Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China

Zhonghe Zhou and Fucheng Zhang

Abstract: Two new, nearly completely articulated skeletons of *Sapeornis chaoyangensis* provide much new information about the anatomy of this basal avian, particularly in the skull, pectoral girdle, forelimb, and hind limb. This new material shows that the hand of *Sapeornis*, with a phalangeal formula of "2–3–2," was more derived than previously reconstructed. The skeleton of *Sapeornis* has several unique features, such as a distinctively elongated fenestra on the proximal end of the humerus, a robust furcula with a distinctive hypocleidum, and an elongated forelimb. *Sapeornis* exhibits a combination of derived and primitive features, including a short, robust non-strut-like coracoid and a fibula reaching the distal end of the tarsal joint (as in *Archaeopteryx*), a pygostyle, reduced manual digits, and a well-fused carpometacarpus (as in more advanced birds). These features further indicate the mosaic pattern in the early evolution of birds and confirm the basal position of *Sapeornis* near *Archaeopteryx* and *Jeholornic* in the phylogeny of early birds. The preservation of gastroliths in one of the new specimens also represents the first Chinese Mesozoic bird with such evidence, indicating a herbivorous feeding habit and providing further evidence for our understanding of the diet diversification in early avian evolution.

Résumé : Deux nouveaux squelettes presque complètement articulés de *Sapeornis chaoyangensis* fournissent beaucoup de nouvelles informations à propos de l'anatomie de cet oiseau de base, surtout en ce qui concerne le crâne, la ceinture thoracique ainsi que les membres antérieurs et postérieurs. Ce nouveau matériel montre que la main de *Sapeornis,* avec une formulation « 2–3–2 » des phalanges, était plus dérivée que reconstruite antérieurement. Le squelette de *Sapeornis* présente plusieurs caractéristiques uniques telles qu'une fenêtre allongée distinctive sur l'extrémité proximale de l'humérus, une fourchette robuste avec un hypocleidum distinctif et un avant-bras allongé. *Sapeornis* montre une combinaison de caractéristiques dérivées et primitives incluant une coracoïde courte, robuste et ne servant pas de support ainsi qu'un péroné qui atteint l'extrémité distale de l'articulation du tarse (tel que chez *Archaeopteryx*), un pygostyle, des doigts de la main réduits et une masse basilaire bien soudée (tel que chez les oiseaux plus évolués). Ces caractéristiques indiquent le patron mosaïque dans l'évolution précoce des oiseaux et confirment sa position à la base, près de *Archaeopteryx* et *Jeholornic*, dans la phylogenèse des premiers oiseaux. La préservation des gastrolites dans un des nouveaux spécimens représente aussi le premier oiseau chinois datant du Mésozoïque présentant une telle évidence, indiquant des habitudes alimentaires herbivores et fournissant d'autres évidences pour notre compréhension de la diversification du régime alimentaire dans l'évolution de la faune avienne précoce.

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Introduction

The Early Cretaceous birds from the lake deposits in western Liaoning Province and neighboring areas in northeast China are well known for their exceptional abundance, diversity, and preservation. Two lacustrine formations belonging to the Jehol Group, the lower one, Yixian Formation, and the upper one, Jiufotang Formation, have produced hundreds of bird specimens. Most of these can be referred to the oldest known beaked bird *Confuciusornis* (Hou et al. 1995; Chiappe et al. 1999), but many others belong to the most prevalent Mesozoic avian group, Enantiornithes, including *Sinornis* (Sereno and Rao 1992), *Cathayornis* (Zhou et al. 1992), *Boluochia* (Zhou 1995), *Liaoxiornis* (Hou and Chen 1999), *Eoenantiornis* (Hou et al. 1999), *Protopteryx* (Zhang and Zhou 2000), *Longipteryx* (Zhang et al. 2001*a*, 2001*b*), and *Eocathayornis* (Zhou 2002). A few of these birds are referable to the more advanced avian group Ornithurae, for example, *Chaoyangia* (Hou and Zhang 1993), *Songlingornis* (Hou 1997), *Liaoningornis* (Hou et al. 1996), and *Yanornis* and *Yixianornis* (Zhou and Zhang 2001). Ornithurine fossils are generally believed to have given rise to all extant birds (Martin 1983; Hou et al. 1996; Norell and Clarke 2001).

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Sapeornis chaoyangensis is one of the most recently described avian species from the Jiufotang Formation. The holotype was collected by the field crew of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, in the summer of 2000 in the Shangheshou area near Chaoyang City, Liaoning Province (Fig. 1). This locality was first discovered in the spring of 2000. Shortly afterwards, many more fossil birds and dinosaurs were discovered from another locality also in Chaoyang City, about 40 km from the Shangheshou locality. *Sapeornis* was named and briefly described based on an incomplete postcranial skeleton (Zhou and Zhang 2002*a*). Two new specimens described here were recently collected and preserve information that was lacking in the holotype. With this new material, we are able to provide a comprehensive description of the major anatomic features of this basal bird.

Phylogenetic analysis indicates that *Sapeornis* is the most basal known bird except for *Archaeopteryx* and *Jeholornis* (Zhou and Zhang 2002*a*, 2002*b*). It is very distinctive from other known Early Cretaceous birds not only because of its exceptional large size but also because of its extremely long wings when compared with the hind limb. *Sapeornis* also retains some primitive characters such as a coracoid comparable to that of *Archaeopteryx*. Associated with *Sapeornis* from the same localities are the recently discovered long-tailed seed-eating birds *Jeholornis* (Zhou and Zhang 2002*b*) and *Confuciusornis* (Hou et al. 1995, 1996; Chiappe et al. 1999), *Longipteryx* (Zhang et al. 2001*a*), abundant enantiornithines, ornithurines (Zhou and Zhang 2001), feathered dromaeosaurs (Norell et al. 2002), pterodactyloid pterosaurs (Wang and Zhou 2002), and abundant teleost fishes (Zhang et al. 2001*b*). These new localities are now increasingly important for at least two reasons: the deposits belong to the Jiufotang Formation, which overlies the famous bird- and dinosaur-bearing Yixian Formation; and they have produced fossils of greater diversity and abundance than those from the previously known localities in western Liaoning Province, northeast China.

Systematic palaeontology

Aves Linnaeus, 1758
***Sapeornis chaoyangensis*** Zhou and Zhang, 2002

HOLOTYPE: Postcranial skeleton comprising some vertebrae, pygostyle, pectoral girdle, furcula, forelimbs, pelvic girdle, and the hind limb (IVPP V12698).

REFERRED SPECIMENS: IVPP V13275, a nearly completely articulated skeleton, lacking only the sternum and some toes of the left foot (Fig. 2*a*); IVPP V13276, a nearly completely articulated skeleton, lacking the sternum, left pectoral girdle, left forelimb, and distal portion of the left hind limb (Fig. 2*b*).

LOCALITY AND HORIZON: Shangheshou and Dapingfang areas, Chaoyang City, Liaoning Province, China (Fig. 1); Jiufotang Formation, Early Cretaceous (Aptian).

DIAGNOSIS: Furcula robust with a slender hypocleidum, and two furcular rami form an angle of about 105° (a robust furcula in other basal birds such as *Archaeopteryx*, *Jeholornis*, and *Confuciusornis* lacks a hypocleidum). Forelimb extremely

Fig. 1. Map showing the Shangheshou and Dapingfang localities of *Sapeornis chaoyangensis* in Liaoning, northeast China.
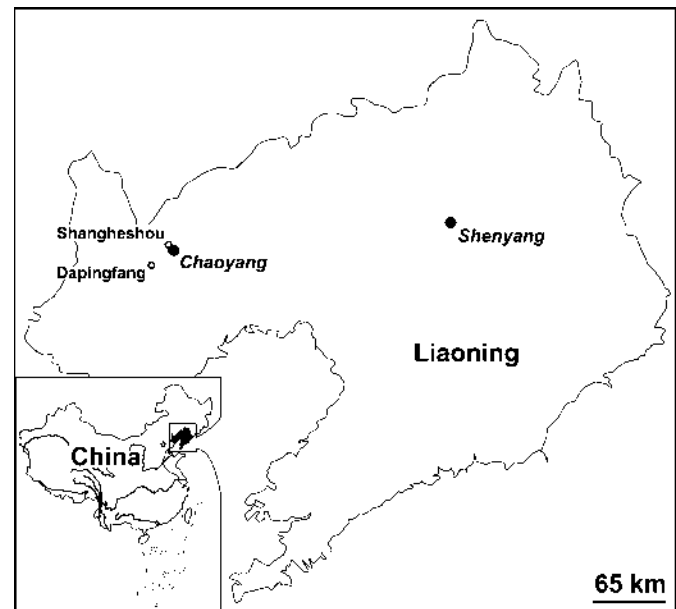
elongated; forelimb (humerus + ulna + carpometacarpus) about one and one half the length of the hind limb (femur + tibiotarsus + tarsometatarsus). Proximal end of the humerus with an elliptical fenestra (the only other known Mesozoic bird with a fenestra at the proximal humerus is *Confuciusornis*, but it is nearly rounded in shape). The third manual digit comprises two slender phalanges.

INSTITUTIONAL ABBREVIATION: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

DESCRIPTION:

Skull: The skull is not preserved in the holotype; fortunately, nearly complete skulls are preserved in both IVPP V13275 (Fig. 3*a*) and IVPP V13276 (Fig. 3*b*). The skull is generally similar in shape to that of *Archaeopteryx* and most enantiornithines. There are four teeth in the premaxilla as in *Archaeopteryx* and most enantiornithine birds. The teeth are short and conical in shape; they lack serrations (Fig. 3*c*). The premaxilla has a slender nasal process and maxillar process. The nasal is broad and unreduced. The nasal opening is elongated. The maxilla is unreduced and triangular; it is not clear how many teeth are present in the maxilla. The jugal is slender but has a dorsal expansion behind the orbit. The quadratojugal is small, with a slender ascending process. The lacrimal is long, dividing the antorbital fenestra and the large orbit. The antorbital fenestra is relatively large as in *Archaeopteryx*, *Jeholornis* (Zhou and Zhang 2002*b*), and *Confuciusornis* (Martin et al. 1998).

The frontal is expanded as in other basal birds. The parietal is short and square-shaped. The squamosal is tightly attached to the parietal in IVPP V13275; it has a pointed ventral process. A large Y-shaped postorbital is present and contacts both the squamosal and jugal as in *Confuciusornis*, indicating the presence of a complete temporal bar separating the upper and lower temporal fenestrae. *Archaeopteryx* probably preserves

Fig. 2. *Sapeornis chaoyangensis*. Two new specimens, IVPP V13275 (*a*) and IVPP V13276 (*b*). cav, caudal vertebra; cmc, carpometacarpus; co, coracoid; cv, cervical vertebra; dv, dorsal vertebra; fe, femur; fi, fibula; fu, furcula; ga, gastralia; gs, gizzard stone; hu, humerus; il, ilium; is, ischium; pu, pubis; py, pygostyle; r, radius; ri, rib; sc; scapula; sk, skull; sy, synsacrum; ti, tibiotarsus; tmt, tarsometatarsus; u, ulna.

Fig. 3. *Sapeornis chaoyangensis.* Skull of IVPP V13275 in dorsal and lateral view (*a*, *d*); skull of IVPP V13276 in dorsal view (*b*, *e*); and tip of skull of IVPP V13275, showing teeth of the upper jaws (*c*, *f*). af, antorbital fenestra; an, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; mp, maxillar process of the premaxilla; mx, maxilla; na, nasal; no; nasal opening; np, nasal process of the premaxilla; or, orbit; p, parietal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sp, splenial; sq, squamosal; sur, surangular; t, tooth.
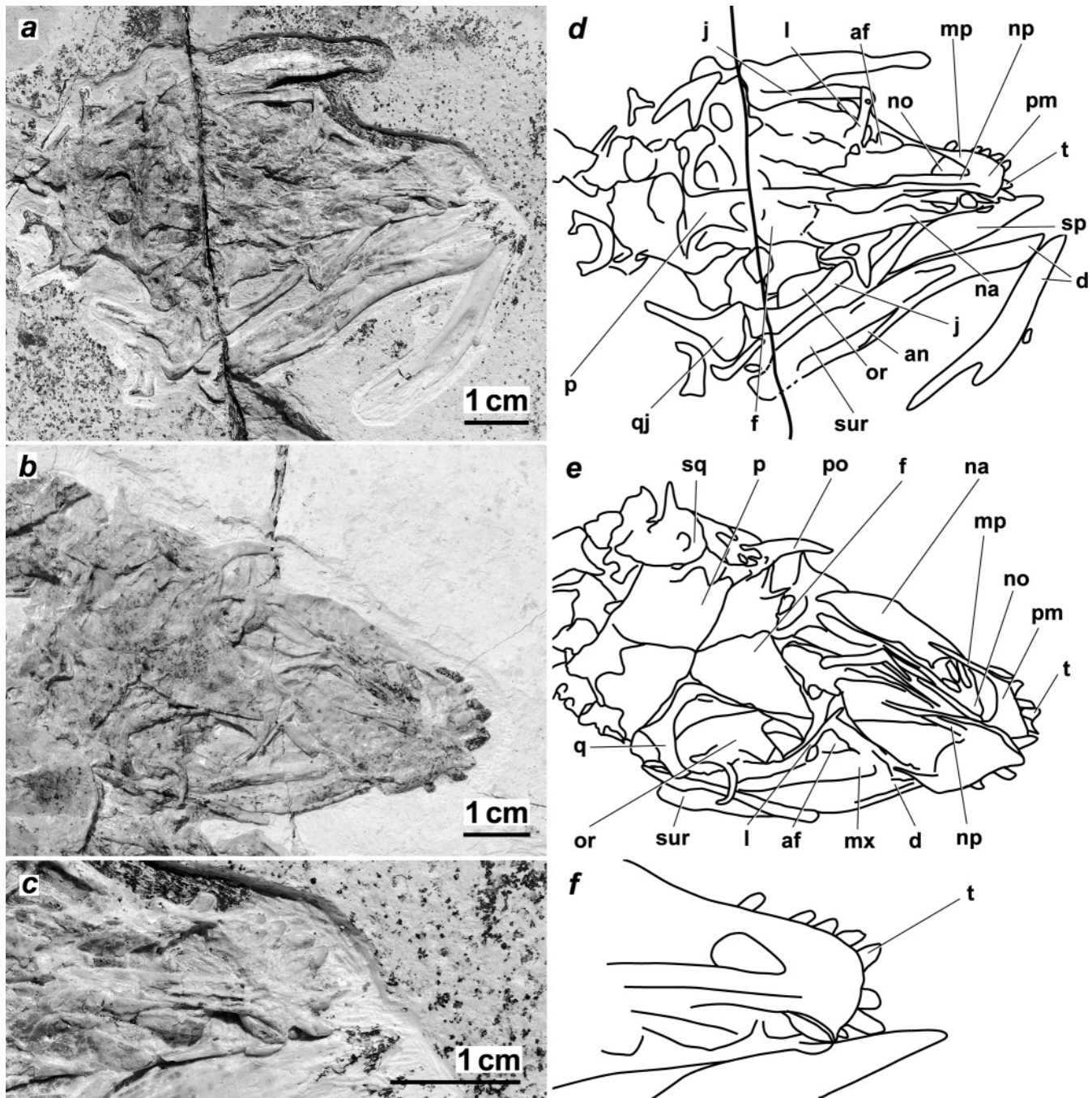
the same situation, and it is reduced in Early Cretaceous enantiornithines (Sanz et al. 1997).

The quadrate has a slender and long orbital process. The lower jaw is robust and straight. The mandibular symphysis is short. The dentary is posteriorly forked; it is about half the length of the mandible. Teeth are absent in the dentary. There is no mandibular fenestra.

Vertebrae column: All three specimens preserve vertebrae. Between IVPP V13275 and IVPP V13276 is preserved a nearly completely articulated vertebral column, including cervicals (Fig. 4*a*), thoracics, synsacrum, free caudals, and the pygostyle.

The total number of cervicals is estimated to be 10 or 11. The cervicals are elongate. The cervical vertebrae are heterocoelous, and thus exhibit a more derived condition than in *Archaeopteryx* (Wellnhofer 1988, 1993).

There are 13 thoracic vertebrae as in *Archaeopteryx*; there are 12 thoracic vertebrae in *Confuciusornis* and less in more

Fig. 4. *Sapeornis chaoyangensis*. Cervical vertebrae of IVPP V13276 (*a*, *e*), dorsal vertebra of IVPP V12698 in lateral view (*b*, *f*), synsacrum of IVPP V13275 in dorsal view (*c*, *g*), and caudal vertebrae and pygostyle of IVPP V13276 in lateral view (*d*, *h*). ac, articular surface of centrum; ce, centrum; fe, femur; hp, haemapophysis; il, ilium; ns, neural spine; plp; pleurapophysis; poz, postzygapophysis; prz, prezygapophysis; py, pygostyle; 1–7, transverse processes of first through seventh sacral vertebrae of the synsacrum.
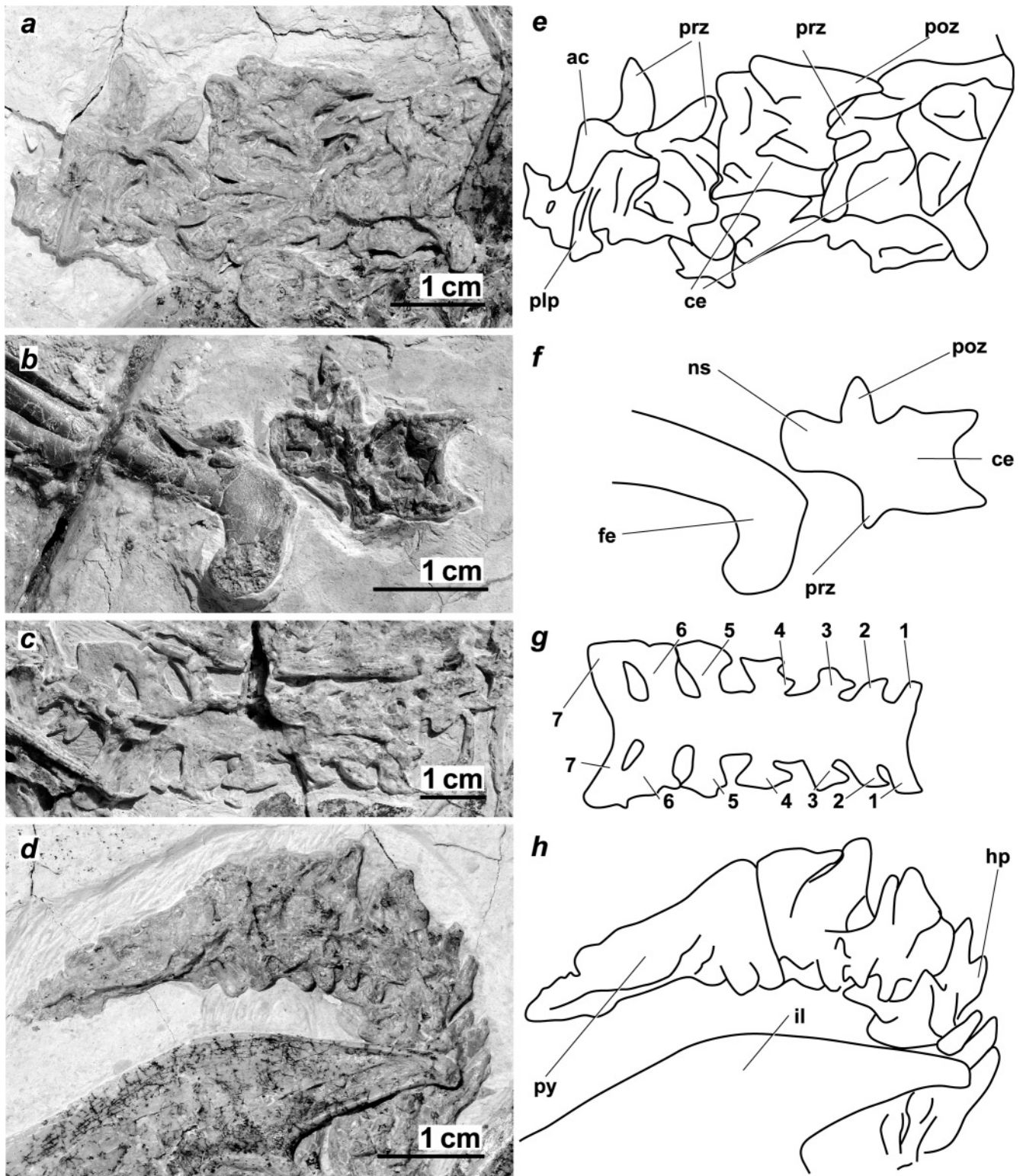
advanced birds (Chiappe et al. 1999). The thoracics have biconcave centra as in other primitive birds. Most of the thoracic vertebrae of *Sapeornis* lack pleurocoels (lateral excavations) as in *Archaeopteryx* (Fig. 4b); however, the last two thoracics appear to possess deep excavations in IVPP V13275. *Confuciusornis* and nearly all enantiornithines such as *Cathayornis* and *Concornis* possess such lateral excavations.

The synsacrum is best preserved dorsally in IVPP V13275 (Fig. 4c). It is composed of seven sacral vertebrae as in *Confuciusornis* and the most primitive enantiornithine *Protopteryx* (Zhang and Zhou 2000); there are eight sacrals in *Cathayornis* and nine in the ornithurine *Yanornis* (Zhou and Zhang 2001). There is a deep spinal crest along the full length of the synsacrum. The transverse processes of the sacral vertebrae become progressively longer and more robust towards the caudal end. The transverse processes of the first three sacrals have relatively small distal expansions and are mainly inclined cranially; the fourth sacral has a large distal expansion of its transverse process; and the transverse processes of the last three sacrals are significantly expanded and inclined caudally. The distal ends of the transverse processes of the second through fifth sacrals do not contact with that of the preceding sacrals; however, the distal ends of the transverse processes of the sixth sacral contact that of both the fifth and seventh, forming two pairs of nearly elliptical fenestra.

There are about six or seven free caudal vertebrae in IVPP V13275. They are short and small compared with the sacral vertebrae. The transverse processes of the caudal are long, caudally directed, and become progressively shorter caudally.

The pygostyle is long and triangular, which is generally similar to that of *Confuciusornis* and early enantiornithines (Fig. 4d). Ornithurine birds such as *Yixianornis* typically have a much shorter pygostyle (Zhou and Zhang 2001).

Ribs and gastralia: Ribs and gastralia are most completely preserved in IVPP V13276 and are nearly completely preserved in IVPP V13275. The vertebral ribs are long and slender; they are much more curved than in the oviraptotosaurid *Caudipteryx* (Zhou and Wang 2000), indicating a laterally expanded rib cage. The first two pairs are shorter than the posterior ribs; the last four pairs of vertebral ribs are also short, and are approximately half as long as the preceding ones.

It is noteworthy that neither of these two specimens has preserved convincing evidence of the uncinate process. It is unknown if this structure is absent in *Sapeornis* as in *Archaeopteryx* or due to the fact that it is unossified. It is notable, however, that the uncinate process has been reported in non-avian theropods (Clark et al. 1999; Zhou and Wang 2000; Zhou et al. 2000) and more advanced birds such as *Confuciusornis* and all ornithurine birds including *Chaoyangia* (Hou and Zhang 1993). No sternal rib has been positively recognized in *Sapeornis*.

The gastralia are nearly completely preserved in IVPP V13276 (Fig. 5). We counted about 15 pairs of gastralia from this specimen, although the exact number is difficult to obtain. Unlike vertebral ribs, which are consistent in width throughout their length, gastralia are expanded at the cranial end and taper significantly towards the needle-shaped caudal end. They are generally more slender and much shorter than the vertebral ribs; however, the cranial ends of most of the anterior gastralia are as wide as or even wider than the distal portion of the vertebral ribs. The gastralia become progressively shorter toward the caudal end.

Pectoral girdle: In IVPP V12689, the scapula and coracoid are articulated and exposed lateroposteriorly. The scapula and coracoid form an angle of less than 90° as in all volant birds (Olson and Feduccia 1979) (Fig. 6a). The scapula lacks a prominent acromion. The scapular shaft is relatively straight and tapers slightly towards the distal end (Figs. 6a, 6b) similar to that of *Jeholornis* (Zhou and Zhang 2002b). The distal end of the scapula is neither pointed nor expanded. In *Archaeopteryx* and dromaeosaurs the scapular shaft is slightly expanded distally, and in *Confuciusornis* the distal end is approximately as wide as the proximal portion.

In IVPP V13276, the cranial surface of the coracoid is exposed. The coracoid is generally similar to that of *Archaeopteryx* and theropod dinosaurs; it is broad and non-strut-like (Fig. 6c). *Jeholornis* has a more elongated coracoid as in *Confuciusornis* and more advanced birds (Zhou and Zhang 2002b). The coracoid of *Sapeornis* has a concave lateral margin and convex medial and distal margins. There appears to be a supracoracoid foramen in the middle position near the dorsal margin of the coracoid. The glenoid facet of the coracoid lies ventral to the acrocoracoid process as in *Jeholornis*, *Confuciusornis*, and more advanced birds. In *Archaeopteryx*, however, the acrocoracoid process ("biceps tubercle") lies ventral to and cranial to the glenoid facet (Wellnhofer 1988).

The furcula is preserved in all known specimens of *Sapeornis*. However, the overlapping of the furcula with the humerus in the holotype prohibits the recognition of the hypocleidum of the furcula (Zhou and Zhang 2002a). Without the hypocleidum, the furcula is nearly identical to that of *Archaeopteryx*, *Jeholornis* (Zhou and Zhang 2002b), and *Confuciusornis* (Chiappe et al. 1999); this is another reason why the hypocleidum was not recognized in the previous description. The two new specimens clearly show that the furcula has a moderately long and slender hypocleidum, comparable to that of enantiornithine birds; however, the rest of the furcula is stout and U-shaped (Figs. 6b, 6c). The furcular ramus is wide and its width is consistent throughout its length; there is no obvious excavation or groove on the anterior surface of the furcula. The two furcular rami form an angle of about 105°. The hypocleidum is about twice as long as the width of the clavicle.

The sternum has not been preserved in any of the known specimens of *Sapeornis*. This is similar to the situation with *Archaeopteryx* in which only one specimen preserves the sternum out of the seven skeletons (Wellnhofer 1993).

Forelimb: The forelimbs of *Sapeornis* are extremely elongated compared with the hind limbs. The ratio of the forelimb length (humerus + ulna + carpometacarpus) to the hind limb length (femur + tibiotarsus + tarsometatarsus) in known specimens is 1.54 (IVPP V12689), 1.54 (IVPP V13275), and 1.53 (IVPP V13276). The same ratio is 0.91 in the Solnhofen specimen of *Archaeopteryx*, 1.2 in *Jeholornis* (IVPP V13274), and 1.0 in *Confuciusornis* (IVPP V11619) (Zhou and Zhang 2002a, 2002b). The ratio of the ulna length to the femur length in *Sapeornis* is 1.66 (IVPP V12689), 1.66 (IVPP V13275), and 1.72 .(IVPP V13276) (Table 1), and the same ratio is 1.03 in *Archaeopteryx* (the Solnhofen specimen), 1.40 in *Jeholornis* (IVPP V13274), and 1.00 in *Confuciusornis* (IVPP V11619). However, it is only 0.66 and 0.74 in the

Fig. 5. *Sapeornis chaoyangensis*. Gastralia of IVPP V13276. ga, gastralia; ri, rib.
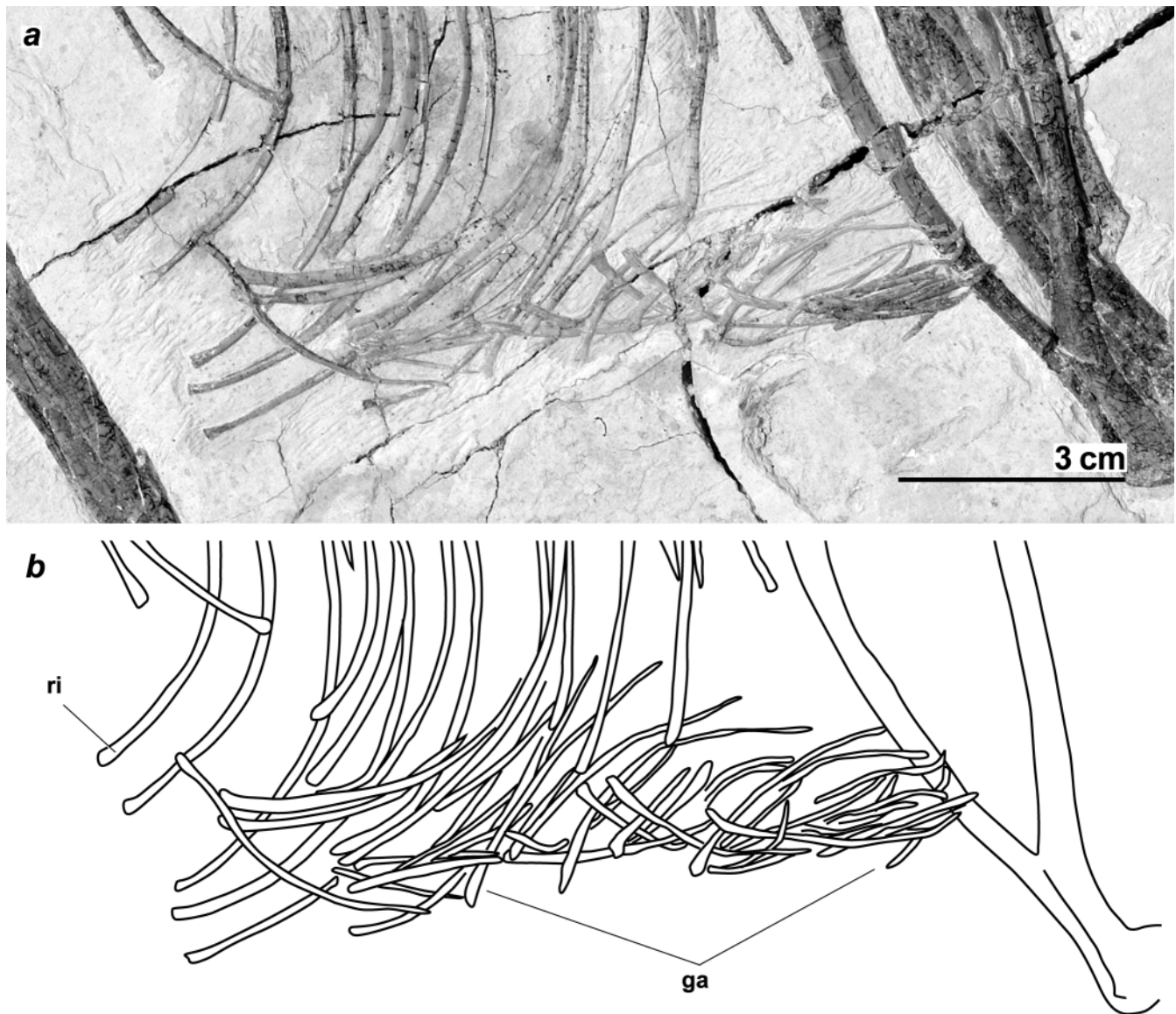
dromaeosaurs *Microraptor* (Xu et al. 2000) and *Sinornithosaurus* (Xu et al. 1999), respectively.

The humerus has a distinctive fenestra at the proximal end; it is proximodistally elongated, and nearly half the length of the deltoid crest; its width is only about one third of its length (Fig. 7*a*). In the initial description of the holotype, such a structure was not recognized because the region of the specimen is either crushed or overlapped by the furcula. The new specimens clearly preserve such a fenestra and after reexamination we also confirmed the presence of the fenestra in both of the humeri of the holotype with more careful observations. Both *Confuciusornis* and *Changchengornis* have a similar fenestra at the proximal end of the humerus (Hou et al. 1995; Ji et al. 1999); however, the fenestrae in these confuciusornithid birds are more or less rounded as compared to a much more slender shape in *Sapeornis*.

The humerus has a prominent and rounded head, as best shown in the left side of IVPP V13275. In proximal view the head has a less marked midline convexity. The humerus lacks the capital incisure and the pneumotricipital fossa. The deltoid crest is large, with a straight dorsal margin; it does not protrude strongly cranially as in *Archaeopteryx* and *Confuciusornis*; the distal margin of the deltoid crest is concave as in *Confuciusornis*, but its dorsodistal portion tapers into a distinctive acute angle. The dorsal tubercle is recognizable in both IVPP V12698 and IVPP V13276. The ventral tubercle is not visible in all the specimens available. The bicipital crest is small and flat.

Distally, the humerus lacks the impression of brachialis anticus. The distal condyles are mainly positioned on the anterior side of the humerus as in advanced birds; the ventral condyle is prominent and ball-shaped, and the dorsal condyle appears smaller and does not project far proximally as in extant birds. The ventral supracondylar tubercle is observable in IVPP V13276. The dorsal supracondylar process is absent. Both the ectepicondyle and entepicondyle are apparent in IVPP V13276.

The forearm is best preserved in IVPP V13276. The ulna

Fig. 6. *Sapeornis chaoyangensis*. Left scapula and coracoid of IVPP V12698 in lateral view (*a*, *d*), pectoral girdle and furcula of IVPP 13275 in dorsal view (*b*, *e*), and furcula and right coracoid of IVPP V13276 in cranial view (*c*, *f*). ac, acrocoracoid of the coracoid; co, coracoid; fu, furcula; hp, hypocleidum; hu, humerus; sc, scapula.
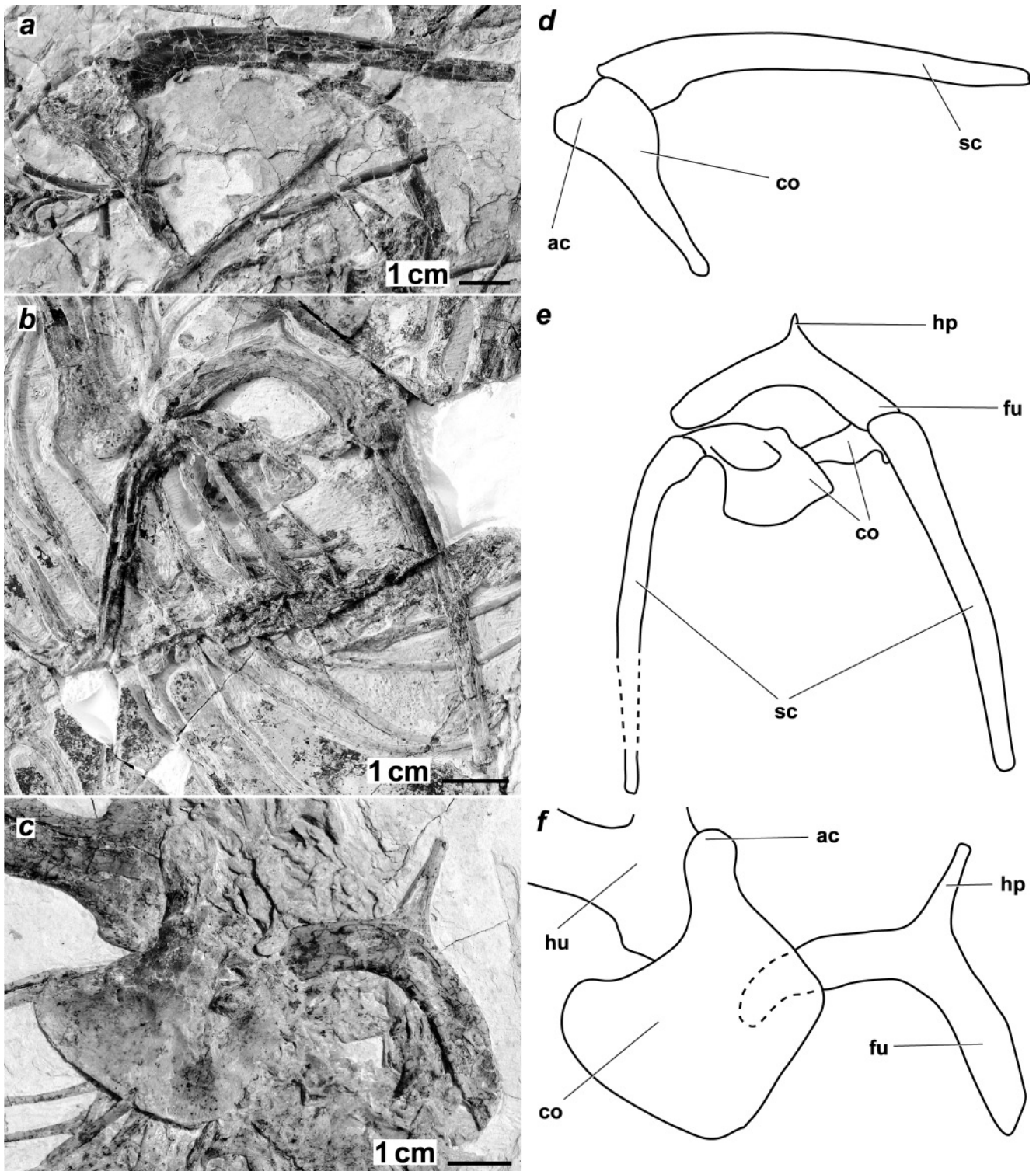
is slightly longer than the humerus in all known specimens, which is similar to that of more advanced birds; however, in both *Archaeopteryx* and confuciusornithids, the ulna is significantly shorter than the humerus (Ji et al. 1999; Chiappe et al. 1999). In *Jeholornis*, however, the ulna is approximately the same length as the humerus (Zhou and Zhang 2002*b*). The ulna is curved along its proximal two thirds, but the distal portion is straight (Fig. 7*b*). Papillae for the attachment of the remiges are absent on the ventral side, as in most primitive birds. The olecranon is short and stout.

Table 1. Length (mm) of some skeletal elements of *Sapeornis chaoyangensis*.

	IVPP V12698 (holotype)	IVPP V13275	IVPP 13276
Skull		62*	64*
Scapula	75(l)*, 75(r)	71(l)*, 71.5(r)*	
Coracoid	40(r)*	36.7(l)	39.5(r)
Furcula (width)	43.1	41.5*	42.4
Humerus	126.5(l), 129.6(r)	122.6(l)	123.2(r)*
Ulna	133.1(l), 135.1(r)	123.6(l)*, 124(r)*	124(r)
Radius	133(l), 131.9(r)	120(l), 120.4(r)	123.3(r)
Carpometacarpus	61.9(l)	56.5(l)	58(r)
Metacarpal I	14.3(l)	11(l)*, 12(r)*	12(r)
Metacarpal II	57.1(l)	52(l)*, 51.3(r)	52.9(r)
Metacarpal III	54.6(l)	49(l)*, 47(r)	48.2(r)
Manual digit I-1	33.6(l)	28.7(l), 30(r)	27(r)*
Manual digit I-2 (ungual)	19(l)*	18.6(l)*	18.8(r)
Manual digit II-1	30(l), 32.2(r)	29(r)*	30.6(r)
Manual digit II-2	27.7(l)	26(l)*, 25.9(r)	26.6(r)
Manual digit II-3 (ungual)	18(l)*	17.4(l)	17.7(r)*
Manual digit III-1		10.6(r)	10(r)
Manual digit III-2			9(r)
Ilium	56(l)*	55.3(l), 53(r)*	55.9(l)
Ischium	42.1(l)	41.9(l)*	
Pubis	85.4(l), 87(r)	77.5(l)*	80.0(l)
Femur	80.4(l)	74.4(l), 73.7(r)*	72.1(r)
Tibiotarsus	83.6(l)	80.6(l), 81.7(r)	85.3(r)
Fibula	72.4(l)*	71(l)*, 68(r)*	
Metatarsal I		10.8(l)	
Metatarsal V		9.6(r)	
Tarsometatarsus	44.6(l)	41.5(l)*, 42(r)*	42(r)
Pedal digit I-1		16(l)	16.4(r)
Pedal digit I-2 (ungual)		17.9(l)	17(r)*

Note: Asterisks indicate estimated measurement; l and r indicate left and right sides, respectively.

The distal end of the ulna is as wide as the midshaft, but not as expanded as in advanced birds. As in *Archaeopteryx*, the dorsal condyle is not developed as a semilunate ridge.

The radius is relatively straight and rod-shaped. In IVPP V13276, the radius and ulna are tightly attached at both ends, leaving a space between the two bones restricted mainly along the proximal half. The radius is anteroposteriorly compressed. The anteroposterior width of the midshaft of the radius is only about one third that of the ulna. The proximal end of the radius is dorsoventrally compressed and possesses a bicipital tubercle. The radius is rounded and expanded distally.

The manual elements are articulated in IVPP V13276 (Fig. 7c). The total length of the manus approximately equals that of the ulna. The ulnare in the left hand of IVPP V13275 shows a well-developed V-shape as in extant birds (Vazquz 1992). IVPP V13276 has a radiale that is about the size of the ulnare, with articulating facets for both the carpometacarpus and the radius. The distal carpals and the proximal end of metacarpals II and III are fused into carpometacarpus, as in *Jeholornis* (Zhou and Zhang 2002b) and *Confuciusornis* (Zhou and Farlow 2001). Metacarpal I is short, straight, and about one fourth the length of metacarpal II; it lacks the extensor process and is not fused with the carpometacarpus, although it is tightly attached to the latter in all three known specimens of *Sapeornis*. Proximally, the carpometacarpus has a well-developed carpal trochlea. Metacarpal II is slightly longer than metacarpal III; metacarpal II extends distally past metacarpal III; by contrast, in all known enantiornithine birds, metacarpal III extends distally past metacarpal II. Metacarpal II is more than twice the midshaft width of metacarpal III. Metacarpal III is mediolaterally compressed; proximally it is dorsoventrally much wider than the midshaft and is dorsoventrally flattened as is typical of all birds. Metacarpals II and III are unfused distally; they are both straight and so tightly attached to each other that there is no intermetacarpal space. Metacarpal II lacks an intermetacarpal process.

The manual digits are not completely preserved in the holotype of *Sapeornis*. Due to the incompleteness and disarticulation of the phalanges, the phalangeal formula of *Sapeornis* was incorrectly reconstructed in our preliminary report as compared to that of *Archaeopteryx* and *Confuciusornis*, i.e., "2–3–4." Fortunately, both IVPP V13275 and IVPP V13276 have preserved completely articulated manual phalanges, which clearly point to a phalangeal formula of "2–3–2."

The first manual digit comprises two phalanges; the first phalanx is long, slender, and curved. Although it is more than half the length of metacarpal II, it does not extend to the distal end of metacarpal II. The second phalanx (ungual) is large and curved but is much shorter than the first phalanx.

The second manual digit is significantly longer than the

Fig. 7. *Sapeornis chaoyangensis*. Right forelimb of IVPP V13276. Humerus in cranial view (*a*, *d*), ulna and radius in cranial view (*b*, *e*), and manus in ventral view (*c*, *f*). cmc, carpometacarpus; dc, deltoid crest of the humerus; fe, fenestra at the proximal humerus; hu, humerus; mc-I, mc-II, and mc-III, metacarpals I–III; r, radius; ra, radiale; se, semilunate carpal; u, ulna; ul, ulnare; I-1 and I-2, first and second phalanges of manual digit I; II-1, II-2, and II-3, first through third phalanges of manual digit II; III-1 and III-2, first and second phalanges of manual digit 3.
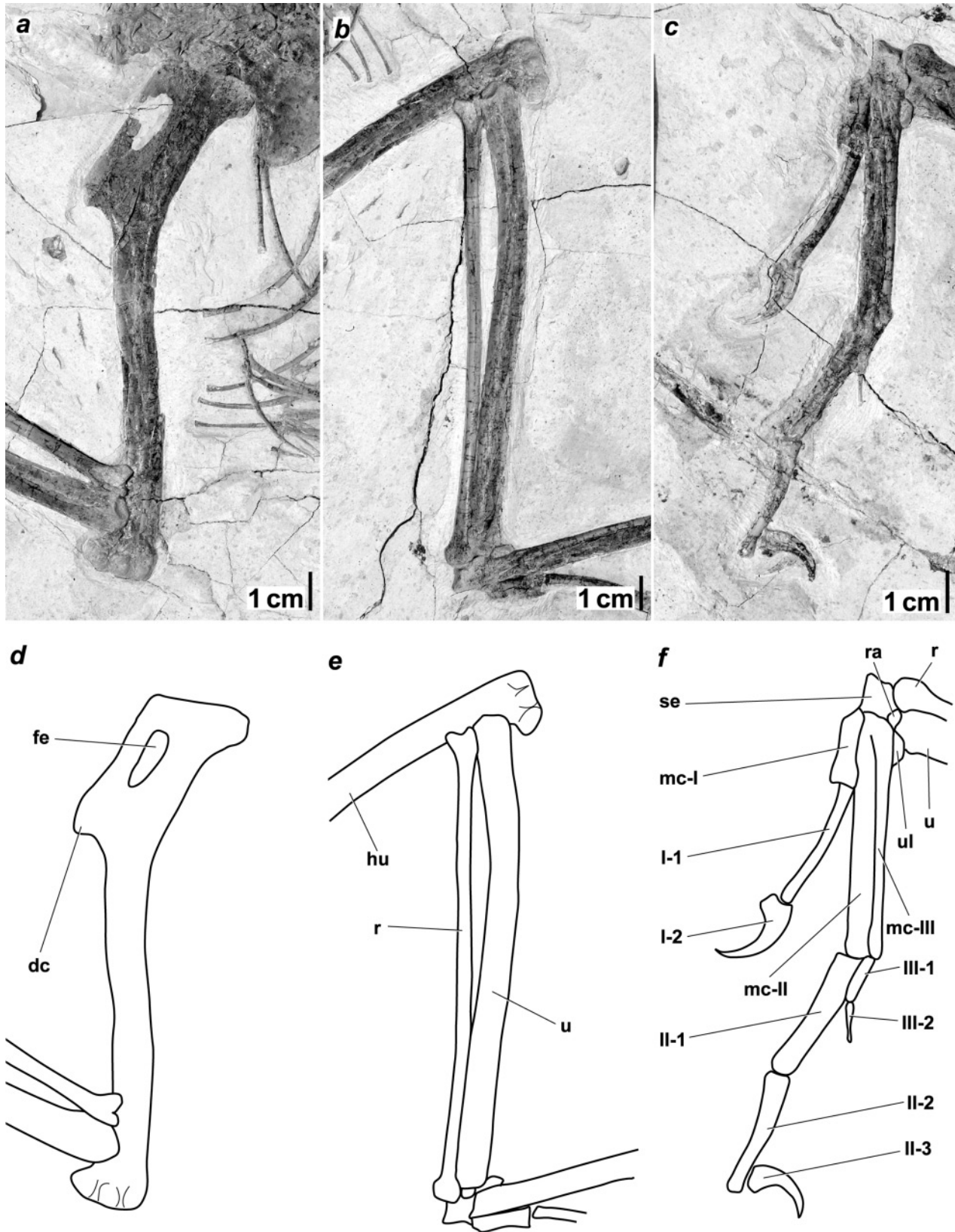
carpometacarpus. It is comprised of three long phalanges. Unlike *Archaeopteryx* and *Confuciusornis*, the first phalanx is slightly longer than the second, although the third phalanx (ungual) is the shortest in all these birds. The first phalanx is robust and as wide as metacarpal II; it is slightly expanded at the distal end in the holotype, but this expansion is not clear in the other two specimens. The second phalanx is much more slender, rod-shaped, and curved than the first phalanx of the first digit, but it tapers distally. The ungual is curved and only slightly smaller than the ungual of the first digit.

The third manual digit is comprised of two reduced phalanges, in contrast to four in *Archaeopteryx* (Wellnhofer 1988), *Confuciusornis* (Hou et al. 1995; Chiappe et al. 1999), and *Jeholornis* (Zhou and Zhang 2002*b*). The two phalanges are approximately the same length; both are a lot more slender than other phalanges. The first phalanx is tightly attached to both the distal portion of metacarpal III and the proximal part of the first phalanx of the second digit. The total length of the third digit is only about 27% of that of the second digit (Table 1).

Pelvic girdle: The pelvis is more or less completely preserved in the three known specimens of *Sapeornis*. The ilium, ischium, and pubis are not fused with each other as in other most primitive birds (Wellnhofer 1993; Chiappe et al. 1999; Zhou and Zhang 2002*b*) (Fig. 8).

The ilium is generally similar to that of *Archaeopteryx*, *Confuciusornis*, and enantiornithines (Figs. 8*a*, 8*b*). The two ilia appear to be separate from each other, and neither is fused with the synsacrum, as in other basal birds. The preacetabular portion of the ilium is longer than the postacetabular portion; the former is large and expanded dorsoventrally, and the latter tapers and curves ventrally towards the distal end. The ilium forms about the upper half of the acetabular foramen. The antitrochanter is not developed. The pubic peduncle is robust and a lot wider than the ischiatic peduncle; the ischiatic peduncle is short and small.

The ischium is long, straight, and tapers slightly towards the distal end; it has a well-developed strut-like dorsal process as in *Jeholornis* (Zhou and Zhang 2002*b*), *Confuciusornis*, and enantiornithines (Martin et al. 1998) (Fig. 8*c*); this process nearly contacts the posterior portion of the ilium near the posterior end. The two ischia might be in contact at the distal end as shown in IVPP V13276, but they are not fused.

The pubes are exposed dorsally in the holotype (Fig. 8*d*) but are laterally preserved in IVPP V13276 (Fig. 8*a*). The pubis is posteriorly directed as in all birds and dromaeosaur dinosaurs. The pubis is much longer than the ischium; it is rod-shaped along much of its length, and the midshaft is suboval in cross section. The pubic symphysis is about one third the length of the pubis, as in *Confuciusornis* (Martin et al. 1998; Chiappe et al. 1999). The pubic symphysis is more than one third the length of the pubis in *Archaeopteryx* (Wellnhofer 1988) and *Jeholornis* (IVPP V13353), and even longer in dromaeosaurs, *Caudipteryx*, and other dinosaurs (Norell and Makovicky 1997, 1999; Xu et al. 1999; Zhou et al. 2000). The two pubes are symphysized, but not fused caudally. In lateral view, the distal portion of the pubis is curved dorsally, with a distinctive pubic foot, which is somewhat similar to that of *Archaeopteryx*, *Jeholornis*, and enantiornithines, but not to that of *Confuciusornis* (Chiappe et al. 1999). The

reduced pubic foot of *Confuciusornis* most likely evolved independently of more advanced birds. Ornithurine birds such as *Yanornis* and *Yixianornis* also seem to retain a small pubic foot (Zhou and Zhang 2001).

Hind limb: The hind limb is short compared with the forelimb, similar to that seen in the enantiornithine *Longipteryx* (Zhang et al. 2001*a*, 2001*b*). The femur is only slightly shorter than the tibiotarsus; the ratio of femur length to tibiotarsus length is 0.96 (IVPP V12689), 0.92 (IVPP V13275), and 0.85 (IVPP V13276). In *Longipteryx*, the same ratio is about 0.95 (IVPP V12325).

The femur is stout and curved (Fig. 9*a*). The greater trochanter is not prominent. Distally, there is a well-developed fibular trochlea, and the intercondylar sulcus is shallow.

The tibiotarsus is relatively short. It lacks a well-developed cnemial crest. Unlike *Archaeopteryx* and *Jeholornis* (Zhou and Zhang 2002*b*), the proximal tarsals of *Sapeornis* are well fused with the tibia into tibiotarsus as in more advanced birds, and the medial condyle is as large as the lateral condyle. The intercondylar groove is broad and about one third the width of the distal tibiotarsus (Fig. 9*b*). The supratendinal bridge is absent as in other basal birds. The fibula is extremely slender and long; it nearly reaches the distal end of the tibiotarsus as in *Archaeopteryx* and *Jeholornis.* The fibula is also long in the primitive enantiornithine *Protopteryx*, but it is much reduced in *Confuciusornis*, ornithurines, and most enantiornithine birds.

The tarsometatarsus is preserved and well fused at the proximal end (Figs. 9*c*, 9*d*). One free tarsal is recognized in the holotype (Fig. 9*d*), but not in other specimens. It is likely that it is fused with the metatarsals in the adult individual. The tarsometatarsus is slightly constricted in its distal one third. The hypotarsus is absent. The fifth metatarsal is present as in *Archaeopteryx*, *Jeholornis* (Zhou and Zhang 2002*b*), and *Confuciusornis* (Zhou and Hou 1998); it is short, slender, and less than one fourth the length of the tarsometatarsus. Metatarsal I is J-shaped in dorsal view. Metatarsals II, III, and IV are straight and not fused at the distal end. Metatarsal III is slightly longer than metatarsals II and IV, which are approximately the same length. Metatarsal II bears no tubercle on the dorsal surface. Metatarsal III is not pinched at the proximal end. There is no distal vascular foramen on the tarsometatarsus. The trochleae for metatarsals II, III, and IV are about the same width. Trochleae for metatarsals II and IV are slightly projected medially and laterally, respectively.

The pedal digits are approximately as long as the tarsometatarsus (Fig. 9*c*). All the unguals are large and semicircular, with sharp and needle-shaped horny sheaths. Digit I is reversed as in all birds; it is long, with two nearly equally long phalanges. The ungual of digit I has a relatively large extensor process. Digits II, III, and IV are approximately the same length, with the unguals longer than the penultimate phalanges. Digit III is the longest of the four pedal digits. In digit III of IVPP V13276, the second and third phalanges are nearly identical in length; both are only slightly shorter than the first phalanx; and all of the first three phalanges are much shorter than the ungual.

Gastroliths: In IVPP V12375, dozens of gastroliths are present, mainly distributed in the region posterior to the gastralia and ventral to the pelvis, although some of them are spread into the areas of the pectoral girdle or foot. They

Fig. 8. *Sapeornis chaoyangensis*. Pelvis of IVPP V13276 in ventrolateral view (*a*), right ilium of IVPP V12698 in lateral view (*b*), left ischium of IVPP V12698 in medial view (*c*), pubes of IVPP V12698 in dorsal view (*d*), and line drawings of *a–d* (*e*). ai, articulation for the ischiatic process of the ilium; ap, articulation for the pubis; dp, dorsal process of the ischium; il, ilium; is, ischium; pf, pubic foot; pp, pubic peduncle of the ilium; ps, pubic symphysis; pu, pubis.
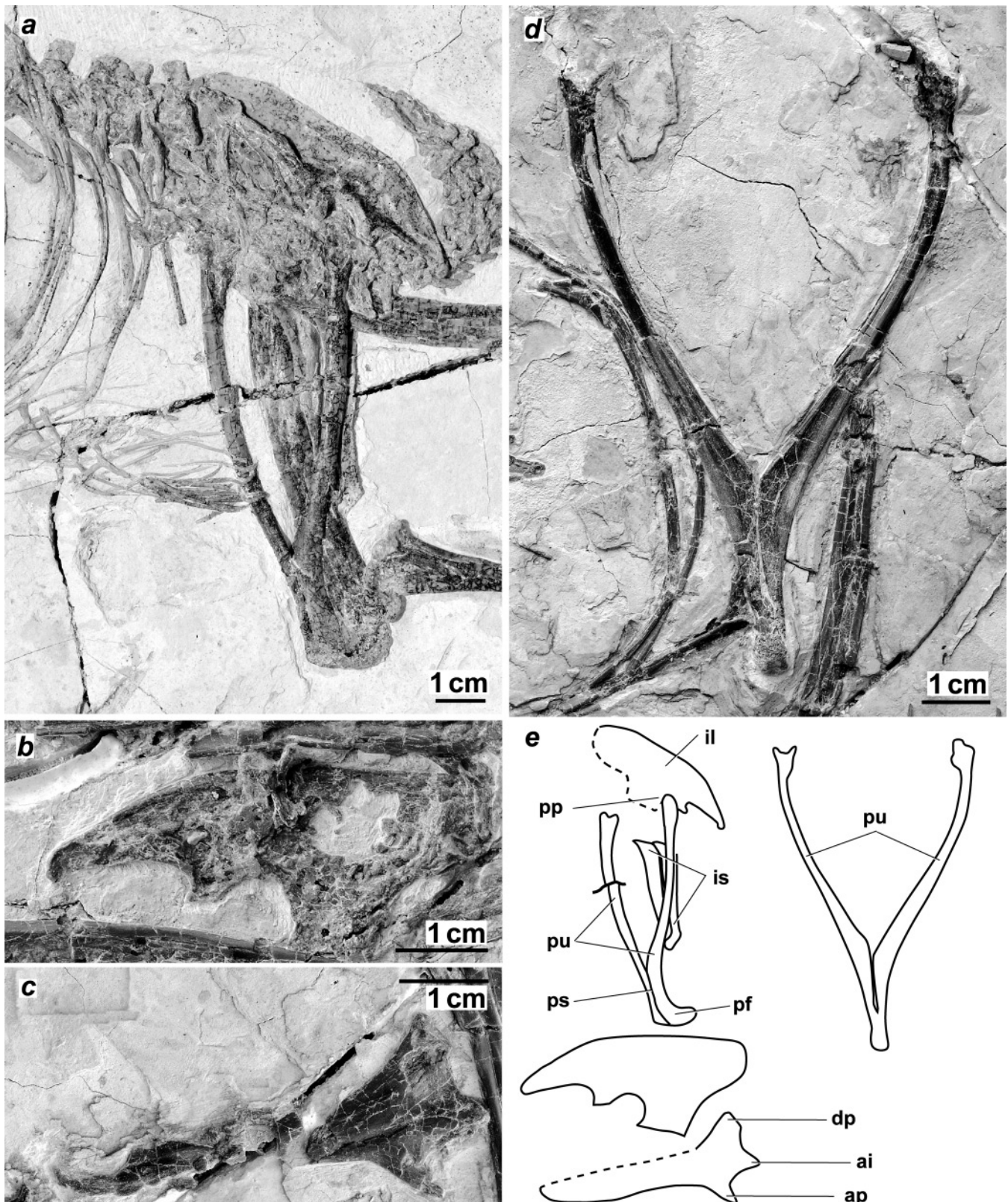
Fig. 9. *Sapeornis chaoyangensis*. Left femur of IVPP V12698 in caudal view (*a*, *e*), tibiotarsus and fibula of IVPP V12698 in cranial view (*b*, *f*), right foot of IVPP V13276 in cranial view (*c*, *g*), and left tarsometatarsus of IVPP V12698 in caudal view (*d*, *h*). fh, femoral head; fi, fibula; lc, lateral condyle of the tibiotarsus; mc, medial condyle of the tibiotarsus; mtII, mtIII, mtIV, and mtV, metatarsals II–V; t, tarsal; ti, tibia; 1–4, first through fourth pedal digits.
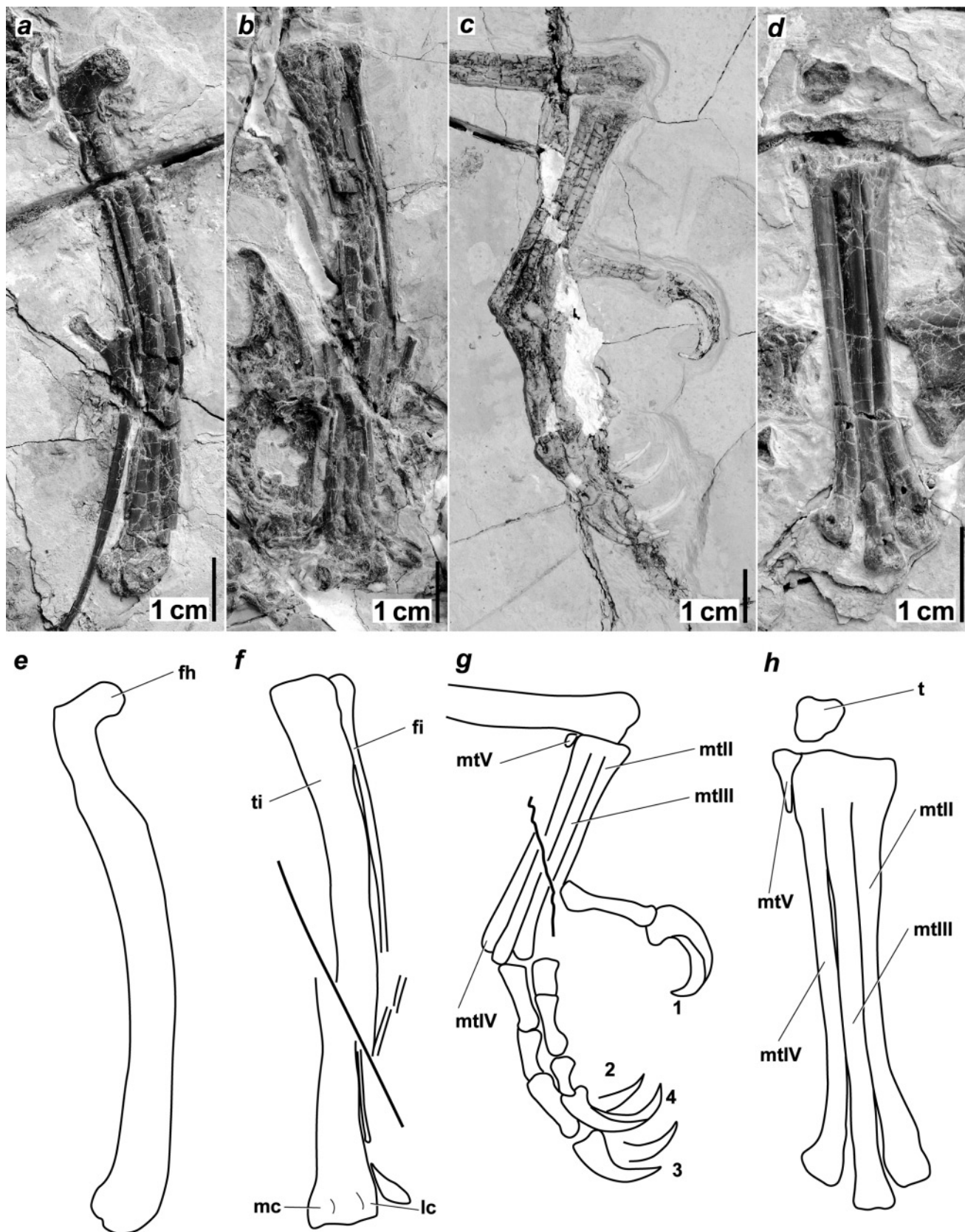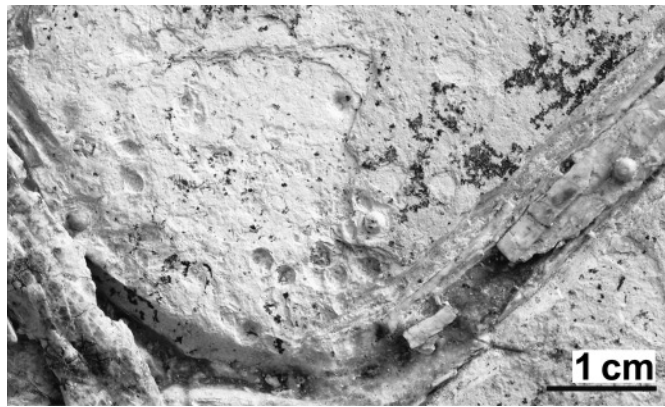
Fig. 10. *Sapeornis chaoyangensis*. Gastroliths and their impressions of IVPP V13275.

are nearly rounded in shape and measure about 2.0–2.5 mm in diameter (Fig. 10). These gastroliths resemble those found associated with specimens of *Caudipteryx* from the Yixian Formation, but are smaller in size (Zhou and Wang 2000; Zhou et al. 2000).

Discussion

The new material of *Sapeornis* described here provides substantial new information regarding the anatomy of this recently described basal bird (Fig. 11). It confirms some aspects of the unique features shown in the holotype, such as the large body size and the elongated forelimbs compared with the hind limbs. Further, it also illustrates many important features that were either unknown or misinterpreted in the holotype, in particular, those in the skull, furcula, humerus, hand, and foot.

Recent phylogenetic analysis indicated that *Sapeornis* is the most basal known bird except for *Archaeopteryx*, *Rohonavis* (Forster et al. 1998), and *Jeholornis* (Zhou and Zhang 2002*b*). *Sapeornis* therefore represents the most basal bird with a pygostyle. On the other hand, its coracoid is short and robust, rather than strut-like as in *Confuciusornis*, enantiornithines, and ornithurines. The furcular feature is also consistent with its phylogenetic position between these basal birds and more advanced forms such as enantiornithines.

Since the skull is not preserved as part of the holotype, this new *Sapeornis* material clearly shows that this taxon had a skull typical of basal birds. For instance, the skull retains a relatively large antorbital fenestra, large maxilla, and unreduced nasal. On the other hand, the skull is different from that of other known basal birds in that, although it lacks teeth in the lower jaw, it retains them in the premaxilla and maxilla. *Sapeornis* confirms that teeth reduction had happened many times independently in early avian evolution (Chiappe et al. 1999).

The furcula of *Sapeornis* is unique among birds and is also different from that of any dinosaurs (Norell et al. 1997; Xu et al. 1999). It combines both primitive characters (*Archaeopteryx*, *Jeholornis*, and *Confuciusornis*) and derived characters (enantiornithine birds). In other words, the long and slender hypocleidum of the furcula is similar to that of enantiornithines, but the rest of the furcula is similar to that of the stout U shape of *Archaeopteryx*, *Jeholornis*, and

Confuciusornis. *Sapeornis* is the most basal bird known to possess a furcula with a distinctively long hypocleidum. All known early ornithurines birds such as *Yanornis*, *Yixianornis*, and *Ambiortus* have a U-shaped furcula similar to that of modern birds, but none of them has a distinctive hypocleidum (Zhou and Zhang 2001).

The pectoral girdle of *Sapeornis* is nearly as primitive as that of the oldest known bird *Archaeopteryx*. The coracoid is short and stout, rather than strut-like as is the case in more advanced birds. The scapular shaft is relatively straight and its distal end is neither expanded nor pointed. Obviously, the triosseal canal for the supracoracoideus muscles is absent in *Sapeornis* and in many other basal birds including *Archaeopteryx*, *Jeholornis*, *Confuciusornis*, and enantiornithines (Zhou and Farlow 2001). Ornithurine birds like *Yanornis* and *Yixianornis* from the same age possess a much more derived coracoid, with such advanced features as a distinctive procoracoid, thus a triosseal canal is most likely present in these birds.

The humerus of *Sapeornis* is also unique in possessing an elongated elliptical fenestra. Among the known Mesozoic birds, *Confuciusornis* and *Changchengornis* also preserve a fenestra at the proximal end of the humerus. The fenestrae in these early birds were probably adapted for the reduction of weight. No enantiornithine bird has been reported with such a structure. It is also absent in *Archaeopteryx*, *Jeholornis*, and ornithurine birds.

The hand of *Sapeornis* was previously incorrectly reconstructed due to incomplete and disarticulated preservation of the phalanges in the holotype (Zhou and Zhang 2002*a*). Two major revisions have been made in this paper based on the two nearly completely articulated skeletons. First, contrary to previous reconstruction, the second phalanx of the second digit is in fact slightly shorter than the first. This is obviously an advanced feature compared to the primitive state in *Archaeopteryx*, *Confuciusornis*, and theropod dinosaurs, where the reverse is true. Second, the third digit actually comprises only two reduced phalanges, which is significantly different from previous reconstruction of four phalanges obviously based on the phalangeal formula of *Archaeopteryx* and *Confuciusornis*. It is noteworthy that the oviraptorosaurid theropod *Caudipteryx* also has a reduced third manual digit, with two very reduced phalanges (Zhou et al. 2000). All known enantiornithines and ornithurines have a reduced third manual digit comprising one or two phalanges, and the second is always very small. The reduced third digit in *Sapeornis* again confirms the trend of the manual digits starting from the third digit in birds and even non-avian theropods. Clearly, this must be related to the attachment of the primary feathers to the second manual digit; the third digit had not only lost its original function but also came in the way of the attachment of primary feathers in these creatures.

The first manual digit is long but, unlike *Archaeopteryx*, *Confuciusornis*, and *Protopteryx*, it does not extend to the distal end of metacarpal II, which is more similar to more advanced enantiornithines and ornithurine birds. Since feathers have not been found associated with the skeleton in known specimens, there is yet no evidence of whether the alula is present, as in *Protopteryx* (Zhang and Zhou 2000) and *Eoalulavis* (Sanz et al. 1996), or absent, as in *Archaeopteryx* and *Confuciusornis*. What is certain is that the alula had appeared before the reduction of the alular digit, as indicated

by *Protopteryx*; in view of this fact, *Sapeornis* might have already possessed an alula.

None of the three known specimens of *Sapeornis* preserves the sternum. This reminds us of the situation in *Archaeopteryx*: only one individual is now known to have preserved the sternum. Although an ossified sternum is most likely present in this bird, it is unclear why only the sternum is not preserved while all other bones are preserved, and most of them are even well articulated in some specimens. This might be explained by the lack of a strong articulation between the sternum and coracoid. Obviously, the coracoid of *Sapeornis* is among the most primitive features of this bird. The sternum of *Sapeornis* most likely lacks the coracoidal sulci for a tight connection with the coracoid. Another possible explanation is that the sternum is not well ossified in known specimens.

Sapeornis was recognized as the largest known bird from the Early Cretaceous (Zhou and Zhang 2002*a*). Two new specimens are approximately the same size as the holotype. They are all larger than the largest known individual of *Archaeopteryx*. The recently described long-tailed bird *Jeholornis* is also relatively large but is slightly smaller than *Sapeornis* (Zhou and Zhang 2002*b*). Early Cretaceous enantiornithines are generally smaller than *Archaeopteryx* and *Confuciusornis*. For instance, the tibiotarsus of the Early Cretaceous Australian bird *Nanantius* (Molnar 1986) is only about half as long as that of *Sapeornis*, and the tibiotarsus of *Concornis* (Sanz et al. 1995) from Spain is even smaller. Early Cretaceous ornithurines birds are generally larger than the contemporaneous enantiornithines. Among the known ornithurine types, *Yanornis* and *Yixianornis* are most completely articulated in preservation (Zhou and Zhang 2001): *Yanornis* is approximately the same size as *Gansus* and *Chaoyangia* from China and *Ambiortus* (Kurochkin 1985) from Mongolia, and *Yixianornis* is smaller. The humerus of *Yanornis* is only about 61–64% that of *Sapeornis*, and the femur of *Yanornis* is about 65–72% that of *Sapeornis*. The humerus of *Yixianornis* is 37–39% that of *Sapeornis*, and the femur of *Yixianornis* is about 51–57% that of *Sapeornis* (see Zhou and Zhang 2001) (Table 1).

It has been generally concurred that the reduction of body size has been a trend in the early evolution of birds (Sanz and Buscalioni 1992; Zhou and Hou 1998). In other words, relatively large body size was probably a synapomorphy for all birds, as shown by the most basal bird *Archaeopteryx* and *Jeholornis*; early birds with less well developed flight structures could probably take advantage of the small size while launching their first flapping flight. This is particularly true in the case of the Early Cretaceous enantiornithine birds; they are generally small in size. Ornithurine birds are relatively large and have a flight apparatus that is nearly modern in appearance (in this context, the large size of *Sapeornis* could be explained as a secondary adaptation, as it is much more advanced than *Archaeopteryx*).

Despite the primitive appearance of the coracoid and lack of feather evidence, the flight capability of *Sapeornis* is probably more developed than that in *Archaeopteryx*. *Sapeornis* has, among many more derived features, a pygostyle, a furcula with a hypocleidum, a better developed humeral head and deltoid crest, a well-fused carpometacarpus with a well-developed carpal trochlea, reduced manual phalanges, and an extremely elongated wing.

Fig. 11. *Sapeornis chaoyangensis*. Reconstruction of the whole skeleton mainly based on IVPP V13275 and V13276.
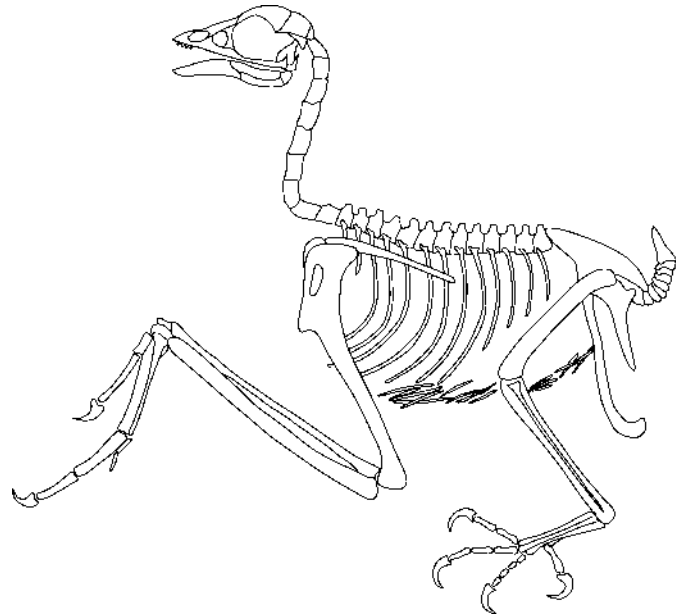
The foot of *Sapeornis* has an opposable hallux as in all known birds; the first pedal digit is long; all pedal unguals are large and strongly curved, indicating strong perching capability.

By the time of the Early Cretaceous, early birds had diversified significantly, not only in morphology and habit, but also in diet. For instance, most enantiornithines are toothed and arboreal forms, and many of them probably ate insects; however, unlike other Early Cretaceous enantiornithines, *Longipteryx* has an elongated snout and distinctively long wing, thus it was probably adapted to eating fish (Zhang et al. 2001*a*, 2001*b*). Early Cretaceous ornithurine birds probably lived near the water, as indicated by their toe proportions (Zhou and Zhang 2001). Among known ornithurines, *Yanornis* also possesses an elongated snout and a lot of densely arrayed teeth in both the upper and lower jaws. Recently discovered material of *Yanornis* preserves fish fragments in the stomach, clearly indicating that it was another piscivorous bird (Zhou et al. 2002). Nothing is known about the habit of *Confuciusornis*, but its robust, toothless jaws suggest it could have been a seed-eater. The recently discovered long-tailed bird *Jeholornis* preserves direct evidence of seed-eating adaptation (Zhou and Zhang 2002*b*). Therefore, by the Early Cretaceous early birds had differentiated in diets, morphology, and flight mode and skills.

The presence of gastroliths and the reduced teeth in *Sapeornis* probably indicate that it mainly fed on plants, which is consistent with its arboreal habit as evidenced by its foot structure. Although *Sapeornis* occupied a habit similar to that of the contemporaneous enantiornithines, they must have had a different flight mode and living space. Enantiornithines, with relatively well developed flight structures such as keeled sternum, strut-like coracoid, and alula, could perform nearly modern flapping flight, which may have made them capable of catching flying insects; however, *Sapeornis* has a pectoral girdle almost as primitive as that in *Archaeopteryx*, and its unreduced manual digits also prohibit it from being an able

flapping flier. Further, the long wings of *Sapeornis* prohibit it from living in dense vegetation such as a forest, thus it most likely occupied an open or semiopen environment (King and King 1979; Welty 1982; Gill 1990). Therefore, a herbivorous or an omnivorous habit appears to be a better strategy for survival of *Sapeornis*, especially when the competition for resources came not only from birds but also from arboreal dromaeosaurs, pterosaurs, and mammals that have been discovered from the same horizon of the region.

Acknowledgments

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