

Confuciusornis sanctus* Compared to *Archaeopteryx lithographica

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Confuciusornis sanctus [1–2] and *Archaeopteryx lithographica* [3] are the only known birds that share sophisticated anatomy designed to facilitate tree trunk climbing [2–4]. They are the most primitive known flying birds and probably had limited ability to ascend from flat surfaces. *C. sanctus* shows clear evidence of complex social behavior totally unexpected in such an ancient bird [5].

C. sanctus joins *A. lithographica* in providing a model for the earliest birds. Described by us 3 years ago on the basis of partial specimens, it is now known from hundreds of examples, including males with two long tail feathers, and we can now compare it in detail with *A. lithographica*. As with *A. lithographica*, it is a window into the early diversification of birds, but neither genus can be considered basal to our modern birds. One of the great revelations resulting from the discoveries in China is that birds had already diversified by the Late Jurassic, and we must search earlier rocks to find their beginnings [5, 6]. Unlike *A. lithographica*, *C. sanctus* was a highly gregarious, social bird, as evidenced by the large numbers preserved.

In *C. sanctus* (Fig. 1B) the toothless premaxilla is about one-third the total length of the skull, compared to about one-fifth in *A. lithographica*

(Fig. 1A) The premaxilla and dentary are covered anteriorly by a field of large nutrient foramina indicative of a horny bill. The antermost foramina open into distinct grooves. The ridges between the grooves have been confused with degenerate teeth and the nutrient foramina as sockets of tiny teeth. Examination of nearly 200 individuals failed to demonstrate any evidence of teeth. The premaxilla extends posteriorly, overlapping a slender toothless maxillary. The maxillary sends a process behind the narial opening to join the ventral process of a small nasal. The dorsal process of the premaxillary extends backwards until it overlaps the frontals. It thus resembles modern birds in separating the nasals. The premaxillaries fuse anteriorly but are separate for most of their posterior length. Posteriorly the dorsal process of the premaxillary is flattened and probably flexible. The narial opening is large but more rounded than in *A. lithographica*.

The lacrimal is small, C shaped, and surprisingly slender. It has proven difficult to elucidate its exact outline in a sample of over 100 skulls. It appears to join the nasal at the front of the orbit and curves posteriorly to form the back of a very small triangular antorbital fenestra.

The frontals extend a shelflike ridge over the orbit as in *A. lithographica* [7]. Posteriorly the frontals join short parietals. The back of the orbit is

formed by a Y-shaped postorbital bone that extends ventrally to a small rounded projection on the jugal bar. The jugal is slender and overlaps dorsally the posterior arm of the maxilla. The posterior process of the postorbital joins the squamosal forming a complete diapsid arch. The quadratojugal appears to be a small L-shaped bone as in *A. lithographica* [8]. The quadrate is slender and lacks a distinct orbital process, but near the base a large flat process turns in towards the midline. The palate is not clearly exposed in the specimens examined, but short pterygoids and elongate rodlike palatines may be present.

The edentulous dentary expands ventrally at the beginning of a long fused symphysis. The mandible is broad anteriorly. There is no indication of a predentary bone as in *Hesperornis*. The dentary has a long ventral process running under the surangular, practically to the articular. There is also a long dorsal process running above the surangular. The angular runs anteriorly underneath the ventral dentary process. A row of five foramina mark the position of the articular suture and another foramen lies anterior to it. There is an elongate mandibular foramen in the surangular. No other Mesozoic bird has this feature. The retroarticular process is short and flat, curving inwards posteriorly, and a pneumatic foramen seems to be present. The splenial is remarkably similar to that of a chicken (*Gallus*), being long and rodlike with a dorsal process showing through the mandibular fenestra (Fig. 1B).

The vertebrae are amphicoelous, with large pleurocoels. No postcranial pneumatic foramina have been recognized. There are 8 cervicals, 11 or 12 thoracics, 7 fused sacrals, 4 or 5 free caudals, and a pygostyle (Fig. 2E,F). The pygostyle contains some ten fused vertebrae. The anterior three sacral vertebrae have wide transverse processes that join to form a lateral bar that abuts the anterior ilium (Fig. 2J). The pygostyle is triangular with central and transverse ridges. It lies just above the elongate pubic symphysis. *A. lithographica* has 9 cervicals, 14 thoracics, 5 sacrals, and 22

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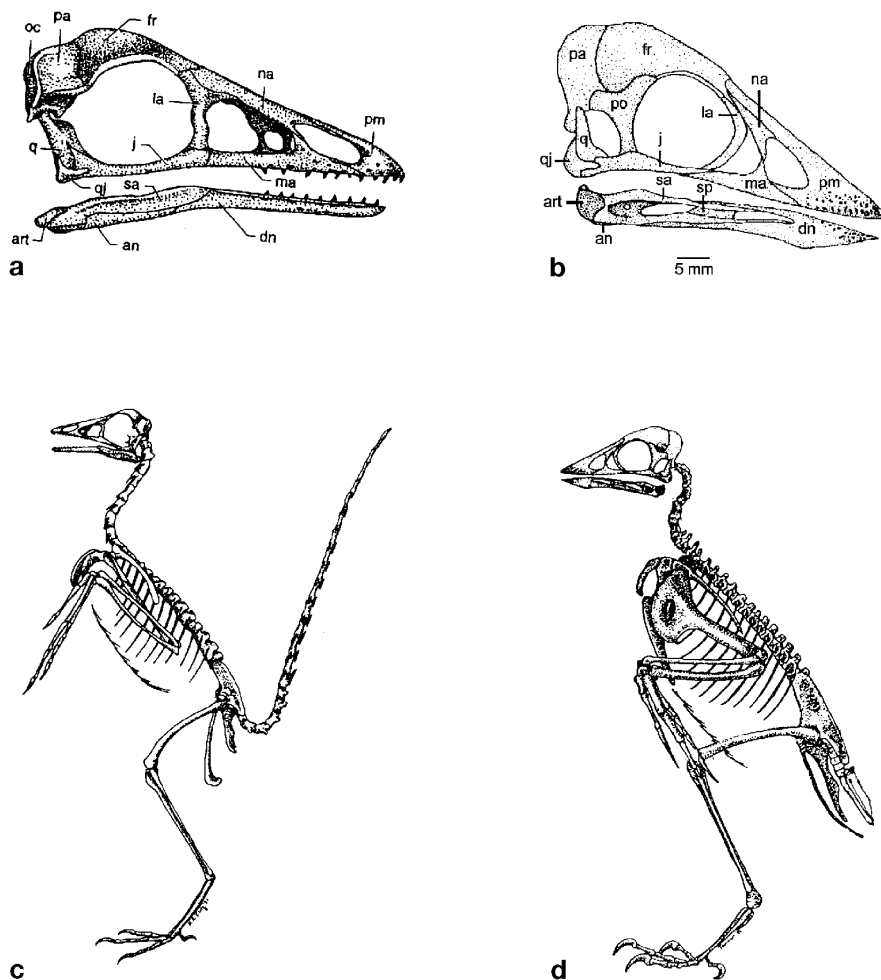


Fig. 1. a) Reconstruction of the skull of *A. lithographica*. b) Reconstruction of the skull of *C. sanctus*. c) Reconstruction of the skeleton of *A. lithographica*. d) Reconstruction of the skeleton of *C. sanctus*. an, Angular; art, articular; dn, dentary; fr, frontal; j, jugal; la, lacrimal; ma, maxilla; na, nasal; oc, occipital; pa, parietal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial

caudals [3], indicating a reduction in vertebrae number in *C. sanctus*.

The sternum is flat, and the coracoid abuts directly against an oval facet on the anterior margin, rather than in a slot as in modern birds (Fig. 2B). This relationship holds for *A. lithographica* [3] as well as for the enantiornithine birds [5] and may account for the curled sternal margin seen in coracoids of enantiornithine birds. There is a small costal margin attaching four short costal ribs. The costal ribs converge towards a broad projection on the lateral margin of the sternum and become progressively shorter posteriorly. The sternum is slightly notched and followed by ten pairs of gastralia (Fig. 2B). The posterior ribs are free

from the sternum and pointed ventrally.

The coracoids are more slender than in *A. lithographica* but not elongated. They have a flat, oval sternal edge. The bicipital process is huge and extends slightly dorsal to the glenoid. In some specimens the bicipital process is found articulated to a special downward turned facet on a heavily built and inflexible furcula (Fig. 2A,B). The furcula is grooved posteriorly. It is similar in overall shape to that of *A. lithographica* (Fig. 2B). The coracoid and scapula seems to fuse and *C. sanctus* is the only known Mesozoic bird to do this. The elongate glenoid has a raised rim and projects laterally. The scapulae lie parallel to the verte-

bral column and expand slightly posteriorly. The humeri are short and thick with enormously expanded deltoid crests on the proximal ends (Fig. 2D). The bicipital area has a circular depression that is often incorrectly prepared as a hole. The radius and ulna are about the same length as the humerus.

The hand of *C. sanctus* resembles that of *A. lithographica* and other birds in consisting of two proximal carpals, an L-shaped ulnare, a large radiale, and a single distal carpal with a semilunate shape on metacarpal III (II of many authors). In older individuals it fuses to metacarpal III forming a carpometacarpus although the three metacarpals (II–IV) do not fuse together. We accept the developmental evidence that shows convincingly that the avian hand is composed of digits II–III–IV [9, 10]. A small pisiform is present and associated with metacarpal IV. The semilunate carpal has distinct trochlear ridges. Metacarpal II is broad but short. It has a bulge in the position of the flexor process. The distal end has large condylar ridges for an elongate phalanx. The claw is highly recurved and enormous, and is with its horny sheath about the length of the carpometacarpus. The middle metacarpal is the largest and has the strongest finger. The first phalanx has condylar ridges locked to the metacarpal and a flat shelf to support the feathers. The penultimate digit is elongated as in *A. lithographica*. The middle claw is reduced in comparison to the other claws. The outer metacarpal extends even with the middle distally. It is slightly flattened. The first phalanx of the fourth digit is very short, the second longer, and the third much elongated. There is a long highly recurved claw.

The ilium broadens anteriorly and turns slightly anteroventrally. There is a broad articular surface on the anterior margin of the acetabulum and a small one on the back. Apparently when walking or climbing the back was nearly vertical as in *A. lithographica*, but the femur could also extend forwards to help leg folding when flying and this may have facilitated shortening of the bony tail. The posterior ilium is short and pointed. The ischium has an anterior antero-

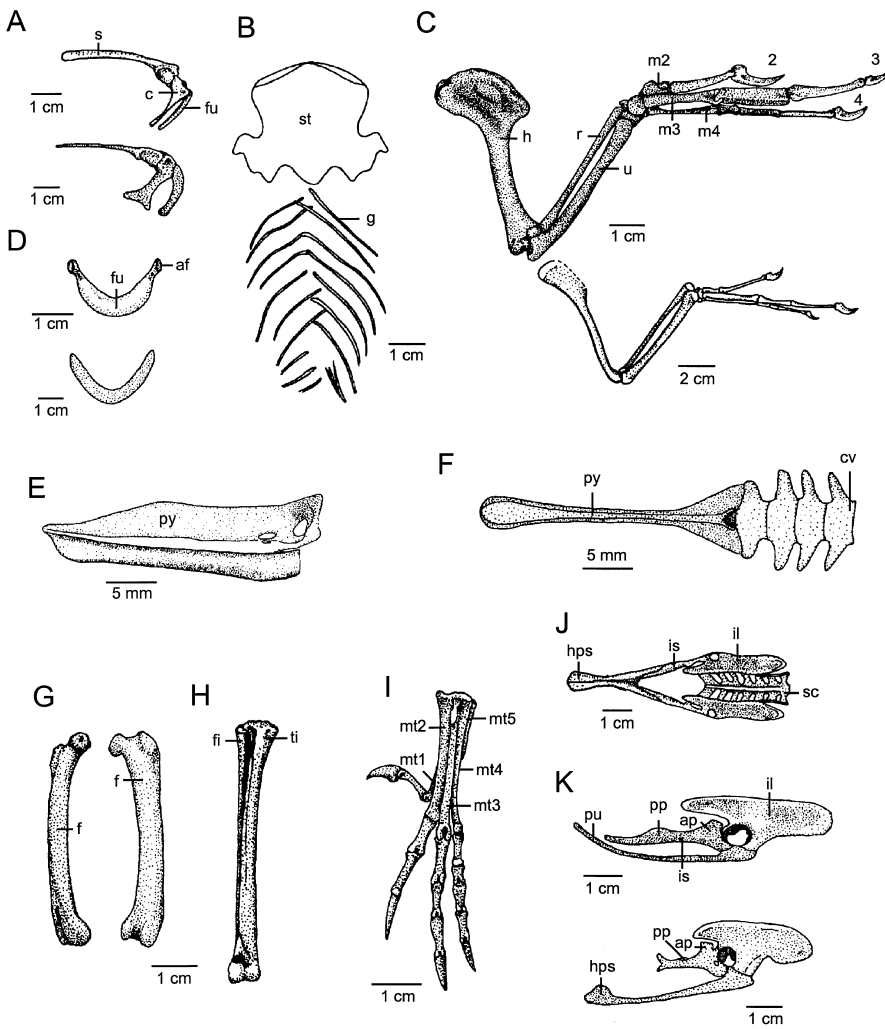


Fig. 2. a) Comparison of the right pectoral girdle of *A. lithographica* (top) and *C. sanctus* (below) in lateral view. b) Comparison of the furcula of *C. sanctus* (top) and *A. lithographica* (below) in anterior view. c) Sternum and gastralia of *C. sanctus*. d) Comparison of the left wing of *C. sanctus* (top) and *A. lithographica* (below) in posterior view. e) Pygostyle of *C. sanctus* in right lateral view. f) Caudal vertebrae and pygostyle of *C. sanctus* in ventral view. g) Right femur of *C. sanctus* in medial and posterior views. h) Right tibiotarsus and fibula of *C. sanctus* in anterior view. i) Left foot of *C. sanctus* in anterior view. j) Pelvis and synsacrum of *C. sanctus* in dorsal view. k) Comparison of the right pelvis of *C. sanctus* (top) and *A. lithographica* (below) in lateral view. *af*, Articulating facet; *ap*, anterior anterodorsal process; *c*, coracoid; *f*, femur; *fi*, fibula; *fu*, furcula; *g*, gastralia; *h*, humerus; *hps*, hyperpubic spoon; *il*, ilium; *is*, ischium; *mt1-5*, metatarsals I-V; *m2-4*, metacarpals II-IV [18]; *pp*, posterior anterodorsal process; *pu*, pubis; *py*, pygostyle; *r*, radius; *s*, scapula; *sc*, synsacrum; *st*, sternum; *cv*, caudal vertebra; *ti*, tibiotarsus; *u*, ulna; 2-4, manual digits II-IV

dorsal process abutting against the ilium as in *A. lithographica* and a small posterior process (Fig. 2K). The ischium is parallel with the ilium. The pubis is strongly reflected and fused distally into a long pubic apron. There is a small hyperpubic spoon as in *A. lithographica*, and is unlike the condition in theropod dinosaurs. The absence of a dorsal articular shelf on

the acetabulum indicates that the posture found in dinosaurs was not possible.

The femur (Fig. 2G) has a small separate trochanter as in *A. lithographica*, but the head is turned at a right angle to the shaft as in later birds and has a ball-shaped head with a large popliteal depression. The acetabulum was completely open. The fibula does not

extend to the ankle. It fits proximally against a prominent fibular crest. The pretibial bone lies across the co-ossified calcaneum and astragalus as in the enantiornithine birds. It bears a distinct papilla for the supratendinal ligament (Fig. 2H).

The tarsometatarsus (Fig. 2I) is fused proximally but not distally, resembling *A. lithographica* and all enantiornithine birds. A papilla for tibialis anticus is present, but there are no proximal foramina. No hypotarsal cap as is found in ornithurine birds is present. The reflexed hallux bears a large claw as in *A. lithographica* and is positioned at about the same level. The middle trochlea is the largest and most distal. The claws with their horny sheaths are highly recurved demonstrating a climbing rather than a running bird.

C. sanctus is the only bird in addition to *A. lithographica* to retain large climbing hands and a boomerang-shaped furcula. The skull retains the primitive diapsid condition of its archosaur ancestors, a feature already greatly modified in *A. lithographica*, *Cathayornis*, and the Spanish enantiornithines [7, 8, 11]. It is likely that *C. sanctus* and *A. lithographica* are the only known birds to retain gastralia. The gastralia of *Sinornis* may be incorrectly identified [13]. *C. sanctus* along with the enantiornithine *Vorona* and *A. lithographica* are the only known birds to retain metatarsal V. It is clearly the most primitive known bird next to *A. lithographica*. Coupled with this primitive suite of features are several that are amazingly precocious. Most notable is the loss of teeth and the formation of a horny bill, a feature not seen again until the upper Cretaceous *Gobipteryx*. *C. sanctus* also has a short bony tail with a distinct pygostyle [14].

New information permits a considerable improvement (Fig. 1D) in our previous reconstructions of the skeleton of *C. sanctus* [2, 5]. It is a curious evolutionary mosaic. The anterior part of the skull is more advanced than *A. lithographica* and *Cathayornis* [8, 15, 16], but the posterior of the skull is less advanced. The shoulder girdle and the hand resemble more those in *A. lithographica* than in other birds, but the pleurocoels on the ver-

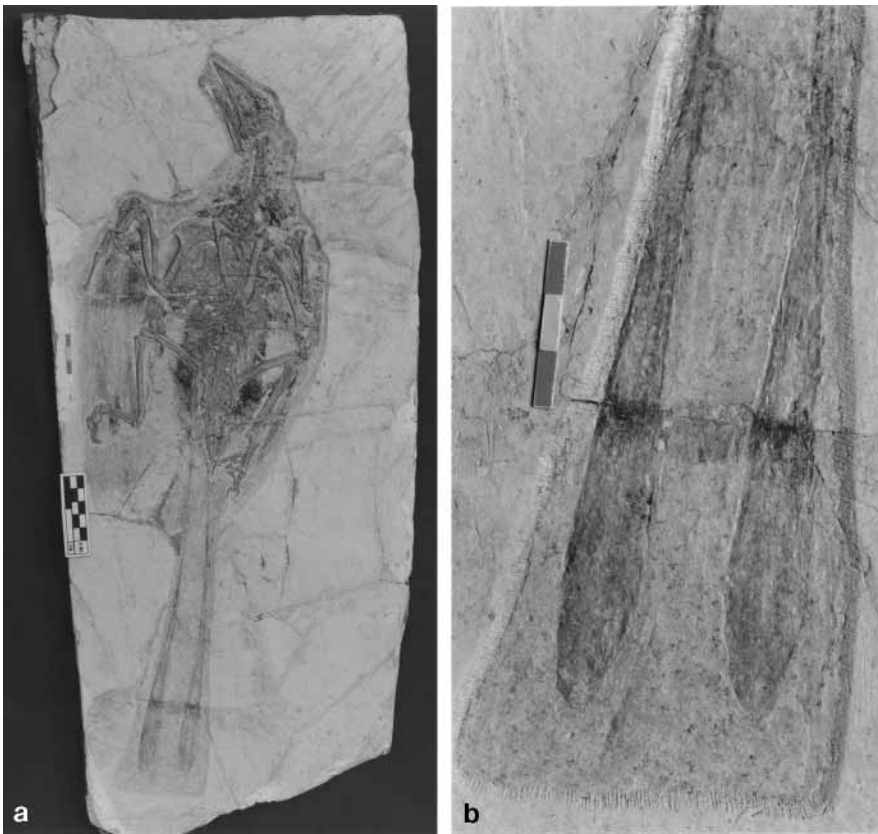


Fig. 3. a) Male specimen of *C. sanctus* showing the characteristic two long tail feathers. b) Enlargement of the tail feathers. (Photos by Zhang Jie)

tebrae and the pygostyle are derived towards enantiornithines. It is apparently a side group to the main line of enantiornithine evolution and provides further evidence that early birds include many extinct lines independently developing evolutionary innovations that became standard features in later birds.

Many of the several hundred known *C. sanctus* specimens come from a single layer, and single slabs with two birds are not uncommon. Such a distribution would be possible only if the birds gathered in flocks, and a mass mortality occurred, possibly due to the volcanic activity so often documented in the rocks at the *C. sanctus* site. Some specimens have two greatly elongated tail feathers (Fig. 3). These represent between 5% and 10% of the sample and might reasonably be considered males involved in "lek display" and harem formation. The presence of sophisticated social behavior was unexpected in such early birds, and this is the old-

est evidence of such avian behavior. We now know *C. sanctus* from many complete specimens with feathers. We can say with some certainty that it had a broad, upturned horny bill and long slender primary feathers attaching to the hand. The highly recurved pedal claws and elongate tail feathers confirm arboreal habits for *C. sanctus*. It must have lived in flocks along the margin of a fresh water lake and may have made daily visits for drinking water or other resources as some tropical parrots do today. It seems likely that such a flock was unlucky enough to be over the water during a catastrophic and deadly event. In our original descriptions [1, 5] we assigned the *C. sanctus* bearing Yixian Formation to the latest Jurassic or earliest Cretaceous. This interpretation was challenged by argon-argon dates on basalt in these deposits [17]. Field examinations of these basalts conducted by our Chinese colleagues and ourselves demonstrated that they are intruded into the lake sediments

containing *C. sanctus* (passing through sediments as vertical dikes and spreading out in sills baked both top and bottom). The dated basalts are thus younger by some unknown amount than the sediments that enclose them. This does not mean that they are much younger, and it is possible that a wide range of ages occurs in those deposits. Additional work is needed to establish the age and palaeontological sequences [18].

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1. Hou L, Zhou Z, Gu Y, Zhang H (1995) Chinese Sci Bull 40:726–729
2. Hou L, Zhou Z, Martin LD, Feduccia A (1995) Nature 277:616–618
3. Wellnhofer W (1993) *Archaeopteryx*. 11:1–48
4. Feduccia A (1993) Science 259:790–793
5. Hou L, Zhou Z, Martin LD, Feduccia A (1996) Science 274:1164–1167
6. Feduccia A (1996) The origin and evolution of birds. Yale University Press, New Haven
7. Martin LD (1991) In: Schultze H-P, Trueb L (eds) Origins of the higher groups of tetrapods, controversy and consensus. Comstock, Ithaca, p 485
8. Martin LD, Zhou Z (1997) Nature 389:556
9. Burke AC, Feduccia A (1997) Science 278:666–668
10. Hinchliffe R (1997) Science 278:596–597
11. Martin LD (1983) In: Brush AH, Clark GA (eds) Perspectives in ornithology. Cambridge University Press, London, pp 291–338
12. Sanz JL, Chiappe LM, Perez-Moreno BP, et al (1997) Science 276:1543–1546
13. Sereno P, Rao C (1992) Science 255:845–848
14. Peters DS (1996) Natur und Museum 126:298–302
15. Zhou Z (1995) Acta palaeornithologica. 181:9–22
16. Zhou Z, Jin F, Zhang J (1992) Chinese Sci Bull 37:1365–1368
17. Smith PE, York NM, Chang M, Jin F, Li J, Cumberbaa, S, Russell D (1995) Can J Earth Sci 32:1426–1431
18. Jin F (1996) Vertebrata Pal Asiatica 34:102–122