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A diapsid skull in a new species of the primitive bird *Confuciusornis*

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Since the description of *Confuciusornis* (the oldest beaked bird) in 1995, based on three partial specimens, large numbers of complete skeletons have been recovered^{1,2}. Most new material of *Confuciusornis*^{3,4} can be assigned to a single sexually dimorphic species, *C. sanctus*. Here we report a new species based on a

remarkably well preserved skeleton with feathers and, for the first time in the Mesozoic record, direct evidence of the shape of a horny beak. It has a complete and large preserved postorbital that has a broad contact with the jugal bone. This character is presently only known in *Confuciusornis*, and may confirm previous suggestions of a postorbital in *Archaeopteryx*⁵. The squamosal is in tight contact with the postorbital. These two bones form an arch dividing the upper and lower temporal fenestrae, as in other diapsid reptiles⁶. The presence of a typical diapsid cheek region with two openings in *Confuciusornis* may preclude the presence of prokinesis (upper jaw mobility against the braincase and orbital area), a feeding adaptation found in most modern birds. The presence of a horny beak, characteristic of modern birds, coupled with a primitive temporal region provides new evidence for a mosaic pattern in the early evolution of birds.

Aves Linnaeus 1758
 Sauriurae Haeckel 1866
 Confuciusornithiformes Hou *et al.* 1995
 Confuciusornithidae Hou *et al.* 1995
Confuciusornis Hou *et al.* 1995
Confuciusornis dui sp. nov.

Etymology. The species name is dedicated to Mr. Wenya Du, who collected and donated the specimen to the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) for scientific research.
Holotype. A nearly complete skeleton. IVPP Collection Number V 11553.

Paratype. IVPP 11521, a partial skeleton consisting of a sternum, ribs, vertebrae, pelvis, femora and tail.

Horizon and locality. A two-metre thick interval within the Yixian Formation (Late Jurassic-Early Cretaceous); Libalanggou, Zhangjiying, Beipiao, Liaoning, northeast China.

Diagnosis. The holotype, a presumed male, is about 15% smaller than the holotype of *C. sanctus* (a small individual and presumed female). Large male individuals of *C. sanctus* are about 30% larger than the new species. The mandible is more slender anteriorly,



Figure 1 Cast of the elongate tail feathers of *C. dui* (IVPP Collection V 11553) whitened with ammonium chloride, showing that it was probably male.

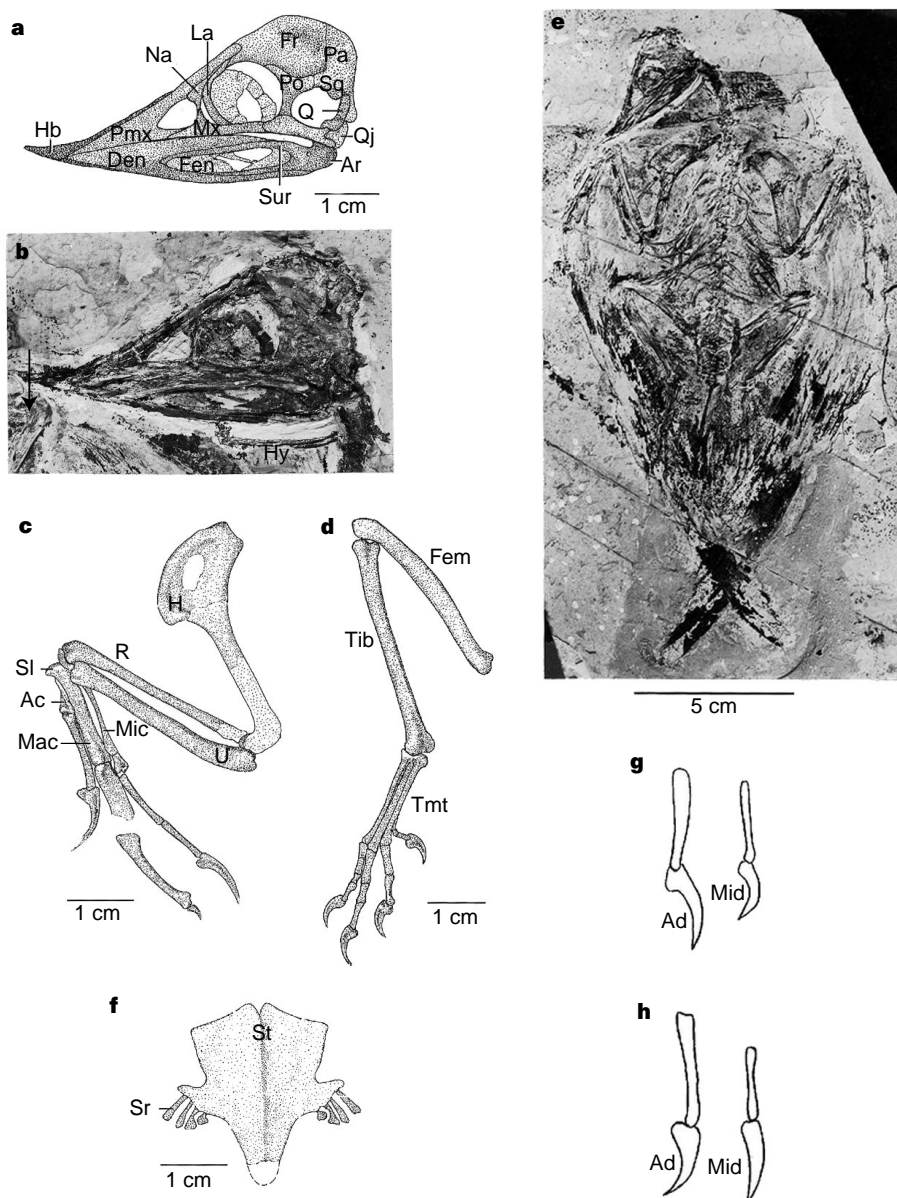


Figure 2 *Confuciusornis dui*. **a**, Reconstruction of the skull. **b**, Photograph of the skull (IVPP Collection V 11553); the arrow indicates the horny beak. **c**, Forelimb (IVPP Collection V 11553). **d**, Hindlimb. **e**, Photograph of the holotype (IVPP Collection V 11553). **f**, Reconstruction of the sternum and sternal ribs (based on IVPP Collection V 11521). **g**, Alular and minor manual digits of *C. sanctus*. **h**, Alular and minor manual digits of *C. dui*. Abbreviations: Ac, alular metacarpal; Ad, alular manual digit; Ar,

articular; Den, dentary; Fen, fenestra of the lower jaw; Fem, femur; Fr, frontal; H, humerus; Hb, horny beak; Hy, hyoid bone; J, jugal; La, lacrimal; Mac, major metacarpal; Mic, minor metacarpal; Mid, distal minor manual digit; Mx, maxilla; Na, nasal; Pa, parietal; Po, postorbital; Q, quadrate; Qj, quadratojugal; R, radius; Sl, semilunate bone (fused with major metacarpal); Sq, squamosal; Sr, sternal ribs; St, sternum; Sur, surangular; Tib, tibiotarsus; Tmt, tarsometatarsus; U, ulna.

without the distinctive anteroventral expansion of the dentary found in *C. sanctus*. The upper jaw is also more pointed anteriorly than that of *C. sanctus*. The claw of the alular digit is not enlarged as in *C. sanctus*. The sternum is more elongate with an anterior notch and a pair of short lateral processes. The tarsometatarsus is relatively shorter than in *C. sanctus*, and is shorter than the pygostyle.

Measurements of holotype (mm). Wing chord, 201; length of lower jaw 40; length of humerus, 42; length of ulna, 39; length of femur, 35; length of tibiotarsus, 41; length of tarsometatarsus, 19.5; length of pygostyle, 23; length of carpometacarpus, 19.

Description. This is a smaller, more gracile species than *C. sanctus*. The tarsometatarsus is fused proximally, and the semilunate bone is fused to the major metacarpal, indicating that this is an adult specimen. Like other *Confuciusornis*, it lacks teeth. Impressions of a

single pair of long tail feathers (Fig. 1) indicate that IVPP V11553 was a male.

The skull (Fig. 2a, b) is well preserved and shows some critical features of *Confuciusornis*. The impression of the horny rhamphotheca is preserved (Fig. 2a, b). The horny bill extends in front of the bony core with a long and pointed tip. The distal end of the beak curves dorsally and the bill was not raptorial. It is likely that *Confuciusornis* was an herbivore. The nasal processes of the premaxillae separate the nasals and overlap the anterior end of the frontals. The lacrimal joins the nasal above a small slit-shaped antorbital fenestra. The postorbital is large and 'Y' shaped; it contacts the jugal, squamosal and frontal. The contact on the jugal for the postorbital appears to be a rounded process. The quadrate is similar to that of *Archaeopteryx* and lacks an orbital

process. The quadratojugal seems to be small and 'L' shaped, as in *Archaeopteryx*. The maxillary process of the premaxilla tapers posteriorly and overlaps the maxilla below the middle of the narial opening. The maxilla has a dorsal ascending process in contact with the nasal, forming the anterior margin of the antorbital fenestra. There is a 'V'-shaped groove formed by backwards-extending processes of the dentary surrounding a large fenestra in the surangular.

The neck is relatively short. The exact number of cervical vertebrae in the new species is unclear, but it is probably fewer than eight. The vertebrae are short with deep pleurocoels. The pygostyle is longer than the tarsometatarsus and is well fused. The exact number of vertebrae that are fused into the pygostyle is unknown in the new species, but we have counted between 8 and 10 in *C. sanctus*. The sternal plate, which is visible on the holotype but best seen in the referred specimen (Fig. 2f), is longer than it is wide. It is relatively flat and lacks an obvious keel, as in *C. sanctus*. There are a pair of short lateral processes that serve as attachment sites for four short sternal ribs (Fig. 2f). Gastralia are present. The flight feathers (Fig. 2e) are very asymmetric with a wing chord of about 201 mm. The twin tail feathers are clearly visible in low-incidence lighting and resemble those of other *Confuciusornis* (Fig. 1).

The humerus is typical of *Confuciusornis* in having a very expanded proximal end with an oval depression (it is not clear whether any of the many specimens of *Confuciusornis* shown with a humeral perforation had that character before preparation). The humerus (Fig. 2c) is slightly longer than the ulna, as in *Archaeopteryx* but different from later birds where the ulna is usually longer than the humerus. The ulna is nearly twice as wide as the radius. The semilunate bone is fused to the major metacarpal, forming a carpometacarpus, but not to the alular metacarpal, indicating that the semilunate bone in *Confuciusornis*, as in modern birds, is a single distal carpal. The major and minor metacarpals are of nearly equal length and the major metacarpal is more robust than the other two. The minor metacarpal is significantly narrower proximally than distally, as in *C. sanctus*. There are three clawed fingers and the claw of the alular digit is about the same size as that of the minor digit, rather than about one-third larger as in *C. sanctus* (Fig. 2g, h). The middle manual claw is reduced, as in other *Confuciusornis*, although it is not completely preserved. The first phalanx of the alular digit is almost as long as the major and minor metacarpals. As is typical of *Confuciusornis*, the first phalanx of the minor digit is short (the first and second are short in *Archaeopteryx*); the others of the same digit are long, and the second is longer than the penultimate phalanx.

The pelvis is narrow and opisthopubic. The femur (Fig. 2d) is almost as long as the tibiotarsus. The tarsometatarsus is fused only proximally, as in *C. sanctus* and other saururine birds. The foot has highly recurved claws and a reversed hallux.

Discussion. The evolution of the skull in early birds is less known than that of the postcranial skeleton. This is particularly true of the temporal region. The cheek region in modern birds is reduced, owing to an expanded brain and enlarged orbit. Fossils of the oldest bird, *Archaeopteryx*, have unfortunately not preserved the postorbital and provide little information about the transition from the typical diapsid skull to the situation in modern birds.

Confuciusornis dui preserves a large 'Y'-shaped postorbital with a broad contact with the jugal bone. The postorbital process of the jugal does not lie behind the postorbital in contrast to that of *Dromaeosaurus*⁷. The postorbital has not been found in *Archaeopteryx*, but its presence has been extrapolated on the basis of the postorbital process on the jugal bone and the shape of the squamosal^{5,8}. The jugal bone in *Confuciusornis* is strong and relatively short compared with that of modern birds, where it is slender and fused with the quadratojugal bone, forming a rod-like bar. The postorbital was probably absent in the Chinese Early

Cretaceous enantiornithine *Cathayornis*^{9–11}. The only other Mesozoic bird that has retained this structure is an Early Cretaceous bird from Spain¹². However, in this bird the postorbital is much more reduced and has lost its contact with the jugal bar.

The squamosal is in tight contact with the postorbital. They form an intact intertemporal arch separating the upper and lower temporal fenestrae. The unreduced postorbital and its contacts with the jugal bone and the squamosal might prevent prokinesis; this may be confirmed by the fact that the quadrate has no orbital process and the quadratojugal is reduced so it cannot participate in a prokinetic push-rod. The presence of two derived quadrate systems indicates that a streptostylic quadrate with an orbital process would not have been a feature of the first bird.

Although *Confuciusornis* retains an intact diapsid temporal region, it shows several cranial modifications also found in more advanced birds. The enlargement of the frontal and reduction of the parietal make the frontal the major contributor to the skull internal to the upper arch, whereas in typical diapsid animals the parietal extends further anteriorly. The dorsal process of the jugal bone is low and has a rounded contact with the postorbital. The quadrate of *Confuciusornis* is single-headed; it lacks the prominent orbital process that is present in modern birds but is also lacking in the Early Cretaceous enantiornithine *Cathayornis*¹¹.

Although the sternum has no obvious keel, the shape of the wing and flight feathers are highly adapted for powered flight. *Confuciusornis* probably lived in large aggregations along the margin of a freshwater lake, as shown by hundreds of individuals found in a limited area. There is abundant evidence for lush forested conditions and the freshwater mudstones contain a variety of conchostracans, insects, fishes, amphibians, reptiles and mammals. The long tails on the presumed males seem to preclude much activity on the ground or the water surface and, along with the highly recurved pedal claws and reversed hallux, indicate that *Confuciusornis* was a perching bird. None of the many specimens preserve stomach contents but it seems likely that *Confuciusornis* was herbivorous.

The Early Cretaceous saururine birds from younger geological sections are smaller than the Late Jurassic *Archaeopteryx* and the Late Jurassic–Early Cretaceous *Confuciusornis*. The new species of *Confuciusornis* is smaller than *C. sanctus*. It has been proposed that size reduction was important in the early evolution of avian flight¹³. The early ornithurine birds and Early Cretaceous enantiornithines are smaller than *Archaeopteryx* and *Confuciusornis*. In addition, the new species has a more elongated sternum.

The findings of different species of *Confuciusornis* show that the oldest known beaked bird was not only abundant but had also diversified, as had *Archaeopteryx*, with at least two species in both genera⁵. A recently found enantiornithine bird¹⁴ from the same locality as *Confuciusornis* and *Liaoningornis* indicates that Enantiornithes had a longer history than previously known. Thus, the origin and early diversification of birds might be earlier and more significant than expected^{15,16}.

All known Late Jurassic–Early Cretaceous ornithurines such as *Chaoyangia* and enantiornithines have retained teeth in the jaw¹, and only *Confuciusornis* lost its teeth completely in favour of a horny beak. It provides an unusual mosaic of primitive and derived features with the anterior skull more like that of a modern bird than in any other Late Jurassic–Early Cretaceous bird, but with a temporal region nearly unchanged from its remote archosaurian ancestors. Like the early evolution of mammals, the original diversification of birds was probably also a complicated bush with many extinct lines that may at one time have been more advanced in some features than their ultimately more successful contemporaries¹⁷. The combination of distinctively advanced and primitive features found in the skull provides new evidence for a mosaic pattern in the early evolution of birds. *Confuciusornis* is not the progenitor of either modern birds or later enantiornithines,

but must be regarded as an early twig in a bush-like radiation of birds. □

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Cultures in chimpanzees

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As an increasing number of field studies of chimpanzees (*Pan troglodytes*) have achieved long-term status across Africa, differences in the behavioural repertoires described have become apparent that suggest there is significant cultural variation^{1–7}. Here we present a systematic synthesis of this information from the seven most long-term studies, which together have accumulated 151 years of chimpanzee observation. This comprehensive analysis reveals patterns of variation that are far more extensive than have previously been documented for any animal species except humans^{8–11}. We find that 39 different behaviour patterns, including tool usage, grooming and courtship behaviours, are

customary or habitual in some communities but are absent in others where ecological explanations have been discounted. Among mammalian and avian species, cultural variation has previously been identified only for single behaviour patterns, such as the local dialects of song-birds^{12,13}. The extensive, multiple variations now documented for chimpanzees are thus without parallel. Moreover, the combined repertoire of these behaviour patterns in each chimpanzee community is itself highly distinctive, a phenomenon characteristic of human cultures¹⁴ but previously unrecognised in non-human species.

Culture is defined in very different ways in different academic disciplines¹⁵. At one extreme, some cultural anthropologists insist on linguistic mediation, so that culture is constrained to be a uniquely human phenomenon¹⁶. In the biological sciences, a more inclusive definition is accepted, in which the significance of cultural transmission is recognized as one of only two important processes that can generate evolutionary change: inter-generation transmission of behaviour may occur either genetically or through social learning, with processes of variation and selection shaping biological evolution in the first case and cultural evolution in the second. From this perspective, a cultural behaviour is one that is transmitted repeatedly through social or observational learning to become a population-level characteristic¹⁷. By this definition, cultural differences (often known as 'traditions' in ethology) are well established phenomena in the animal kingdom and are maintained through a variety of social transmission mechanisms¹⁸. Well documented examples include dialects in song-birds^{12,13}, sweet-potato washing by Japanese macaques (*Macaca fuscata*) at Koshima¹⁹, and stone handling by Japanese macaques at Arashiyama²⁰. However, each case refers to variation in only a single behaviour pattern.

Tabulations of population differences amongst chimpanzees have indicated that multiple behavioural variants may exist^{2–7}. However, these tabulations have been based on published reports, which, although they record the presence of behaviours, remain problematic in three respects: they are incomplete; they frequently do not clarify the extent to which each behaviour pattern is habitual in the community; and they do not systematically document the absence of behaviour patterns present elsewhere. We therefore adopted a different strategy in our attempt to provide a definitive assessment of what is now known of chimpanzee cultural variation.

Phase 1 of the study established a comprehensive list of candidate cultural variants, which are behaviours suspected by research workers to be specific to particular chimpanzee populations. Beginning with a list drawn from literature review by A.W. and C.B., the research directors of the major chimpanzee field projects (Table 1) added and defined unpublished candidate patterns. The patterns were then split and lumped as appropriate. This complex, collaborative and iterative process produced a listing of candidate cultural variants that were fully and consensually defined (see Supplementary Information; Table 1 gives abridged descriptions). The scope of this list, differentiating 65 categories of behaviour, represents a unique record of the inventiveness of wild chimpanzees.

In phase 2, the research directors assigned to each of these behaviour categories one of the following six codes, as applicable at their site: (1) customary, for which the behaviour occurs in all or most able-bodied members of at least one age-sex class (such as adult males); (2) habitual, for which the behaviour is not customary but has occurred repeatedly in several individuals, consistent with some degree of social transmission; (3) present, for which the behaviour is neither customary nor habitual but is clearly identified; (4) absent, for which the behaviour has not been recorded and no ecological explanation is apparent; (5) ecological explanation, for which absence is explicable because of a local ecological feature; and (6) unknown, for which the behaviour has not been recorded, but this may be due to inadequacy of relevant observational opportunities. These codings were cross-checked and confirmed by senior colleagues at each site. Our results are for the seven chimpanzee