiornis zhangii* gen. et sp. nov. (IVPP V18116), from the Middle Eocene Huayong Formation of Guangdong Province, south China, in dorsal ( $A_1$ ) and plantar ( $A_2$ ) views. **B.** Ciconiid bird *Eociconia sangequanensis* Hou, 1989 (holotype, left tarsometatarsus, IVPP V7649), from the Middle Eocene Yixibaila Formation of Xinjiang, China, in dorsal ( $B_1$ ) and plantar ( $B_2$ ) views.

sulcus for the tendon of musculus flexor digitorum longus. The two sulci between cristae 2 and 4 are shallower, and presumably are the sulci for the tendons of musculus flexor perforatus digit II, and musculus flexor hallucis longus respectively. The widths of these three sulci are roughly the same. In *Rhynchaetes messelensis*, as in *Sanshuiornis zhangii*, the medial crista is the most developed, but the remaining three cristae are more weakly developed compared to *Sanshuiornis zhangii*, so that the middle and lateral sulci are not as prominent (compare Fig. 3 with Mayr and Bertelli 2011: fig. 4). The distal end of crista 1 converges with the basis of the remaining three cristae into a single ridge, and extends proximo-distally, which is not the case in *Rhynchaetes messelensis*. This ridge is very wide, measuring nearly one third of the width of the shaft. The medial parahypotarsal fossa is much deeper than the lateral one, and the two fossae extend distally to one fourth of the length of the shaft, where the single ridge begins to be confluent with the shaft. There is a marked tubercle on the mid-section of the proximal rim of

the medial parahypotarsal fossa in a newly reported *Rhynchaetes* sp. (Mayr and Bertelli 2011), but such a tubercle is absent in *Sanshuiornis zhangii* and extant Threskiornithidae.

The dorsal surface of the tarsometatarsus is deeply excavated by the dorsal infracotylar fossa on the proximal end. The extensor sulcus occupies about one third the width of the shaft through most of its length. Its lateral section appears deeper than its medial section, but this may be an artefact of preservation. The sulcus begins to angle gently from the medial to the lateral side of the shaft, at three-fourths of the length of the shaft, and extends into the distal vascular foramen. The fossa infracotylaris dorsalis area is crushed and difficult to discern. The distal vascular foramen is situated just upon the upper margin of the lateral intertrochlear incision, and is situated more distally than in *Eociconia sangequanensis*. The distal vascular foramen is elliptical, with the width being half its length.

In their proportions, the trochleae resemble those of extant Threskiornithidae.

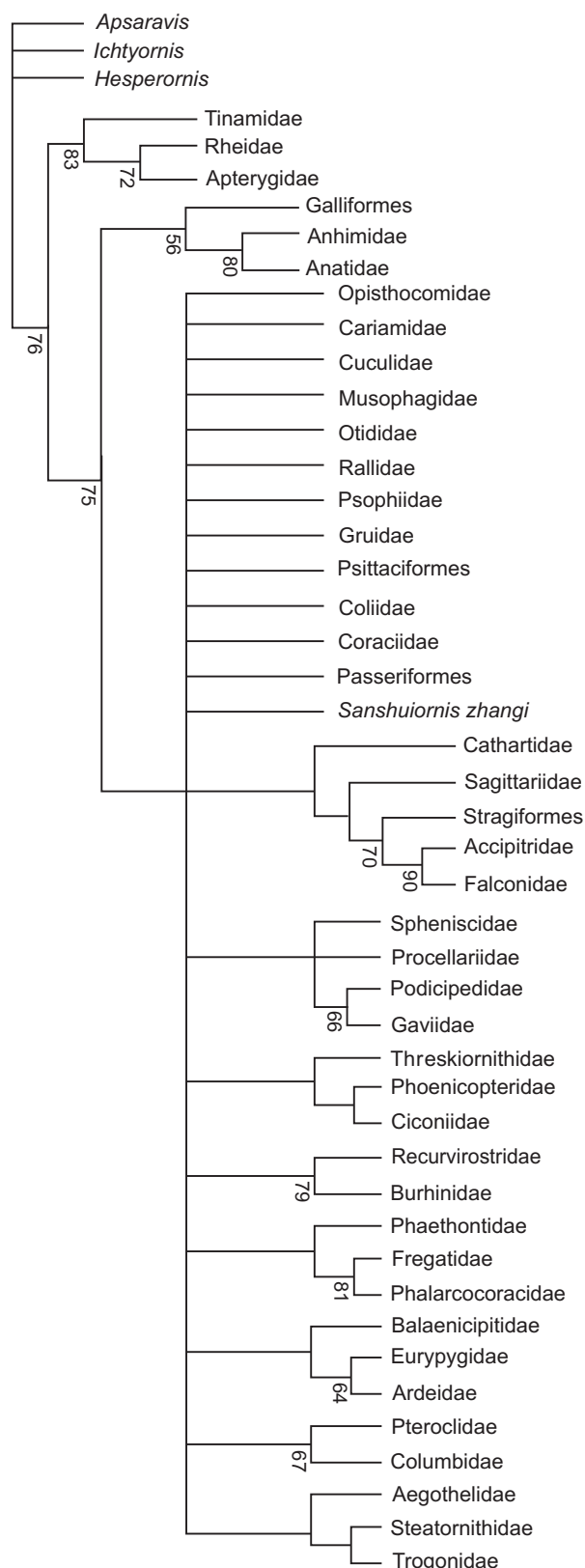


Fig. 6. The strict consensus tree of 39 most parsimonious trees resulting from analysis of the modified matrix of Mayr and Clarke (2003) integrating *Sanshuiornis zhangii*, with three characters ordered (55, 71, 91) following Mayr and Clarke (2003). Length = 728, Consistency index (CI) = 0.23, Retention index (RI) = 0.48, Homoplasy index (HI) = 0.77. Bootstrap values of more than 50% are shown next to the corresponding nodes.

The distal end of the trochlea for the second toe is expanded and ball-shaped in both dorsal and distal view, lacking an articular furrow on its dorsal surface. There is, however, a groove on the plantar surface, and the medial section of the trochlea is plantarly deflected. The collateral ligamental fovea on its medial side is exposed. The distal articular facet is medially deflected, forming an angle of  $33^\circ$  with the longitudinal axis of the tarsometatarsus. The medial intertrochlear incision is not as deep as the lateral one, but mediolaterally wider. The trochlea metatarsi III projects more dorsally and distally than the other trochleae, which reach almost the same dorsal and distal level. It is grooved on its dorsal surface, and even more strongly so on the plantar surface. The width of the groove decreases slowly in the disto-dorsal direction. On the proximal end of this trochlea there is a fossa, which is wider than the distal vascular foramen; its proximal boundary is at the same distal level with the distal end of the distal vascular foramen. The distal articular facet of the trochlea for the fourth toe projects laterally, forming an angle of  $20^\circ$  with the longitudinal axis of the tarsometatarsus. Its dorsal surface is grooved, but the plantar groove is only very shallow. The dorsal groove is wider than that of the third trochlea, but less deep. The distal end of the trochlea bears a curving groove, and the groove becomes shallower distally. The proximal end of the trochlea metatarsi IV is not expanded significantly, meeting with the shaft of the tarsometatarsus with little demarcation. The trochlea metatarsi IV projects a little more dorsally than the trochlea metatarsi II, but less so than the trochlea metatarsi III. There is a distal interosseous canal opening into the lateral intertrochlear incision, which is connected with distal vascular foramen in plantar view, but cannot be seen in dorsal view.

**Metatarsal I** measures about two-thirds of the length of the first phalanx of digit I and attaches to the tarsometatarsus tightly throughout most of its length. It is "J" shaped in dorsal view, and also exposes its lateral side, where a collateral ligamental fovea can be seen. The plantar supratrochlear fossa is shallow, and demarcated medially by a high ridge, which separates the base of metatarsal I and the trochlea metatarsi II.

**Pedal phalanges.**—The pedal digits are almost completely preserved in articulation, except that digits II, III are displaced. Like in most birds, the phalangeal formula is 2-3-4-5.

Digit I is well developed and reaches about half the length of digit III. Assuming that the unguals are roughly similar in length for all the digits, which is confirmed by the unguals of digit I, III and IV, digit II is shorter than digit III. The proximal phalanx of digit I, as well as the proximal phalanx of digit II, are the longest phalanges; both are proportionally shorter than the corresponding phalanges of *Rhynchaetites messelensis*. The proximal phalanges of digit I and IV are slimmer than the proximal phalanges of the other toes.

The proximal phalanx of digit II measures 133% of the length of its penultimate one, and both are compressed in the mid section, with expanded distal and proximal ends.



Digit III is the longest and measures more than half of the length of the tarsometatarsus, and 195% and 122% of the length of digits I and IV respectively. Compared with *Rhynchoaeites messelensis*, it is proportional shorter. The estimated length of digit III is nearly equal to the length of the tarsometatarsus in *Rhynchoaeites messelensis*, but because of the longer tarsometatarsus the same ratio for IVPP V18116 is 70%. All phalanges of the third toe are exposed in medial view, and the flexor tubercles and collateral ligamental foveae can be seen. The length of the phalanges decreases proximodistally, with the proximal phalanx being 150% as long as the penultimate one, and the second one being the most robust.

The lengths of the phalanges of digit IV also decrease distally, and the proximal phalanx is twice as long as the penultimate one. The proximal phalanx of digit IV is the shortest, and the last three phalanges including the ungual are equal in length.

The ungual phalanges have a similar morphology, including the developments of the flexor tubercles and vascular sulcus. The unguals of digit I and II are equal in size, and smaller than that of digit IV. The ungual of the third toe is the biggest.

*Stratigraphical and geographical range.*—Huayong Formation, Middle Eocene, Foshan, Guangdong Province.

## Result of phylogenetic analysis

The new species was added to the data matrix of Mayr and Clarke (2003), and fourteen characters were scored for the new fossil. 405 most parsimonious trees were obtained (length = 728, CI = 0.23, RI = 0.48, HI = 0.77), the strict consensus tree of which is shown in Fig. 6. In the strict consensus tree, the relationships of a large number of taxa, including *Sanshuiornis zhangii*, is unresolved. In 66 of the 405 most parsimonious trees, *S. zhangii* is sister taxon of a clade including Threskiornithidae, Ciconiidae, and Phoenicopteridae.

## Discussion

The morphological features displayed by *Sanshuiornis zhangii* rule out some taxa as close relatives. For example, the hypotarsus lacks bony canals, which are present in Galliformes, all Pelecaniformes except Phaethontidae (Mayr and Bertelli 2011), and most psittaciform birds (Mayr 2008). Unlike Accipitridae, Falconidae, Horusornithidae and Sagittariidae (Mayr 2006), the central phalanges of the fourth toe and the proximal phalanx of the second toe are not strongly reduced. The trochleae metatarsorum II and IV extend to the same level distally, which is different from the condition seen in Eogruidae, Gruidae, Rallidae, Procellariidae and Phoenicopteridae (Wetmore 1934; Mayr and Clarke 2003; Clarke et al. 2005).

In overall morphology of the bones, *Sanshuiornis zhangii* most closely resembles some fossil “ciconiiform” birds, especially the poorly known and much larger *Eociconia sangequanensis* and the stem-group threskiornithid *Rhynchoaeites*. The holotype of *E. sangequanensis* preserves only the distal end of the left tarsometatarsus (Fig. 5), and the trochleae metatarsorum are largely broken. *S. zhangii* differs from *E. sangequanensis* in: (i) being much smaller, (ii) width of the medial intertrochlear incision smaller, (iii) trochlea metatarsi III positioned in the center of the tarsometatarsus, not as medially displaced as in *E. sangequanensis*, and (iv) the extensor groove proximal of the distal vascular foramen being deeper.

*Sanshuiornis zhangii* resembles *Rhynchoaeites messelensis* in many respects, especially that (i) the hypotarsus consists of four cristae without bony canals, with the medial crista being the most prominent (compare Fig. 3 with Mayr and Bertelli 2011: fig. 4), and (ii) the length of the phalanges of the three anterior toes decreases distally. The key traits in which *Rhynchoaeites* differs from *Sanshuiornis* are the presence of the tubercle on the proximal rim of the medial parahypotarsal fossa (see Mayr and Bertelli 2011), and the difference in the proportional length of some elements, especially pedal digits (proportionally shorter in *Rhynchoaeites*) and tarsometatarsus (proportionally longer in *Sanshuiornis*).

Unfortunately, the affinities of the fossil are not resolved in our phylogenetic analysis. Although 66 of the 405 most parsimonious trees recover a sister-group relationship between *Sanshuiornis zhangii* and the clade (Threskiornithidae + Ciconiidae + Phoenicopteridae), the evidence for this grouping is weak. Five characters were optimized as apomorphies of this clade: (i) distal rim of medial condyle of tibiotarsus notched (character 102: 1, CI = 0.33, HI = 0.60), (ii) hypotarsus without bony canals for musculus flexor digitorum longus (character 105: 0, CI = 0.14, HI = 0.40) and musculus flexor hallucis longus (character 106: 0, CI = 0.11, HI = 0.38), (iii) presence of distal interosseus canal (character 107: 0, CI = 0.50, RI = 0), (iv) tarsometatarsal trochleae II and IV extending to same dorsal and distal level (character 108: 1, CI = 0.11, HI = 0.42), and (v) hallux not reduced (character 110: 0, CI = 1, RI = 1). At least the latter three of these represent, however, the plesiomorphic condition in neornithine birds, and the first two have a wide distribution and are thus of little significance. Moreover, whereas Threskiornithidae are traditionally considered to be closely related to the Ciconiidae (Mayr and Clarke 2003; Clarke et al. 2005; Livezey 2007), a clade including (Threskiornithidae + Ciconiidae + Phoenicopteridae) is not supported by current phylogenetic analyses, which show Phoenicopteridae to be the sister taxon of Podicipedidae (e.g., Ericson et al. 2006; Hackett et al. 2008).

Although we note morphological similarities with some “ciconiiform birds”, we thus conclude that a definitive phylogenetic placement of the fossil is not possible with the material at hand.



## Acknowledgements

We thank Xianqiu Zhang and Xiaojun Zhang (both SINOPEC Star Petroleum Corporation Limited, Guangdong, China), Zhao Wang and Qiuyuan Wang for help in the field, Yutong Li for fossil preparation, and Wei Gao for photos (all Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, China). The research was supported by National Natural Science Foundation of China and the Chinese Academy of Sciences. We thank Gareth Dyke (School of Biology and Environmental Science, University College Dublin, Belfield Dublin 4, Ireland) and Nathan Smith (Department of Geology, The Field Museum of Natural History, Chicago, USA) for reviewing the manuscript and providing helpful comments.

## References

- Baumel, J.J. and Witmer, L.M. 1993. Osteologia. In: J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Van den Berge (eds.), *Handbook of Avian anatomy: Nomina Anatomica Avium. Publications of the Nuttall Ornithological Club* 23: 45–132.
- Clarke, J.A., Norell, M.A., and Dashzeveg, D. 2005. New avian remains from the Eocene of Mongolia and the phylogenetic position of the Eogruidae (Aves, Gruoidea). *American Museum Novitates* 3494: 1–17.
- Ericson, P.G.P., Anderson, C.L., Britton, T., Elzanowski, A., Johansson, U.S., Källersjö, M., Ohlson, J.I., Parsons, T.J., Zuccon, D., and Mayr, G. 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters* 2: 543–547.
- Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., and Yuri, T. 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 320: 1763–1768.
- Harrison, C.J.O. and Walker, C.A. 1976. Birds of the British Upper Eocene. *Zoological Journal of the Linnean Society* 59: 323–351.
- Hou, L.-H. 1980. New form of the Gastornithidae from the Lower Eocene of the Xichuan, Henan [in Chinese, with English abstract]. *Vertebrata Palasiatica* 18: 111–115.
- Hou, L.-H. 1982. New form of the Threskiornithidae from the Upper Eocene of the Minggang, Henan [in Chinese, with English abstract]. *Vertebrata Palasiatica* 20: 196–202.
- Hou, L.-H. 1989. A Middle Eocene bird from Sangequan, Xinjiang [in Chinese, with English abstract]. *Vertebrata Palasiatica* 27: 65–70.
- Hou, L.-H. 1990. An Eocene bird from Songzi, Hubei province [in Chinese, with English abstract]. *Vertebrata Palasiatica* 28: 34–42.
- Hou, L.-H. 1994. A new Paleocene bird from Anhui, China [in Chinese, with English abstract]. *Vertebrata Palasiatica* 32: 60–65.
- Hou, M.-C., Chen, H.-D., Tian, J.-C., and Wan, L. 2007. Sedimentary facies and palaeogeography of the Sanshui basin, Guangdong during the Palaeogene [in Chinese, with English abstract]. *Sedimentary Geology and Tethyan Geology* 27: 37–44.
- Kurochkin, E.N. 1976. A survey of the Paleogene birds of Asia. *Smithsonian Contributions to Paleobiology* 27: 75–86.
- Li, J.-G., Hong, W.-Y., Wen, Y.-W., and Wang, Y.-D. 2005. Discovery of early–Middle Eocene fresh water biota and its geological significance in Lubao-Datang area, Sanshui, Guangdong province [in Chinese, with English abstract]. *Geology and Mineral Resources of South China* 3: 72–76.
- Livezey, B.C. and Zusi, R.L. 2007. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society* 149: 1–95.
- Mayr, G. 2005. The postcranial osteology and phylogenetic position of the Middle Eocene *Messelastur gratulator* Peters, 1994—a morphological link between owls (Strigiformes) and Falconiform birds? *Journal of Vertebrate Paleontology* 25: 635–645.
- Mayr, G. 2006. A new raptorial bird from the Middle Eocene of Messel, Germany. *Historical Biology* 18: 95–102.
- Mayr, G. 2008. The phylogenetic affinities of the parrot taxa *Agapornis*, *Loriculus* and *Melopsittacus* (Aves: Psittaciformes): Hypotarsal morphology supports the results of molecular analyses. *Emu* 108: 23–27.
- Mayr, G. 2009. *Paleogene Fossil Birds*. 262 pp. Springer, Heidelberg.
- Mayr, G. 2011. On the osteology and phylogenetic affinities of *Morsoravis sedilis* (Aves) from the Early Eocene Fur Formation of Denmark. *Bulletin of the Geological Society of Denmark* 59: 23–35.
- Mayr, G. and Bertelli, S. 2011. A record of *Rhynchaetites* (Aves, Threskiornithidae) from the early Eocene Fur Formation of Denmark, and the affinities of the alleged parrot *Mopsitta*. *Palaeobiodiversity and Palaeoenvironments* 91: 229–236.
- Mayr, G. and Clarke, J. 2003. The deep divergences of neornithine birds: A phylogenetic analysis of morphological characters. *Cladistics* 19: 527–553.
- Stidham, T.A., Holroyd, P.A., Gunnell, G.F., Ciochon, R.L., Tsubamoto, T., Egi, N., and Takai, M. 2005. An ibis-like bird (Aves: Threskiornithidae) from the late Middle Eocene of Myanmar. *Contribution from the Museum of Paleontology, University of Michigan* 31: 179–184.
- Swofford, D.L. 2002. *PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods)*. Version 4. Sinauer Associates, Sunderland.
- Wetmore, A. 1934. Fossil birds from Mongolia and China. *American Museum of Novitates* 711: 1–16.
- Zhang, X.Q. 1999. Geology of the Cretaceous–Tertiary basin in Guangdong [in Chinese]. *Guangdong Geology* 14 (3): 53–57.

## Appendix 1

1. The modified characters in the data matrix (Mayr and Clarke 2003) according to Mayr (2011) are as follows: Gruidae (character 6: 1), Hesperornithidae (character 22: 1), Phoenicopteridae (character 31: 1), Apterygidae (character 32: 1), Phalacrocoracidae (character 57: 0), Rheidae (character 65: 1), Anatidae (character 85: 0), Opisthocomidae (character 85: 1), Apterygidae (character 100: 0), Coliidae (character 105: 0; character 106: 1)
2. *Sanshuiornis zhangii* scoring in Mayr and Clarke (2003) data matrix: 102: 1, 103: 1, 104: 0, 105: 0, 106: 0, 107: 0, 108: 1, 109: 0, 110: 0, 111: 0, 112: 0, 113: 0, 114: 0, 149: 0

3. Character 149 scored for all the taxa:

*Apsaravis*: ?, *Hesperornis*: ?, *Ichthyornis*: ?, Rheidae: 1, Apterygidae: 0, Tinamidae: 0, Galliformes: 0, Anhimidae: 0, Anatidae: 0, Opisthocomidae: 0, Podicipedidae: 0, Phoenicopteridae: 0, Threskiornithidae: 0, Cariamidae: 0, Strigiformes: 2, Recurvirostridae: 0, Burhinidae: 0, Accipitridae: 1, Falconidae: 2, Sagittariidae: 0, Cuculidae: 0, Musophagidae: 0, Cathartidae: 0, Gaviidae: 0, Spheniscidae: 0, Phaethontidae: 0, Fregatidae: 0, Phalacrocoracidae: 0, Balaenicipitidae: 0, Eurypygidae: 0, Ardeidae: 0, Ciconiidae: 0, Procellariidae: 0, Otididae: 0, Pteroclididae: 0, Columbidae: 0, Rallidae: 0, Psophiidae: 0