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Two new skeletons of the enigmatic, rail-like avian taxon *Songzia Hou*, 1990 (Songziidae) from the early Eocene of China

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Two new skeletons of the enigmatic, rail-like avian taxon *Songzia* Hou, 1990 (Songziidae) from the early Eocene of China

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We describe two nearly complete articulated skeletons of a new species of Songziidae Hou, 1990 from the early Eocene of Central China. The specimens provide new anatomical information on this poorly known avian taxon. Songziids were considered most closely related to Rallidae in the original description, but as yet no convincing evidence has been put forth concerning their affinities. Phylogenetic analyses based on two previously published data sets combining data from the new fossils did not provide conclusive evidence concerning the affinities of songziids. Whereas one analysis supported rallid affinities, the other resulted in a clade including Songziidae, Messelornithidae, Rallidae and Heliornithidae. Apart from the proportionally much longer legs, the osteology of *Songzia* is, however, more similar to that of the contemporary Messelornithidae than to Rallidae.

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COMPARED with that of the Cretaceous, the fossil record of birds from the Paleogene of China is very scanty (Mayr 2009). Previously, only eight species in as many genera have been described. In chronological order of their descriptions, these are *Eogrus aeola* Wetmore, 1934 (Eogruidae; e.g., Clarke *et al.* 2005), *Zhongyuanus xichuanensis* Hou, 1980 (Gastornithidae), *Minggangia changgouensis* Hou, 1982 (?Threskiornithidae), *Eociconia sangequanensis* Hou, 1989 ('Ciconiiformes' incertae sedis), *Wanshuina lii* Hou, 1994 (family incertae sedis), *Songzia heidangkouensis* Hou, 1990 (Songziidae), *Jilinornis huadianensis* Hou & Ericson, 2002 (*cf.* 'Charadriidae') and a new species of a ciconiiform-like bird (Wang *et al.* in press). Apart from the Paleocene *Wanshuina lii*, all of these species stem from early or middle Eocene localities and, except for *S. heidangkouensis*, all are represented by fragmentary remains.

The incomplete holotype of *S. heidangkouensis* from the early Eocene Yangxi Formation was assigned to the new taxon Songziidae by Hou (1990) and tentatively assumed to be related to Rallidae. Its affinities have, however, not been

conclusively resolved (Mayr 2009). In particular, songziids have so far not been compared with the contemporary rail-like Messelornithidae (Messel rails), which are very common in the early Eocene of Europe and North America, and which possess an at least superficially similar osteology (Hesse 1990, Mayr 2009, Weidig 2010, Bertelli *et al.* 2011).

The early Eocene Yangxi Formation represents lacustrine deposits, from which plants, invertebrates and vertebrate fossils have been collected; it contacts unconformably and conformably, respectively, with the underlying Paomagang Formation and overlying Pailougou Formation in Songzi.

Here, we describe two new, largely complete skeletons of songziids from the type locality of *S. heidangkouensis* (Fig. 1), which differ from *S. heidangkouensis* in size and the shape of the ungual phalanges. Features, such as a smooth surface of the long limb bones, fusion of the uncinat processes with the ribs and the synsacrum with the pelvic bones, respectively, together with the completely fused tarsometatarsus, indicate that both are adult specimens. The new *Songzia* fossils are better preserved than the holotype of *S. heidangkouensis* and yield important complementary information about the skull, thoracic girdle, humerus and pelvic girdle. Consequently, they allow for a more detailed description of the anatomical features of *Songzia*

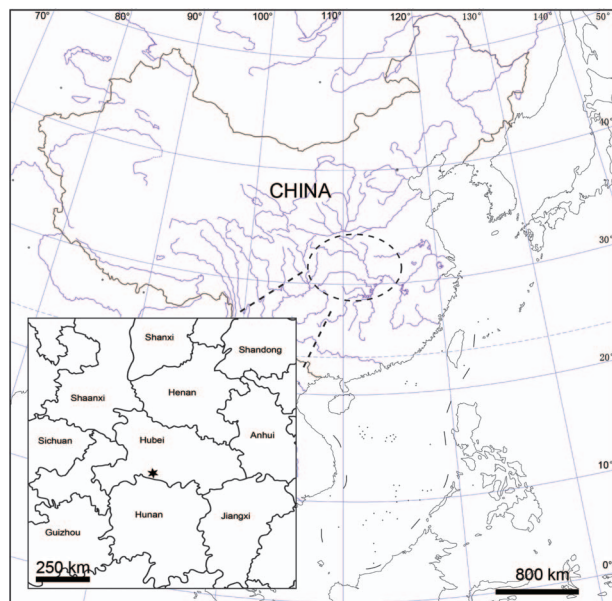


Fig. 1. Map of China showing the fossil locality.

and a refined assessment of its phylogenetic affinities.

Material and methods

The two fossils, each preserved as an articulated skeleton on a single slab, are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China (IVPP). Anatomical terminology follows Baumel & Witmer (1993). Length measurements represent the maximum length along the longitudinal axis; concerning the ungual phalanges, the distance between the tuberculum extensorium and the tip of the claw was measured.

In order to assess the phylogenetic affinities of Songziidae, we performed two phylogenetic analyses based on previously published data matrices from Livezey (1998) and Bertelli *et al.* (2011) respectively. Livezey's (1998) matrix is composed of 381 primarily osteological characters and 76 taxa. It samples all genera of Psophiidae, Aramidae, Gruidae, Heliornithidae and Rallidae; Charadriiformes and a hypothetical ancestor were used as outgroup. This matrix was used in a phylogenetic analysis at genus level of Gruiformes by Livezey (1998, appendix A). Applying this data set, 100 characters could be scored for *Songzia* (Appendix 1), and 12 characters of *Messelornis* (characters 1:1, 50:?, 176:0, 182:0, 184:1, 189:1, 194:0, 201:0, 240:0, 250:?, 265:0, 271:?) were modified according to Mayr (2004), Bertelli *et al.* (2011) and Worthy & Boles (2011). The matrix of Bertelli *et al.* (2011) includes 27 taxa and 83 morphological characters; outgroup comparisons were performed with Tinamidae; 27 characters can be scored for *Songzia* (Appendix 2).

The phylogenetic analyses were performed with TNT [version 1.1] (Goloboff *et al.* 2008). We used unconstrained heuristic searches, with 1000 replicates of random stepwise addition (branch swapping: tree-bisection-reconnection), holding ten trees at each step. All characters were given equal weight. Branches were collapsed to create polytomies if minimum branch lengths were zero. Bootstrap analysis was conducted with 1000 replicates with the same settings as in the primary search.

Systematic palaeontology

AVES Linnaeus, 1758

NEOGNATHAE Pycraft, 1900

SONGZIIDAE Hou, 1990

Songzia Hou, 1990

Type species. *Songzia heidangkouensis* Hou, 1990; early Eocene, Hubei, China.

Emended differential diagnosis. Corncrake (*Crex crex*)-sized birds, which differ from other avian taxa by the combination of the following characters: (1) beak short, measuring about one-third of the length of cranium, (2) limb proportions rail-like (as compared with, e.g., *Gallinula chloropus*), with very long legs and stout ulna not reaching beyond humerus in length, (3) sternum wide and with two shallow caudal incisions on each side, (4) toes very elongated, the longest toe nearly equal to tarsometatarsus in length, and (5) the second phalanx of digit III being longer than the distal third and fourth phalanges.

Species in Songziidae differ from those in Messelornithidae in: (1) the proportionally shorter beak (the distance from the tip of the beak to the rostral margin of the orbit measures 34–37% of the skull length, whereas it is nearly 44% in *Messelornis cristata*), (2) longer forelimbs, with the ratio of (humerus + ulna + carpometacarpus)/(femur + tibiotarsus + tarsometatarsus) being 0.68–0.71 in songziids versus about 0.60 in *Messelornis cristata* (Hesse 1988), (3) proportionally longer femur, with the ratio of femur/tarsometatarsus being 0.83–0.91 in *S. heidangkouensis* versus about 0.67 in *Messelornis cristata* (Hesse 1988), (4) the caudal incisions of the sternum being shallower than in *M. cristata* and *Pellornis mikkelsenii*, (5) the length of the third pedal digit being nearly equal to that of the tarsometatarsus, but measuring not more than half of it in *M. cristata*, and (6) the absence of ossified tendons along the hind limbs and the carpometacarpus (see Bertelli *et al.* 2011 for these tendons in Messelornithidae).

Songzia acutunguis sp. nov.

Holotype. IVPP 18188, an articulated skeleton of an adult individual on one slab (Fig. 2).

Referred specimen. IVPP 18187, largely complete articulated skeleton of an adult from the type

locality and bed, lacking the distal end of the right ulna and radius, right hand and left hindlimb (Fig. 3).

Type locality, unit and age. Songzi, Hubei province; Yangxi Formation; early Eocene (Hou 1990, Zhang 2003).

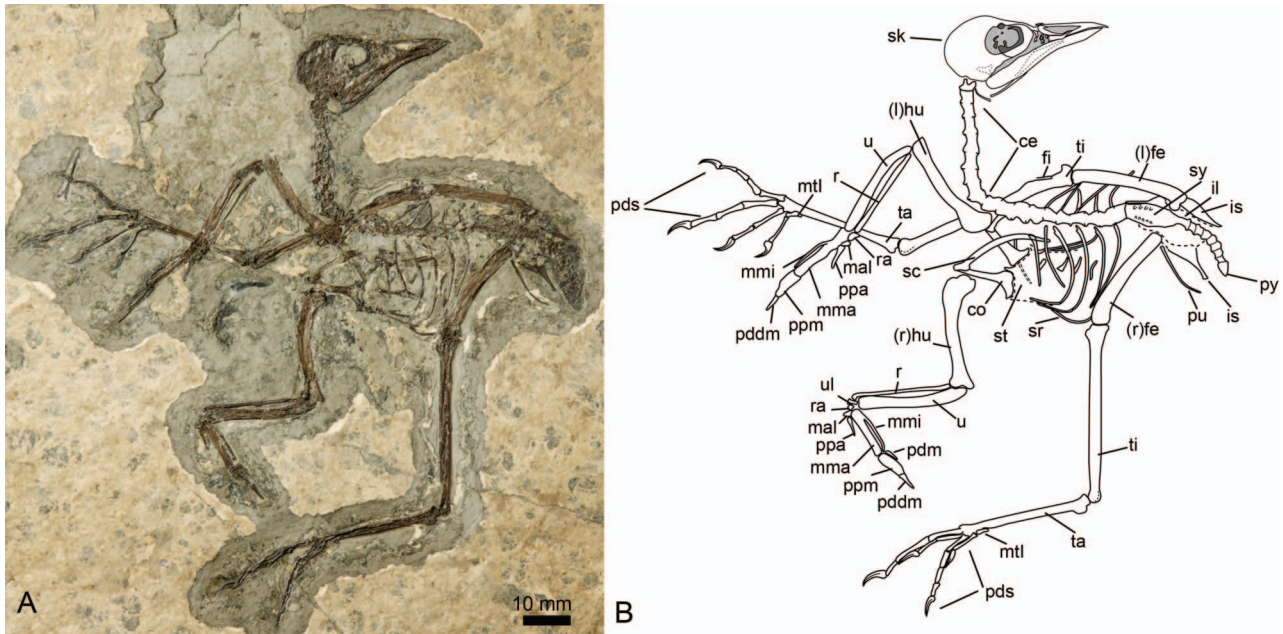


Fig. 2. Holotype of *Songzia acutunguis* sp. nov., IVPP 18188, from the early Eocene Yangxi Formation of Hubei province (China) with interpretative line drawing. Abbreviations: ce, cervical vertebrae; co, coracoid; fe, femur; fi, fibula; hu, humerus; il, ilium; is, ischium; mal, os metacarpale alulare; mma, os metacarpale majus; mmi, os metacarpale minus; mt I, metatarsus I; pu, pubis; py, pygostyle; pdm, phalanx digiti minoris; pds, pedal digits; ppa, phalanx proximalis digiti alulae; ppm, phalanx proximalis digiti majoris; pddm, phalanx distalis digiti majoris; r, radius; ra, radiale; sc, scapula; sk, skull; sr, sternal ribs; st, sternum; sy, synsacrum; ta, tarsometatarsus; ti, tibiotarsus; u, ulna; ul, ulnare; (r/l), (right/left).

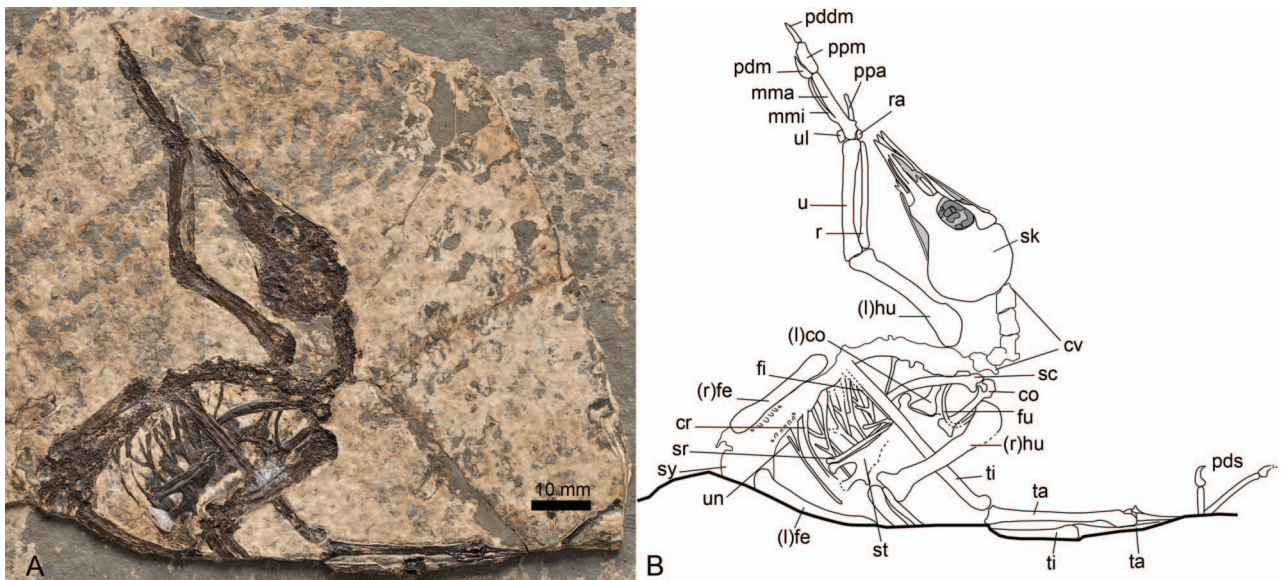


Fig. 3. *Songzia acutunguis*, sp. nov. from the early Eocene Yangxi Formation of Hubei province (China), referred specimen IVPP 18187 with interpretative line drawing. Abbreviations (in addition to those as in Fig. 1): cr, cervical ribs; fu, furcula; un, uncinat process.

Element	IVPP 18188	IVPP 18187	IVPP 8756	<i>Messelornis cristata</i>
Skull (length)	36.5	36.4	37.3	46.6 ± 1.4
Coracoid (length)	13.5	14.5		21.5 ± 0.7
Humerus (length)	25.8/24.9	26.0/25.0		37.9 ± 1.6
Humerus (midshaft width)	3.0/2.9	3.4/3.6		
Ulna (length)	25.2/24.8	23.3	19.4	33.9 ± 1.5
Os metacarpale majus (length)	12.3/13.4	13.9	11.1	20.8 ± 1.1
Os metacarpale majus (midshaft width)	1.7/1.7	2.2		
Phalanx proximalis digiti majoris (length)	5.5/5.8	6.5	6.0	8.8 ± 0.6
Phalanx distalis digiti majoris (length)	4.4/4.4	4.2	5.2	7.4 ± 0.5
Femur (length)	24.5/26.2	22.5	19.7	35.4 ± 0.8
Tibiotarsus (length)	40.0/43.0	39.9	34.1/33.9	64.6 ± 1.5
Tarsometatarsus (length)	28.4/28.9	24.8	23.7/23.5	53.9 ± 1.9
Pedal digit I-1 (length)	6.4/6.7		6.7/6.6	5.0 ± 0.5
Pedal digit I-2 (length)	4.01/4.32		3.3/3.3	3.0 ± 0.5
Pedal digit II-1 (length)	6.8/7.0		7.6/7.5	9.0 ± 0.6
Pedal digit II-2 (length)	5.2/5.1		5.6/5.6	7.5 ± 0.4
Pedal digit II-3 (length)	4.8/4.4		3.1/3.1	4.5 ± 0.4
Pedal digit III-1 (length)	7.4/7.3		7.7/7.7	10.8 ± 0.6
Pedal digit III-2 (length)	6.8/6.5		5.8/5.7	8.8 ± 0.5
Pedal digit III-3 (length)	6.1/6.3		5.5/5.5	7.7 ± 0.5
Pedal digit III-4 (length)	5.7/5.2		3.6/3.5	5.5 ± 0.5
Pedal digit IV-1 (length)	5.1/5.0		5.2/5.2	6.5 ± 0.4
Pedal digit IV-2 (length)	3.9/4.0		3.5/3.6	4.6 ± 0.3
Pedal digit IV-3 (length)	3.4/3.2		2.3/2.3	3.9 ± 0.2
Pedal digit IV-4 (length)	3.4/3.5		3.8/3.8	4.4 ± 0.5
Pedal digit IV-5 (length)	3.9/4.0		2.6/2.7	3.8 ± 0.5

Table 1. Selected measurements (right/left, in mm) of the holotype, IVPP 18188, and referred specimen, IVPP 18187, of *Songzia acutunguis* sp. nov. in comparison with the holotype, IVPP 8756, of *Songzia heidangkouensis*, and *Messelornis cristata*. Measurements of *Messelornis cristata* are from Hesse (1990) and represent mean values with standard deviation.

Differential diagnosis. The new species differs from *Songzia heidangkouensis* in its larger size (Table 1) and the longer and more curved unguis phalanges of the toes (Fig. 4).

Etymology. The species epithet is derived from *acutis* (Lat.), sharp and *unguis* (Lat.), claw.

Measurements. See Table 1.

Description and comparisons

Skull. The skulls of the two *Songzia acutunguis* specimens expose the right lateral and latero-dorsal sides respectively (Fig. 5) and are anatomically more informative than the skull of the holotype of *S. heidangkouensis*, which is preserved in right lateral view with the mandible overlapping the upper jaw (Fig. 5). Unless indicated otherwise, the following descriptions are based on the holotype IVPP 18188. The pointed and stout premaxilla has a slightly ventrally curved tip. The processus frontalis is straight and equal in width along its length, and meets the nasal just rostral of the small depression on the frontal. The processus maxillaris

narrows gradually towards the premaxilla–maxilla joint. The maxilla is slightly crushed, with its processus premaxillaris lying dorsal to the caudal end of the processus maxillaris. The nasal is asymmetrically ‘U’-shaped with a short processus premaxillaris and a long, ventrally curved process, which contacts the processus frontalis of the premaxilla ventrally and the maxilla dorsally. The external naris is holorhinal and measures about 60% of the length of the beak; its oval shape is similar to that of some extant rails (e.g., *Gallinula chloropus* and *Amaurornis phoenicurus*). The area between the orbit and the nasal is crushed, and the lacrimal is partially preserved with a pointed ventral process. The inflated parietal is crushed. Dark-coloured matrix is preserved in the orbits of all the three *Songzia* specimens and may represent melanosome layers in the eyeball (see Vinther *et al.* 2008 for melanosome preservation in fossils). In IVPP 18187, both jugals are preserved, which are straight and rod-shaped in dorsal view, but how they connect with the skull is unclear. Only an impression of the left quadrate is preserved, and the shapes of the orbital and otic processes are not discernible. In *S. heidangkouensis* (IVPP 8756), the



Fig. 4. Hindlimbs of *Songzia*. A, B, Left (A) and right (B) tarsometatarsus of the holotype of *Songzia acutunguis*, sp. nov. (IVPP 18188); C, Tarsometatarsus and D, pedal digits of the holotype of *Songzia heidangkouensis* (IVPP 8756). The arrow in A indicates two to three hypotarsal furrows; whether some of these were originally closed to form a canal can not be decided owing to the poor preservation of the area. The arrows in B and C indicate the well-developed crista medialis hypotarsi of the block-like hypotarsus. The line drawings in A and B show the different shape of the ungual phalanx of digit III in *S. acutunguis* sp. nov. and *S. heidangkouensis*. Abbreviations as in figure 1.

quadrate-jugal articulation is on a peg-like prominence as in charadriiform birds (Fig. 5A).

The pointed and stout mandible curves slightly in a dorsal direction, and widens gently toward its caudal end. The dorsal ramus of the dentary extends caudally to the mid-length point of the mandible, and the ventral ramus accounts for three-quarters of the length of the mandible. The area between these rami is broken, revealing another bone, which is likely to be the splenial. The caudal part of the mandible is barely discernible. One hyoid branch is preserved in IVPP 18188, broken in its caudal part, and overlapped by the mandible rostrally.

Vertebrae. The preserved vertebrae are largely crushed so that osteological details are not visible. There are 20 free presacral vertebrae in IVPP 18188 (Fig. 2). The cervical vertebrae become longer from the axis to the sixth vertebra (the longest one), and then decrease in length to the last cervical. The thoracic vertebrae do not fuse to form a notarium. Seven free caudal vertebrae can be identified, which, as preserved, are wider than long. The pygostyle is small and triangular.

Sternum. In IVPP 18187, the left half of the sternum is preserved in dorsal view and still articulates with the coracoids (Fig. 6A). Overall, this bone resembles

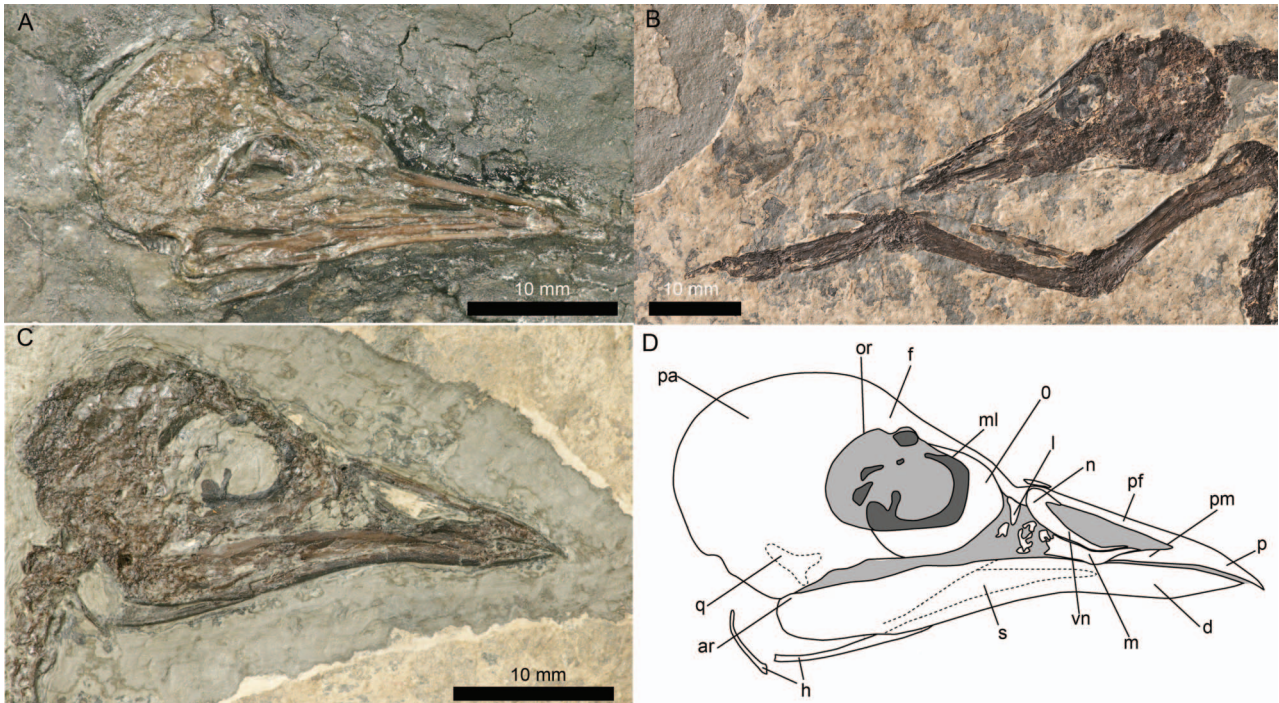


Fig. 5. *Songzia* skulls in comparison. **A**, *Songzia heidangkouensis*, (holotype, IVPP 8756); **B**, the referred specimen of *S. acutunguis*, sp. nov. (IVPP 18187); **C**, the holotype of *S. acutunguis*, sp. nov. (IVPP 18188), and **D**, line drawing of IVPP 18188. Abbreviations: ar, articular; d, dentary; f, frontal; h, hyoid; l, lacrimal; m, maxilla; ml, melanosome layers; n, nasal; o, orbitosphenoid; or, orbit; p, praemaxilla; pa, parietal; pf, processus frontalis; pm, processus maxillaris; q, quadrate; s, splenial; vn, ventral process of nasal.

that of messelornithids in its proportions and is not as elongate and narrow as in species of crown group Rallidae.

The spina externa and the processus craniolaterales are barely discernible. The processus costales are likewise not visible, but six preserved sternal ribs (see below) indicate the presence of six processes (Fig. 7), which is the usual number in species of Gruidae, Rallidae and Charadriiformes (e.g., *Vanellus vanellus*, *Calidris tenuirostris*; Mayr & Clarke 2003: character 71; Livezey 1998: character 152). The connections of the sternal ribs with the processus costalis of the sternum are partially preserved on both sides, demarcating the right and left lateral margins of the sternum, which itself consists only of impressions and several fragments (Fig. 6C, D). There are two caudal trabeculae on each side of the corpus sterni as in messelornithids (Mayr 2009: see fig. 9.2, Bertelli *et al.* 2011), whereas there is only one trabecula in extant and fossil rallids (e.g., Mayr 2006). The distal ends of both trabeculae are slightly expanded. The incisura lateralis is not as deep as in messelornithids (Mayr 2009: fig. 9.2, Bertelli *et al.* 2011: fig. 2), and is located slightly more cranially than the incisura medialis. The trabecula intermedia extends nearly as far caudally as the trabecula lateralis (Fig. 6A).

Ribs. In IVPP 18188, seven left vertebral ribs are found. Four (left side in IVPP 18187) and five (right side in IVPP 18188) sternal ribs that contact the sternum can be recognized (Fig. 6A, C).

Coracoids. In both specimens, the coracoids are preserved in articulation with the scapulae and the sternum. In IVPP 18188, the coracoids are exposed in ventral aspect and their omal extremities are largely broken (Fig. 6C). The coracoids of IVPP 18187 are seen in dorsal view on both sides and the tip of the processus procoracoideus is broken, leaving only its base on the shaft (Fig. 6A). The dorsal surface of the coracoid beneath the processus procoracoideus is crushed and does not allow recognition of the foramen nervi supracoracoidei. The lateral and medial margins of the bone are parallel from the base of the process procoracoideus for over half the length of the bone before diverging sharply to form the broad sternal end. Combining observations from both dorsal and ventral exposures of the coracoid, the shaft appears to have been subround in cross-section. A crista procoracoidei (Livezey 1998), which extends from the processus procoracoideus along the medial side of the coracoid in species of Messelornithidae and in a few other extant groups, including Turnicidae, Psophiidae, Heliornithidae and some Rallidae and Charadriiformes (Mayr

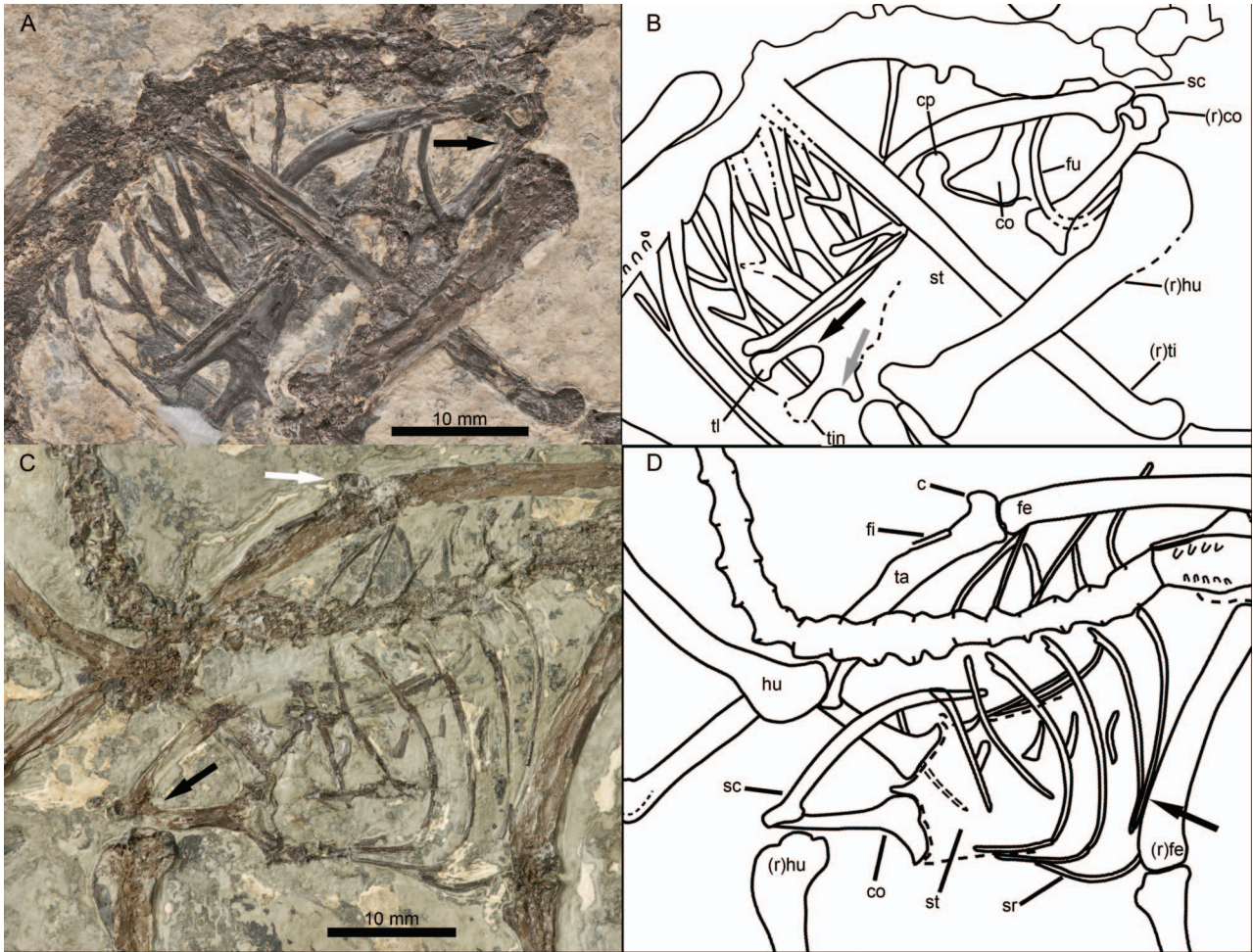


Fig. 6. Pectoral girdle, vertebrae, ribs, sternum and limbs of *Songzia acutunguis*, sp. nov. A, photograph and B, line drawing of the referred specimen, IVPP 18187; C, photograph and D, line drawing of the holotype, IVPP 18188. The black arrows in A and C indicate the processus procoracoideus; note that a crista procoracoidei is absent. The arrows in B point to the shallow incisurae lateralis (black) et medialis (grey) of the sternum. The white arrow in C points to the crista cnemialis lateralis of the tibiotarsus. The arrow in D indicates that the sternal part of the caudal rib does not articulate directly with the sternum, but is adpressed tightly to the ventral side of the cranial rib. Abbreviations (in addition to those in Fig. 1): c, crista cnemialis; cp, processus cranio-lateralis; fu, furcula; pc, processus costalis; se, spina externa; tl, trabecula lateralis; tin, trabecula intermedia.

2004), is absent in *Songzia* (Fig. 6A, C). The facies articularis sternalis appears to be concave. The processus lateralis is upcurved in omal direction and the angulus medialis forms a nearly right angle. The impressio musculi sternocoracoidei is badly preserved in IVPP 18187, preventing determination of whether or not pneumatic foramina were present. Such foramina are absent in Messel rails and extant rallids except *Himantornis* (Mayr & Mourer-Chauviré 2006, Bertelli *et al.* 2011: character 42), but are present in some other gruiform species (Psophiidae, Aramididae and Gruidae; Mayr & Clarke 2003: character 67).

Scapula. The scapula is smoothly curved, with a pointed extremitas caudalis, and resembles that of rallids, such as *Gallinula chloropus*. The shaft

smoothly increases in width from the base of the facies articularis humeralis towards mid-length and then narrows caudally. Details of the cranial part are not visible (Fig. 6A, C).

Furcula. The furcula is preserved only in IVPP 18187 (Fig. 6A). The extremitas sternalis is overlapped by the right coracoid. The bone is widely 'U'-shaped. The exposed cross-section demonstrates that the shaft is oval with slightly dorso-ventral compression, in contrast to the laminar-shaped cross-section seen in extant rallids (e.g., *Rallus aquaticus*, *Gallinula chloropus* and *Amaurornis phoeniceus*).

Humerus. Although the humeri are preserved in articulation with the pectoral girdle in both *S.*

acutunguis specimens, only the right humerus of the holotype allows the recognition of anatomical details (Fig. 8A). In cranial view, the shaft is seen to be arched dorsally. The weakly developed caput humeri is clearly demarcated by the incisura capituli from the well-developed tuberculum ventrale, and by a small fossa from the tuberculum dorsale. The crista deltopectoralis extends about one-third of the length of the bone and its width is about 60% of the

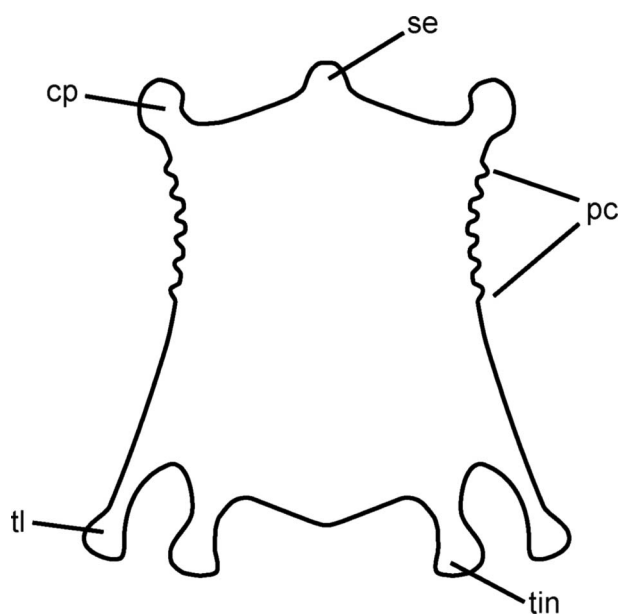


Fig. 7. Reconstructed shape of the sternum of *Songzia acutunguis*, sp. nov. (ventral view). Abbreviations as in Fig. 6.

humerus shaft width. As in Messelornithidae but contrary to Rallidae, the margo dorsalis of the crista deltopectoralis continuously curves without any distinct angulus (see Livezey 1998, character: 204). The long axis of the condylus dorsalis is parallel to the adjacent margo dorsalis, whereas it curves more ventrally in messelornithids (Bertelli *et al.* 2011, fig. 3). The condylus ventralis is broken. The well-developed processus flexorius projects as far distal as the condyli ventralis et dorsalis; regarding the relative distal extension of the processus flexorius and condylus ventralis, rallids are variable (Mayr & Smith 2001, Boles 2005, Mayr 2010, Worthy & Boles 2011).

Ulna. The ulna is bowed and does not exceed the humerus in length. The width of its mid-shaft is about three times that of the radius (Fig. 8B). The proximal and distal ends of the bone slightly widen, and no papillae remigales are visible. The olecranon is moderately developed. At the distal end, the condylus dorsalis is narrow and separated from the well-developed condylus ventralis by a deep sulcus intercondylaris.

Carpometacarpus and distal wing elements. The well-developed processus extensorius of the carpometacarpus projects perpendicular to the longitudinal axis of the os metacarpale majus. The os metacarpale majus is straight and its mid-shaft width is nearly three times that of the os metacarpale minus. The distal end of the os metacarpale minus bends toward the ventral surface of the os metacarpale majus, and

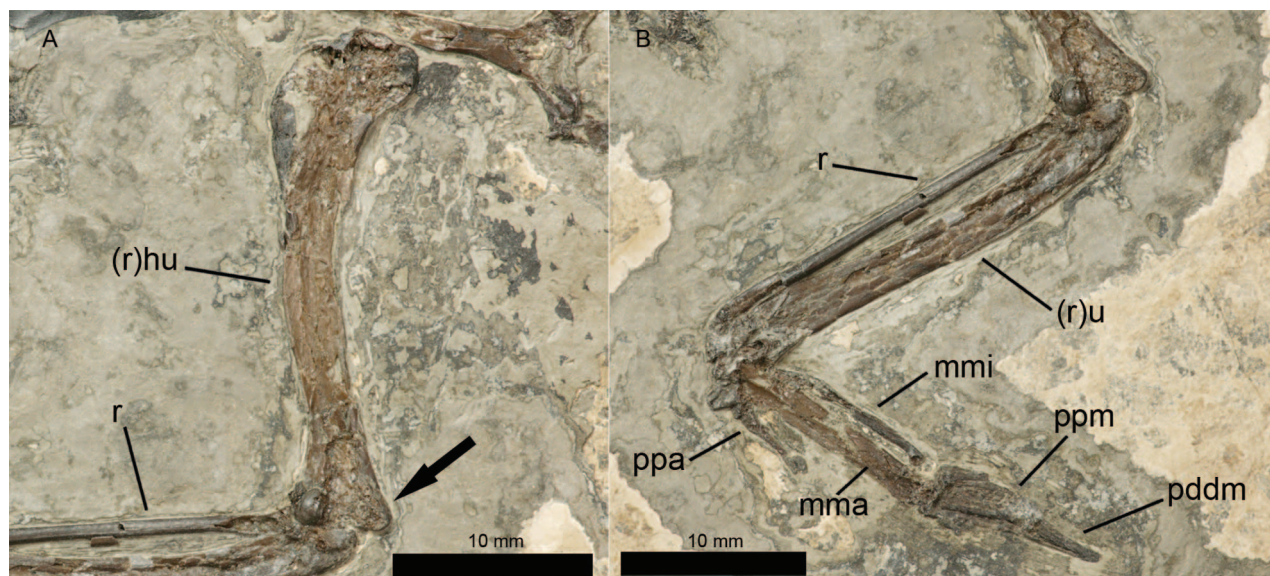


Fig. 8. Right wing of the holotype of *Songzia acutunguis*, sp. nov. (IVPP 18188). **A**, Right humerus in cranial view, the arrow indicates the well-developed processus flexorius, which projects to the distal end of the humerus; **B**, carpometacarpus and distal wing elements in ventral view. Abbreviations as in Fig. 1.

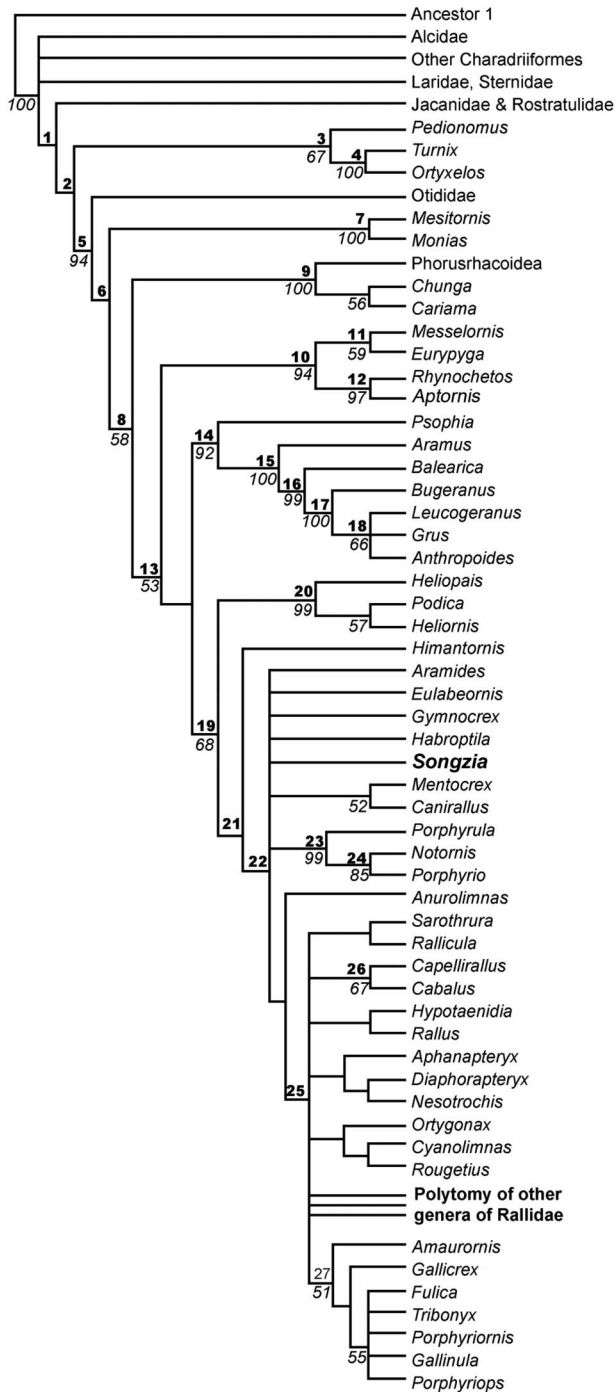


Fig. 9. Strict consensus tree of 2560 most parsimonious trees resulting from analysis of the modified matrix of Livezey (1998) after inclusion of *Songzia* ($L = 886$, $CI = 0.49$, $RI = 0.83$). Bootstrap values of more than 50% are shown below the corresponding branches in italics. Unambiguously optimized synapomorphies of the nodes (asterisked characters have $CI = 1.0$): node 1: 72* (1), 84 (1), 127 (0, 1), 332 (1), 365 (0), 366 (0); node 2: 313 (1); node 3: 57* (1), 134 (2); node 4: 51* (1), 56* (1), 66* (1), 83* (1), 193* (1), 203* (1), 228* (1), 233* (1), 314* (1), 319* (1); node 5: 104 (1), 126* (1), 129 (1), 132 (1), 139 (1), 169 (1), 220* (1), 295* (1); node 6: 195* (1); node 7: 20* (1), 143* (1), 144* (1), 149* (1), 164* (1), 166* (1), 177* (1), 212* (1), 229* (1), 243* (1), 326* (1), 376* (1); node 8: 110 (1),

the distal end of the latter is not inflated. The spatium intermetacarpale is narrow and no processus intermetacarpalis is present (Fig. 8B).

The phalanx digiti alulae does not reach to the middle of the os metacarpale majus in length and lacks an unguis. The phalanx proximalis digiti majoris bears an oval fossa ventralis. The phalanx digiti minoris does not extend distally to the mid-length of the phalanx proximalis digiti majoris (Fig. 8B).

Pelvis. The synsacrum is preserved in ventral view and is largely crushed in IVPP 18188, to which the following description refers (Fig. 2). The region just cranial of the foramen acetabuli is well exposed and the tuberculum preacetabulare is absent. The preacetabular portion of the pelvis is clearly longer than the postacetabular portion. As in Messelornithidae (Mayr 2004), the distal end of the ischium bears a short and tapering processus terminalis ischii. This feature is very unlike the condition in Rallidae, in which the caudal end of the pelvis is straight and the processus terminalis ischii is not well developed.

Femur. In medial view, the shaft of the right femur of IVPP 18188 is slightly bowed cranially. Its proximal and distal ends are damaged. The femur length is 63% of the tibiotarsus length and is slightly shorter than the tarsometatarsus. By contrast, the femur of *M. cristata* is no more than half the tibiotarsus in length (see Mayr 2009:fig. 9.2).

Tibiotarsus. The tibiotarsus is the longest limb element. In his description of the *S. heidangkouensis* holotype, Hou (1990) noted that the cristae cnemiales are not developed, but the proximal ends of the tibiotarsi are not well preserved in this specimen. In IVPP 18188, the crista cnemialis cranialis is well

133 (1), 268* (1), 277 (1), 362 (1); node 9: 5* (1), 22* (1), 29* (1), 30* (1), 36* (1), 42* (1), 54* (1), 63* (1), 91* (1), 213* (1), 227* (1), 245* (1), 340* (1); node 10: 35* (1), 38* (1), 50* (1), 105* (1), 232* (1), 240 (1), 250* (1), 271* (1), 297* (1), 376* (2); node 12: 10 (2), 88* (1), 99* (1), 110 (2), 279* (1), 310* (1), 329* (1); node 13: 320 (1); node 14: 114 (2), 115 (1), 137* (1), 242* (1), 272* (1), 321* (1); node 15: 141* (1), 156* (1), 171* (1), 178* (1), 187* (1), 210* (1), 211* (1), 223* (1), 257* (1), 324* (1); node 16: 59* (1), 103 (4), 155* (1), 224* (1), 234* (1), 325* (1), 341* (1), 371 (2); node 17: 28* (1), 102* (1), 157 (1), 158* (1), 168* (1), 172* (1), 174* (1), 190* (1), 196 (2); node 19: 125 (2), 215* (1), 236* (1), 238* (1), 241 (1), 244* (2), 253* (1), 254* (1), 273* (1), 327* (1), 354* (1); node 20: 160* (1), 183* (1), 315* (1), 316 (2), 334* (1), 350* (1), 355 (2); node 21: 194 (1), 293* (1), 301* (1), 336* (1); node 22: 117* (1); node 23: 60* (1), 331* (1), 347* (1), 356* (1), 369* (2); node 24: 19* (1), 46* (1), 71* (1), 79* (1); node 25: 23 (1), 300 (1); node 26: 24 (2); node 27: 31* (1); 287* (1).

developed (Fig. 6C). The distal end of the tibiotarsus is not well preserved in *S. acutunguis*, but a well-developed sulcus extensorius is evident in *S. heidangkouensis*. The presence of a pons supratendineus was mentioned by Hou (1990), but can not be ascertained in IVPP 18187 and 18188. In IVPP 18187, the well-preserved condylus lateralis of the right tibiotarsus is sub-circular in outline. Also in IVPP 18187, the partially preserved fibula is very slender but its distal extension is unknown.

Tarsometatarsus. The shaft of the tarsometatarsus is straight and the bone measures 71% of the tibiotarsus length in IVPP 18188. The hypotarsi are not completely preserved or well exposed in all specimens of *Songzia*. In the *S. heidangkouensis* holotype, the hypotarsus of the left tarsometatarsus is visible in medial view and the crista medialis hypotarsi is well developed (Fig. 4C). The plantar protrusion of this element measures more than half the dorso-plantar width of the proximal tarsometatarsus, which is also the case in IVPP 18188 (Fig. 4B, C). In IVPP 18188, the plantar aspect of the left proximal end of the tarsometatarsus is exposed. The hypotarsus is compressed but two to three furrows can be determined (whether some of these were originally closed to form a canal can not be determined owing to the poor preservation of the area; Fig. 4A). It is evident, however, that a furrow/canal for the tendon of musculus flexor perforatus digiti II (Mayr 2004) was present in *Songzia*. The eminentia intercotylaris is high. Whether the cotyla lateralis is situated more distally than the medial cotyla, can not be discerned. In the holotype of *Songzia heidangkouensis*, a well-developed sulcus extensorius extends from the fossa infracotylaris dorsalis to the distal end, which makes the shaft appear flattened dorso-plantarly (Fig. 4C). The short trochlea metatarsi II is medioplantarly directed (contra Hou 1994, who incorrectly stated that this trochlea does not project plantarly; Fig. 4A, B). The trochlea metatarsi III projects more distally than the other trochleae and the distal prominence of the trochlea metatarsi II is subequal to the base of trochlea metatarsi IV.

Pedal phalanges and os metatarsale I. The pedal phalanges are completely preserved in articulation in IVPP 18188 and the phalangeal formula is 2-3-4-5 as in most birds. *Songzia acutunguis* and *S. heidangkouensis* share similar proportions and morphology of the pedal phalanges, but the unguis phalanges are longer and more curved in the new species (Fig. 4A, D). The toes are proportionally much longer than those of the messelornithids. Except for digit IV, the

length of the phalanges decreases proximo-distally in all the digits. In digit IV, the proximal phalanx is the longest and the third phalanx the shortest. Digit III is the longest and measures 89% of the tarsometatarsus length, and its second phalanx is longer than the third and fourth phalanges, which contrasts with most fossil and extant genera of Gruiformes except *Fulica*, *Porphyriornis*, *Gallinula* and *Porphyriops* (see Livezey 1998, character: 358).

All unguis phalanges have a similar morphology, including well-developed flexor tubercles and vascular sulcus. The flexor tubercles of the unguis phalanges are better developed on digits I and II than on the other two digits. The unguis of digit III is the longest and digit IV has the shortest one (Fig. 4A).

The os metatarsale I is stout and measures about half the length of the proximal phalanx of the hallux; its distal end is almost ball-shaped without a clear groove for the phalanx on its articulation facet.

Results of phylogenetic analysis

Our analysis of the Livezey (1998) data set resulted in 2560 most parsimonious trees, the strict consensus tree of which is shown in Fig. 9 (CI = 0.49, RI = 0.83, Length = 886). The overall topology of the tree corresponds well with the phylogeny recovered by Livezey (1998), but the intergeneric relationships of Rallidae are less well resolved than documented by Livezey (1998). *Songzia* is placed in an unresolved polytomy together with all rallid taxa except *Himanornis*. The (*Songzia* + Rallidae) clade received a bootstrap support less than 50%. It was supported by five unambiguously optimized characters at node 22 (character 117: 1, free vertebrae with costae complete spuriae present between synsacrum and vertebrae with costae complete verae) and node 21 (character 194:1, crista procoracoidei extending from processus procoracoideus along medial side of coracoid; 293:1, facies renalis ilii flat or convex, delimiting a comparatively dorso-ventrally deep fossa renalis, recessus iliaceus; 301:1, thickening of proximal femur, from facies caudalis to facies articularis antitrochantericus, weakly developed; 336:1, medial lamina of hypotarsus less than or equal to lateral lamina in plantar prominence), respectively. Of these, characters 293, 301 and 336 could not be coded for the fossils, whereas character 194 shows the plesiomorphic state. The more inclusive clade (Heliornithidae + (*Songzia* + Rallidae)) received a bootstrap support of 68% and was supported by 11 unambiguously optimized characters, of which only one character (244: 2, no tuberculum present on os

metacarpale minus, immediately distal to synostosis) could be scored for *Songzia*.

Although we modified some scorings of Messelornithidae according to Mayr (2004), Bertelli *et al.* (2011) and Worthy & Boles (2011), Messelornithidae are still placed as the sister taxon of Eurypygidae as in Livezey's (1998) original analysis (see also Worthy & Boles 2011). Concerning the interrelationships of extant Gruiformes, the topology agrees with that of Livezey (1998). We note, however, that Livezey's phylogeny conflicts in several aspects with the results of recent molecular analyses (Ericson *et al.* 2006, Hackett *et al.* 2008), which do not support a monophyletic 'Gruiformes'.

The analysis of the Bertelli *et al.* (2011) data set resulted in six most parsimonious trees, the strict and 50% majority rule consensus trees of which are shown in Fig. 10 (CI = 0.38, HI = 0.70, length = 240). The strict consensus tree is poorly resolved (Fig. 10A), but the topology of the 50% majority rule consensus tree is largely consistent with that of Bertelli *et al.* (2011). In this latter tree, *Songzia* falls in a polytomy, together with the messelornithids *M. cristata* and *P. mikkelseni* and Rallidae (represented by *Gallinula chloropus* and *Limnocorax flavirostris*; Fig. 10B). Characters (50:0, four notches/fenestrae on the caudal margin of the sternum) and (74:0, trochlea metatarsi II is plantarly deflected and reaches much

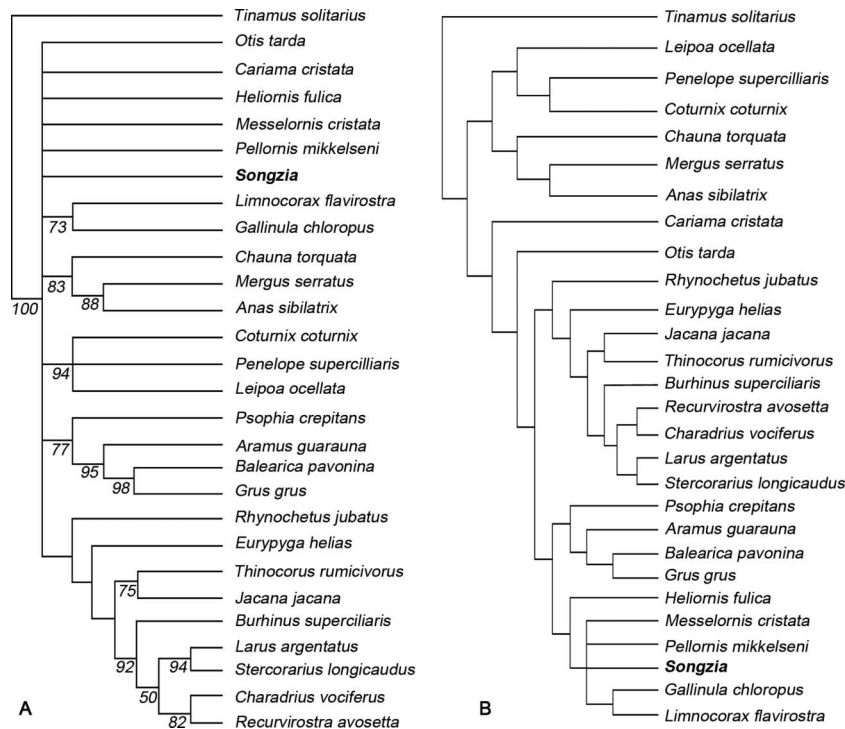


Fig. 10. Strict consensus (A) and 50% majority rule consensus (L = 240, CI = 0.38, RI = 0.70) (B) trees of six most parsimonious trees resulting from analysis of the matrix of Bertelli *et al.* (2011) after inclusion of *Songzia*. Bootstrap values of more than 50% are shown below the corresponding branches.

Ratio	<i>Songzia</i> <i>heidangkouensis</i> IVPP 8756	<i>Songzia</i> <i>acutunguis</i> IVPP 18187	<i>Songzia</i> <i>acutunguis</i> IVPP 18188	<i>Messelornis</i> <i>cristata</i>	<i>Gallinula</i> <i>chloropus</i> IVPP 1893	<i>Amaurornis</i> <i>phoenicurus</i> IVPP1894
Beak/skull	0.36	0.37	0.34	0.44	0.45	0.49
Hum+Uln+Cmc/Fem+Tbt+Tmt		0.71	0.68	0.60	0.71	0.63
Fem/Tmt	0.83	0.91	0.86	0.67	1.09	0.89
Digit III/Tmt	0.95		0.89	0.61	1.53	1.05

Table 2. Selected ratios of elements of *Songzia* spp. (IVPP 8756, 18187, 18188), compared with *Messelornis cristata* and two extant rails. Ratios for *Messelornis cristata* are based on measurements provided by Hesse (1990; see table 1), except for the ratio (beak/skull), which was taken after Mayr (2004: fig. 3A). Abbreviations: Hum = humerus; Uln = ulna; Cmc = carpometacarpus; Fem = femur; Tbt = tibiotarsus; Tmt = tarsometatarsus.

less far distally than the distal end of the trochlea metatarsi IV) support this placement.

Discussion

Relationships

Hou (1990) assumed a close relationship between Songziidae and Rallidae, especially with regard to the short ulna and the long legs and toes, and *Songzia* indeed has very rail-like limb proportions (see also Mayr 2009). The short ulna, which does not exceed the humerus in length, distinguishes the fossil from charadriiform birds, among which Jacanidae have a superficially rail-like external appearance. Inclusion of the taxon in Livezey's (1998) data set also resulted in a clade including *Songzia* and Rallidae. This clade was, however, not supported in the bootstrap analysis and only one of the five characters optimized as apomorphies in support of it could be scored for *Songzia* (character 117:1, CI = 1): free vertebrae with costae complete spuriae (i.e., ribs, whose sternal part does not articulate directly with the sternum) present between synsacrum and vertebrae with costae complete verae (ribs that articulate with sternum; Livezey 1998; fig. 5D); this character is homoplastic among birds and occurs in several other taxa apart from Rallidae.

As yet there are, however, no unambiguous Eocene records of rallids (Mayr 2009) and *Songzia* distinctly differs from crown group Rallidae in several, presumably plesiomorphic features, such as (1) the lack of a crista procoracoidei (coracoid), (2) the much wider sternum with a caudal margin that has four incisions, (3) the elongate crista deltopectoralis, (4) the relative broad pelvis, and (5) the second phalanx of the third digit being much longer than the distal third and fourth phalanges.

Our analysis based on the Bertelli *et al.* (2011) data set supports inclusion of *Songzia* in a clade including Messelornithidae, Heliornithidae and Rallidae in the 50% majority rule consensus tree. Again, this placement was only weakly supported by two characters: (1) sternum, caudal margin with four notches/fenestrae (Bertelli *et al.* 2011: character 50), and (2) tarsometatarsus, trochlea metatarsi II plantarily deflected and distal end reaching much less far distally than distal end of trochlea metatarsi IV (Bertelli *et al.* 2011: character 74).

Songziids differ from messelornithids, which were assumed to be closely related to either Eurypygidae/Rhynochetidae (Hesse 1988, 1990; see also Livezey 1998) or Rallidae/Heliornithidae (Mayr 2004, Bertelli *et al.* 2011), in several features. Most notably, *Songzia*

has proportionally longer legs and toes than the species of Messelornithidae (Table 2); the third toe is nearly as long as the tarsometatarsus, whereas it measures not more than half of the tarsometatarsus in Messel rails (Hesse 1988). The scapi clavicularum appear to be more slender and oval in cross-section (Fig. 5A), whereas the scapi clavicularum are more laminar-shaped and wider in Messel rails. In contrast to messelornithids, a well-developed crista procoracoidei and ossified tendons along the wing and leg bones (Bertelli *et al.* 2011) are absent in songziids. The caudal incisions in the sternum are further shallower than in messelornithids and more closely resemble those of some charadriiform birds (e.g., *Vanellus vanellus*, *Calidris tenuirostris*). The *Songzia* species are also much smaller than any yet known Messel rail. Taking the largest specimen IVPP 18188 as an example, the lengths of humerus and tibiotarsus are only 70% and 64%, respectively, of those of the corresponding elements of *Messelornis cristata* (Hesse 1988).

However, all of these differences do not necessarily preclude messelornithid affinities of songziids, as hindlimb proportions are very variable among closely related birds (e.g., *Scolopax* and *Tringa* among Charadriiformes), and the shorter toes and more strongly ossified tendons in the messelornithids *Messelornis* and *Pellornis* may be related to a more cursorial lifestyle. Thus, we conclude that the affinities of *Songzia* can not be conclusively resolved at present, and among the most crucial issues to be resolved before the affinities of *Songzia* can be established will be a solid placement of messelornithids.

Palaeobiology

The Yangxi Formation at the Songzi locality comprises shallow lacustrine deposits. Other fossils discovered in this formation include ostracods, gastropods, charophytes, pollen and, among vertebrates, teleost fishes (e.g., Osteoglossidae and possible Catostomidae, Zhang 2003, Liu & Chang 2009), trionychid turtles (Chen & Jin 1996) and coryphodont mammals (Zhang *et al.* 1991, Chen & Gao 1992). The formation is composed of deposits of layered sandstones and clay with interbedded marlstone and shales.

Songzia appears to have been a common avian taxon at the locality. In addition to the three specimens discussed here, several other *Songzia*-like birds have been discovered at the locality. Unfortunately, these are in private hands and not available to us for study. With the new species described here, there were at least two species of Songziidae and these birds thus appear to have been diverse by the early Eocene in China.

Because neither the sternum nor the pelvis of *Songzia* is extremely elongated and narrow as in Rallidae, the species was probably not adapted to living in dense cluttered environments as many extant rails. The absence of ossified tendons along the hindlimbs and the proportionally longer toes also suggest that these birds were less cursorial than the forest-dwelling species in Messelornithidae (Hesse 1990) and, by comparison with the equally long-toed rallids, we assume that *Songzia* lived in wetlands, which is also in concordance with the sedimentology of the locality.

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Appendix 1

One hundred and one characters scored for *Songzia acutunguis* in the matrix of Livezey (1998):

1:1. 2:0. 3:0. 7:0. 9:0. 20:0. 21:0. 22:0. 25:0. 26:0. 30:0. 47:0. 57:0. 103:1. 114:1. 115:0. 117:1. 127:2. 130:0. 133:0. 134:0. 135:1. 141:0. 142:0. 145:0. 146:0. 148:0. 149:0. 150:0. 151:0. 152:3. 154:0. 166:0. 168:0. 174:0. 175:0. 176:1. 177:0. 178:0. 179:1. 180:0. 181:0. 187:0. 188:2. 189:0. 193:0. 194:0. 195:1. 196:0. 199:0. 204:0. 205:0. 208:0. 212:0. 213:0. 216:0. 217:1. 219:1. 220:1. 221:0. 228:0. 229:0. 230:0. 235:0. 239:1. 243:0. 244:2. 245:0. 248:0. 249:1. 251:1. 260:0. 270:1. 295:1. 296:0. 297:0. 300:0. 303:0. 304:1. 316:0. 319:0. 325:0. 326:0. 331:0. 335:0. 340:1. 343:0. 344:0. 346:0. 347:0. 349:0. 352:1. 353:2. 355:0. 357:0. 358:1. 359:0. 360:0. 361:0. 362:0.

Appendix 2

Twenty-seven characters scored for *Songzia acutunguis* scoring in the Bertelli *et al.* (2011) data matrix:

15:0. 31:1. 32:0. 36:0. 38:0. 39:0. 43:0. 44:0. 48:1. 49:0. 50:0. 52:0. 57:0. 58:0. 60:0. 62:0. 65:0. 66:1. 70:1. 72:1. 74:0. 75:1. 76:0. 77:1. 78:0. 80:0. 81:0.