

A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers

Fucheng Zhang, Zhonghe Zhou, Xing Xu, Xiaolin Wang, Corwin Sullivan

Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China

Recent coelurosaurian discoveries have greatly enriched our knowledge of the dinosaur-bird transition, but all reported taxa close to this transition are from relatively well-known coelurosaurian groups¹⁻³. Here we report a new basal avialan, *Epidexipteryx hui* gen. et sp. nov., from the Middle-Late Jurassic of Inner Mongolia, China. This new species is characterized by an unexpected combination of characters seen in several different theropod groups, particularly the Oviraptorosauria. Phylogenetic analysis shows it to be the sister taxon to *Epidendrosaurus*^{4,5}, forming a new clade at the base of Avialae⁶. *Epidexipteryx* also possesses two pairs of elongate ribbon-like tail feathers (ETFs), and its limbs lack contour feathers for flight. This finding shows that a member of the avialan lineage experimented with integumentary ornamentation as early as the Middle-Late Jurassic, and provides further evidence relating to this important aspect of the transition from non-avian theropods to birds.

Systematic palaeontology

Theropoda Marsh 1881

Coelurosauria Huene 1914

Maniraptora Gauthier 1986

Avialae Gauthier 1986 (Padian, 2004)

Scansoriopterygidae Czerkas et Yuan 2002

Epidexipteryx hui gen. et sp. nov.

Etymology. *Epidexi* (Greek), display; *pteryx* (Greek), wing, feather; *hui*, in honour of

the late young palaeontologist Yaoming HU, who contributed significantly to the study of Mesozoic mammals from China. Generic name pronounced as ‘ep-id-ecks-IP-ter-icks’.

Holotype. A feathered pigeon-sized skeleton, preserved on part and counterpart slabs, and housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, collection number IVPP V15471 (Figs. 1; see Supplementary Information (SI)).

Locality and horizon. Daohugou, Ningcheng County, Inner Mongolia, north China. The age of the Daohugou sediments is contentious, with possible dates ranging from Middle Jurassic⁷ to Early Cretaceous. However, published radioisotopic dating results span a narrower range from 152 to 168 Ma (Middle to Late Jurassic)⁸⁻¹⁰.

Diagnosis. Medium sized avialan with four ETFs, highly procumbent and significantly enlarged anterior teeth, and a distally tapering pygostyle-like structure formed by 10 unfused caudals at the end of the tail (Figs. 1, 2; see SI). Differs significantly from *Epidendrosaurus*, the only other known scansoriopterygid, in caudal morphology (tail 70% of trunk length in *Epidexipteryx*, compared to more than 300% in *Epidendrosaurus*; 16 caudal vertebrae in *Epidexipteryx*, compared to over 40 in *Epidendrosaurus*; caudal prezygapophyses reduced in *Epidexipteryx* but significantly elongated in *Epidendrosaurus*).

Description and comparisons. *Epidexipteryx* is estimated to be 164 grams in body mass (see SI), smaller than most other basal avialans^{3,11}. The holotype probably represents a subadult individual, since the ends of some of the long bones appear imperfectly ossified.

As in oviraptorosaurs¹², the skull is high in lateral view (height about 60% of length), the external naris is positioned high on the snout, and the parietal is proportionally long. The teeth of both the upper and lower jaws are highly procumbent, a feature previously known only in the ceratosaurian *Masiakasaurus* among theropods¹³. Furthermore, the anterior teeth are much larger than the posterior ones, as in basal oviraptorosaurs¹², basal therizinosaur¹⁴, and probably

Epidendrosaurus^{4,5}. There are probably nine cervicals and fourteen thoracic vertebrae, and the synsacrum is composed of seven vertebrae. The caudal series is much shorter than in non-avian theropods or in other basal avialans. The anterior six caudal vertebrae are proportionally short and wide. The posterior ten caudals bear no transverse processes. They form a structure similar to the elongated, incipient pygostyle in some basal birds^{15,16}, but are not fused to each other (Figs. 1a,1b, 1c, 2a; see SI).

The partially preserved sternum is small and convex anteriorly, and appears to comprise two incompletely fused sternal plates, as in the primitive bird *Jeholornis*¹⁷. The scapula is significantly shorter than the humerus, as in some derived maniraptorans, and the coracoid is sub-rectangular. The pelvis has an unexpected combination of features among theropods, as in *Epidendrosaurus*^{4,5}. The ilium is bird-like in having a long preacetabular process with a strongly convex anterior margin, but differs from the ilia of most non-avian theropods in having a small pubic peduncle. Unusually among theropods, the straight pubis is shorter than the ischium and is significantly shorter than the femur. It is anteroventrally orientated and lacks a pubic boot. The posteriorly curved ischium is laterally compressed, gradually widens towards the distal end, and lacks an obturator process. The humerus is about same length as the femur, proportionally longer than in most other basal avialans. The ulna is posteriorly bowed and the manus is significantly elongated (see SI) as in birds and other derived theropods¹⁸⁻²². The curvature of the manual claws falls within the range known for the pedal claws of ground-based foraging birds (see SI). The femur is about 160% the length of the metatarsus, and 80% the length of the tibia (Figs. 1a, 2a; see SI).

Phylogeny and affinity. Phylogenetic analysis indicates that *Epidexipteryx* and *Epidendrosaurus* form a monophyletic Scansoriopterygidae (see SI), representing a bizarre lineage at the base of the Avialae⁶ (Fig. 3; see SI).

Although possessing many derived features seen in birds, including a humerus as long as the femur, a long preacetabular process of the ilium with a strongly convex

margin, and many other features, *Epidexipteryx* and *Epidendrosaurus* also show some striking similarities to oviraptorosaurs¹² and to a lesser degree therizinosauroids^{14,21}, including a short and high skull, an external naris positioned high on the snout, an anteriorly downturned and strongly dorsally convex mandible, a large external mandibular fenestra, and enlarged anterior teeth. Furthermore, some pelvic features, such as a proportionally very short pubis and a distally widening ischium, are not known in any other theropod. The bizarre appearance of scansoriopterygids indicates that morphological disparity among maniraptorans close to the origin of birds is higher than has previously been assumed, and underscores the importance of Jurassic theropods for understanding avian origins.

Integument. The integument bears feather-like structures of two types, ETFs and non-ETFs, which are roughly comparable to shafted and non-shafted feathers respectively²³. The distal part of each non-ETF is composed of filamentous parallel barbs (Figs. 2e, 2e', 2f), similar to the condition seen in the non-shafted feathers of other feathered dinosaurs and primitive birds^{18,22-25}. However, the free distal barbs of *Epidexipteryx* arise from the edge of a membranous structure (Figs. 2b, 2c, 2d, 2d'), an arrangement that has never previously been reported.

The four ETFs are tightly attached to the last ten caudal segments (Figs. 1a, 2a). These feathers are incomplete distally, but the preserved part of each ETF is identical to the corresponding structure in some primitive birds^{16,26-28}, for example in having a similar central rachis and unbranched vanes (Fig. 1a, 1d, 2a, 2a'; see SI). Elongate tail feathers are a normal component of the ornamental plumage in extant birds. In contrast to other feather types, ornamental plumage is used to send visual signals that are essential to a wide range of avian behaviour patterns, particularly relating to courtship²⁹. For example, experiments have demonstrated that, in some species, males with long tail plumage attract more mates than their short-tailed counterparts³⁰. It is highly probable that the ETFs of *Epidexipteryx* likewise had display as their primary function, rather than serving other purposes such as flight or insulation²⁹. Indeed, pennaceous feathers suitable for flight are not present in *Epidexipteryx*, even though

the bones and integument are well-preserved. Because pennaceous feathers are commonly encountered in other feathered maniraptorans^{2,21,22,25}, their absence constitutes another highly unusual feature of *Epidexipteryx*, as well as strongly implying that this taxon was non-volant. *Epidexipteryx* is the oldest and most phylogenetically basal theropod known to possess display feathers, indicating that basal avialans experimented with integumentary ornament as early as the Middle-Late Jurassic. Unless *Epidexipteryx* is interpreted as secondarily flightless, the absence of pennaceous limb feathers in this taxon suggests that display feathers appeared prior to airfoil feathers and flight ability in basal avialan evolution.

1. Makovicky, P. J. *et al.* The earliest dromaeosaurid theropod from South America. *Nature* **437**, 1007–1011(2005).
2. Xu, X. & Norell, M. A. Non-avian dinosaur fossils from the Lower Cretaceous Jehol Group of western Liaoning, China. *Geol. J.* **41**(3-4), 419–438(2006).
3. Turner, A. H., *et al.* A basal dromaeosaurid and size evolution preceding avian flight. *Science* **317**, 1378–1381(2007).
4. Zhang, F.-c. *et al.* A juvenile coelurosaurian theropod from China indicates arboreal habits. *Naturwissenschaften* **89**, 394–398 (2002).
5. Czerkas, S. A. & Yuan, C. in *Feathered Dinosaurs and the Origin of Flight* (ed Czerkas, S. J.) 63-95 (The Dinosaur Museum, Blanding, 2002).
6. Padian, K. in *The Dinosauria* 2nd edn (eds Weishampel, D. B., Dodson, P., Osmolska, H.) 210–231 (Univ. of California Press, Berkeley, 2004).
7. Gao K.-q & Ren D. Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou Beds, *Acta Geol. Sinica* **80**(1), 42–45 (2006).
8. Chen, W. *et al.* Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geol. Bull. Chin.* **23**, 1165–1169 (2004).
9. He, H.-y. *et al.* ⁴⁰Ar/³⁹Ar dating of ignimbrite from Inner Mongolia, northeastern

- China, indicates a post-Middle Jurassic age for the overlying Daohugou Bed. *Geophys. Res. Lett.* **31**, L20609, doi: 10.1029/2004GL020792 (2004).
10. Liu Y.-x., Liu Y.-q. & Zhang, H. LA-ICPMS Zircon U-Pb Dating in the Jurassic Daohugou Beds and Correlative Strata in Ningcheng of Inner Mongolia. *Acta Geol. Sinica* **80**(5), 733–742 (2006).
 11. Christiansen, P. & Fariña, R. A. Mass prediction in theropod dinosaurs. *Histori. Bio.* **16**, 85-92 (2004).
 12. Xu, X. *et al.* An unusual oviraptorosaurian dinosaur from China. *Nature* **419**, 291–293 (2002).
 13. Sampson, S. D., Carrano, M. T. & Forster, C. A. A bizarre predatory dinosaur from Madagascar: implications for the evolution of Gondwanan theropods. *Nature* **409**, 504–505 (2001).
 14. Kirkland, J. I., *et al.* A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. *Nature* **435**, 84–87 (2005).
 15. Hou, L.-h. & Chen, P.-j. *Liaoxiornis delicatus* gen. et sp. nov., the smallest Mesozoic bird, *Chin. Sci. Bull.* **44**, 834–838 (1999).
 16. Zhang, F.-c., Zhou, Z.-h & Benton, M. J. A primitive confuciusornithid bird from China and its implications for early avian flight. *Sci. China Ser. D* **51**, 625–639 (2008).
 17. Zhou, Z.-h & Zhang, F.-c. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* **418**, 405–409 (2002).
 18. Zhang, F.-c., Zhou, Z.-h & Hou, L.-h. in *The Jehol Biota* (eds Chang, M.-m, Chen, P.-j, Wang, Y.-q. & Wang, Y.) 129–149 (Shanghai Sci. Technol. Publ., Shanghai, 2003).
 19. Zhou, Z.-h., Barrett, P. M. & Hilton, J. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**, 807–814 (2003).
 20. Zhou, Z.-h. & Zhang, F.-c. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Can. J. Earth Sci.* **40**, 731–737 (2003).

21. Weishampel, D. B., Dodson, P. & Osmólska, H. *The Dinosauria* 2nd edn (Univ. of California Press, Berkeley, Los Angeles, London, 2004).
22. Xu, X. in *Originations, Radiations and Biodiversity Changes* (eds Rong, J.-y. et al.) 627–642, 927–930 (Sci. Press, Beijing, 2006).
23. Zhang, F.-c. & Zhou, Z.-h. in *Originations, Radiations and Biodiversity Changes* (eds Rong, J.-y. et al.) 611–625, 923–925 (Sci. Press, Beijing, 2006).
24. Prum, R. O. & Brush, A. H. The evolutionary origin and diversification of feathers. *Q. Rev. Biol.* **77**, 261–295 (2002).
25. Xu, X. Scales, feathers and dinosaurs. *Nature* **440**, 287–288 (2006).
26. Chiappe, L. M. et al. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of Northeastern China. *Bull. Am. Mus. Nat. Hist.* **242**, 1–89 (1999).
27. Zhang, F.-c. & Zhou, Z.-h. A primitive enantiornithine bird and the origin of feathers. *Science* **290**, 1955–1959 (2000).
28. Zheng, X.-t., Zhang, Z.-h. & Hou, L.-h. A new enantiornithine bird with four long rectrices from the Early Cretaceous of northern Hebei, China. *Acta Geol. Sinica* **81**(5), 703–708 (2007).
29. Gill, F. B. *Ornithology* 2nd edn (W. H. Freeman and Co., New York, 1995).
30. Andersson, M. Female choice selects for extreme tail length in a widowbird. *Nature* **299**: 818–820 (1982).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank F. Jin for discussion, Y. Li for specimen preparation, W. Gao for photography, and J. Choiniere for the use of his laptop. This research was funded by the National Natural Science Foundation of China, the Chinese Academy of Sciences, and Major Basic Research Projects of the Ministry of Science and Technology, China.

Author Information Reprints and permissions information is available at

www.nature.com/reprints. The authors declare no competing financial interests.
Correspondence and requests for materials should be addressed to F.Z.
(ZhangFucheng@ivpp.ac.cn)

Figure 1 *Epidexipteryx hui* gen. et sp. nov., IVPP V15471, main slab and close-up photos. **a**, main slab; **b** and **c**, skull in main slab and counterslab respectively; **d**, 4 elongate ribbon-like tail feathers; **b'** and **c'**, line drawings of **b** and **c** respectively. Abbreviations: l1, l2, and l7, 1st, 2nd, and 7th left teeth of upper jaw; l1', r1' and r5', 1st left, 1st right and 5th right teeth of lower jaw; l2 and r2, 2nd left and right teeth of upper jaw; t and t', left and right halves of proximal end of left tibia on main slab and counterslab respectively.

Figure 2 *Epidexipteryx hui* gen. et sp. nov, line drawings and close-up photos. **a**, skeleton and feather outline, based on both main slab and counterslab, showing that the shafted feather is formed by central rachis and two unbranched vanes (**a'**); **b**, **d** and **d'**, proximal regions of non-shafted feathers, barbs are parallel and closely united as an unbranched membranous structure (**d**, **d'**), vanes are either layered, indicated by white arrows (**b**), or arranged irregularly (**c**), red arrow indicates proximal-most end of feather (**d**); **e**, **e'** and **f**, distal regions of non-shafted feathers, in which barbs appear loosely parallel. Abbreviations: as+ca, astragalus and calcaneum; ce, cervical vertebrae; co, coracoid; cv, caudal vertebrae; dt3+4, distal tarsals 3 and 4; f, frontal; fe, femur; fi, fibula; ga, gastralia; hu, humerus; il, ilium; is, ischium; ma, mandible; mtI-IV, metatarsals I-IV; p, phalanges or metacarpals; pa, parietal; pm, premaxilla; pu, pubis; q, quadrate; r, ribs; ra, radius; rc, rachis; sc, scapula; st, sternum; ti, tibia; tv, thoracic vertebrae; u, ungual phalanges; ul, ulna; uv, unbranched vane; 4 ETFs, 4 elongate ribbon-like tail feathers.

Figure 3 Phylogenetic relationships of *Epidexipteryx hui* gen. et sp. nov. The cladogram is simplified from the strict consensus of 9 most parsimonious trees (tree length, 1255; consistency index, 0.35; retention index, 0.75; see Supplementary Information). Scansoriopterygidae is defined as the least inclusive clade including *Epidendrosaurus* and *Epidexipteryx*, Avialae as the most inclusive clade including *Vultur gryphus* but not *Deinonychus antirrhopus*, and Aves as the least inclusive clade

including *Archaeopteryx* and *Vultur gryphus*.





