



## Supplementary Materials for

### **Hind Wings in Basal Birds and the Evolution of Leg Feathers**

Xiaoting Zheng,\* Zhonghe Zhou, Xiaoli Wang, Fucheng Zhang, Xiaomei Zhang, Yan Wang, Guangjin Wei, Shuo Wang, Xing Xu\*

\*Corresponding author. E-mail: xingxu@vip.sina.com (X.X.); ty4291666@163.com (X.Z.)

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Supplementary Text  
Figs. S1 to S10  
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References (40–60)

## Supplementary Text

**Systematics of the specimens described in present paper.** Referrals of STM16-18 and STM16-19 to *Sapeornis* were made on the basis of the following characters: skull relatively deep, rostrum shortened, mandible robust, mandibular symphysis downturned, premaxillary teeth robust and procumbent, ilium with relatively shallow preacetabular process, ischium relatively long and slender, and tibia subequal in length to femur (14, 40). STM13-32, STM13-44, STM13-55, STM13-57, and STM13-331 are referable to the Confuciusornithidae based on the following features: jaws toothless, deltopectoral crest of humerus prominent and subquadrangular, metacarpal I not co-ossified with complex formed by semilunate carpal and other two metacarpals, middle manual claw much smaller than other claws, manual phalanx III-1 much shorter than other phalanges, and posterior end of sternum V-shaped (16). More narrowly, STM13-32 can be referred to *Confuciusornis* based on the presence of a large foramen piercing the deltopectoral crest of the humerus (16). STM7-50, STM7-161, and STM7-215 are referable to the Enantiornithes on the basis of the following features: coracoid with convex lateral margin, Y-shaped furcula with long hypocleideum, clavicular rami L-shaped in cross-section, sternum with distally expanded caudolateral processes, metacarpal III extending distally beyond metacarpal II, and metatarsal IV slender (41, 42). STM9-5 is referable to *Yanornis* based on the following combination of features: carina approaching sternal anterior limit, scapula shorter than humerus, pubic symphysis relatively long, distal tarsals fused to metatarsals and metatarsals co-ossified proximally and distally, pedal digits relatively short and robust, and proximal pedal phalanges relatively long but unguals short (17, 18, 43, 44).

**Location and orientation of paravian leg feathers.** The spatial distribution and orientation of leg feathers in basal paravians are important questions because of their connection to feather function and because of the relationship between leg plumage and leg scalation in extant birds. There are two main difficulties in reconstructing leg feather distribution and orientation: 1) all of the relevant specimens are basically preserved in two-dimensions; and 2) feather orientation may have been variable in the living animal, because in extant birds this parameter is subject to control by muscles associated with the feathers (31). Nevertheless, there is circumstantial data that might be useful in inferring the distribution and orientation of leg feathers.

In specimens that preserve large leg feathers, including those described previously (1-3, 8) and those we have observed in connection with the present study, there are basically two modes of preservation: each skeleton is either preserved in dorsal or ventral view with the legs splayed outward, or preserved in lateral view with the legs in a crouched position under the body.

In the former case, any crural feathers are normally preserved lateral to the lower leg and any pedal feathers are lateral to metatarsal IV. This applies, for example, to the dromaeosaurid STM5-222 in figure 1-10 in (45), the dromaeosaurid specimen on p. 325 in (46), the *Anchiornis* LPM B00169 in (3), the *Pedopenna* holotype (2), the confuciusornithid specimen STM13-331, and the enantiornithine specimens STM7-50, 7-161 and 7-215. However,

exceptions exist. In some confuciusornithid specimens, such as STM13-32, 13-44, and 13-55, large feathers are preserved both medial and lateral to the lower legs. In one enantiornithine specimen (IVPP V13939), large feathers are preserved mainly lateral to the lower legs but some can also be seen medial to the lower legs (8). In the *Sapeornis* specimen STM16-19, most of the preserved large feathers are medial to the pedal elements and only a minority are lateral to them.

In specimens preserved in lateral view, any large feathers are normally preserved posterior to leg bones. This is seen, for example, in the dromaeosaurid IVPP V13352 (1), the *Sapeornis* specimen STM16-18, and the confuciusornithid specimen STM13-57. In the Berlin *Archaeopteryx* specimen, however, large feathers are preserved both anterior and posterior to the lower legs. Taken together, these taphonomic observations suggest that the large leg feathers of basal paravians are most likely to have been attached to the lateral surfaces of the leg bones and extend laterally. However, it is difficult to be certain that they did not arise from the anterior or posterior surfaces of the leg bones and/or extend anteriorly or posteriorly rather than laterally.

In some chick and pigeon breeds, large leg feathers are present along the anterolateral surfaces of the leg bones and are oriented mainly laterally (47, 48), and the posterior surface of metatarsus is rarely feathered in extant birds (31). The available neontological data thus support the conclusion that the leg feathers of extinct taxa are likely to have been oriented laterally.

**Functions of the leg feathers in basal paravians.** It is widely accepted that the large leg feathers of *Microraptor* were used in aerial locomotion, but no consensus has been reached as to how these feathers conferred an aerodynamic advantage (1, 5, 6, 10, 24, 25, 49, 50). Few studies have even addressed this question with regard to other basal paravians. Such morphological features as asymmetrical vanes and curved, robust rachises may be associated with flight, but in no case has this kind of association been strictly demonstrated. For example, the presence of vane asymmetry and curvature has been suggested to have an aerodynamic function (51), but both features are also present in the feathers of at least some flightless birds (52, 53). However, it is still possible to infer the functions of particular feather types based on a synthetic overview of the available data.

The leg feathers of basal paravians probably differed in primary function from the metatarsal feathers that are seen in some modern birds. The latter are fluffy and oriented nearly parallel to the long axis of the metatarsus, and have been suggested to function mainly in insulation or protection (31). The leg feathers of basal paravians are considerably different from modern examples in both general morphology and arrangement, and appear less likely to have served primarily as insulation. It is also unlikely that basal paravian leg feathers were primarily for display. In living birds, any large feathers that have a display function and are not also used in flight are normally located on the head or tail, and they differ from flight feathers in lacking such features as vane asymmetry and shaft curvature. The leg feathers of basal birds and other basal paravians have curved rachises, are nearly perpendicular to the long axis of the leg, and are arranged in a wing-like manner (forming a planar surface). These features suggest that

basal paravian leg feathers are more likely to have been aerodynamic in primary function, perhaps creating lift and/or enhancing maneuverability (1, 5, 6, 10, 24, 25, 49, 50), than to have been used primarily for display or insulation. However, it is possible that the leg feathers of basal paravians combined a primary role in flight with a secondary function such as display.

**Phylogenetic distribution of leg feathers.** Although only limited data on the integument of extinct coelurosaurian theropods are available, we attempted an analysis of the distribution of the various states of two key leg integument characters (see below) among 14 representative members of major groups within the Coleurosauria. We mapped the character states onto two versions of a widely accepted coelurosaurian phylogeny (Figs. S9 and S10), the versions differing only in the placement of *Archaeopteryx* (4, 54-60). All other aspects of the phylogeny are uncontroversial. We built a data matrix by scoring the two characters for each of the 14 taxa (Table 1) and based the subsequent analysis on the two alternative phylogenetic topologies.

Character list:

1. Pedal integument: extensive small filamentous feathers (0), extensive large pennaceous feathers (1), or extensive scutate scales (2)
2. Femoral and crural integument: extensive small filamentous feathers (0), extensive small pennaceous feathers (1), or extensive large pennaceous feathers (2)

We ran parsimony-based analyses using the Mesquite software package (33) in order to reconstruct the ancestral states of the two integumentary characters for the major nodes across both versions of the coelurosaurian phylogeny. Default settings were used for all parameters. The results are given below (Tables 2 and 3). Note that ancestral states are listed by character and by node, and that numbers identifying nodes are shown on Figures S9 and S10.

Supplementary figures



Figure S1 Photographs of confuciusornithid (STM 13-32) and its leg feathers



Figure S2 Photographs of confuciusornithid (STM 13-44) and its leg feathers



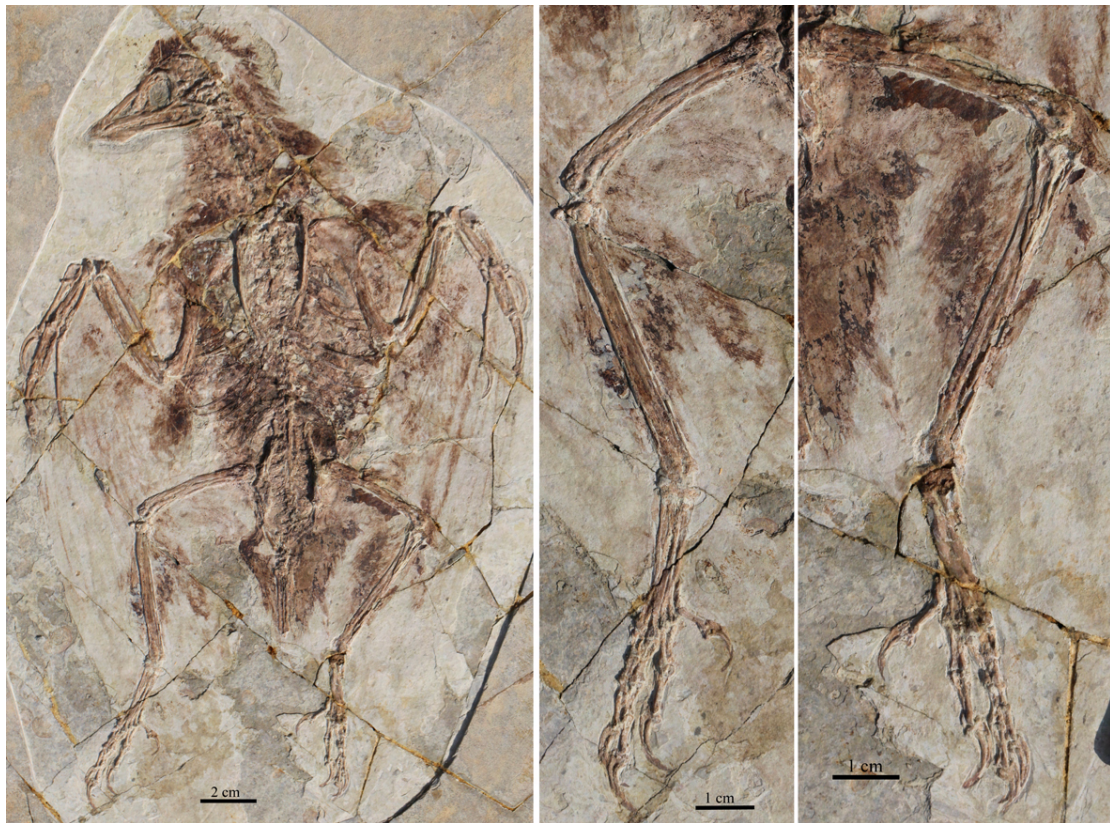


Figure S3 Photographs of confuciusornithid (STM 13-55) and its leg feathers

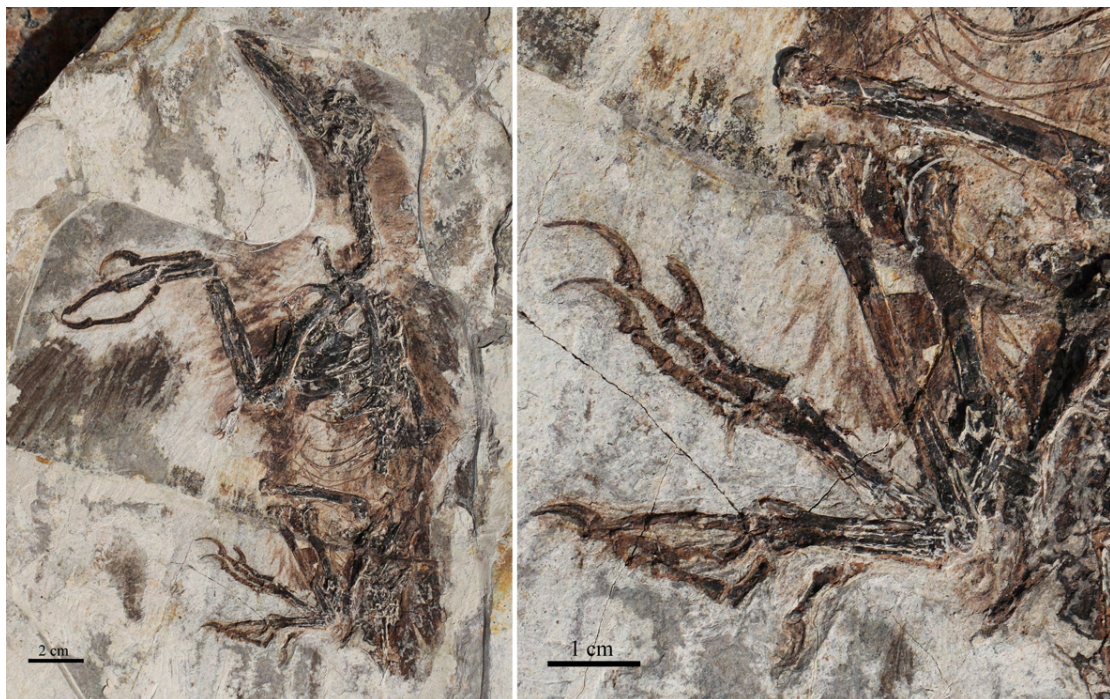


Figure S4 Photographs of confuciusornithid (STM 13-57) and its leg feathers



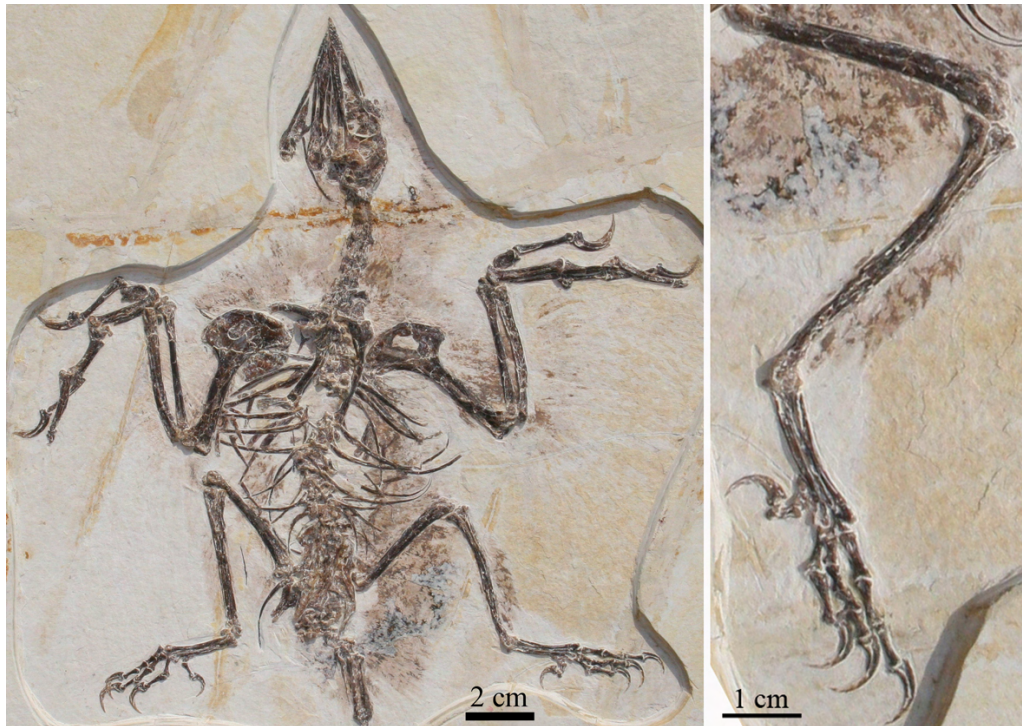


Figure S5 Photographs of confuciusornithid (STM 13-331) and its leg feathers

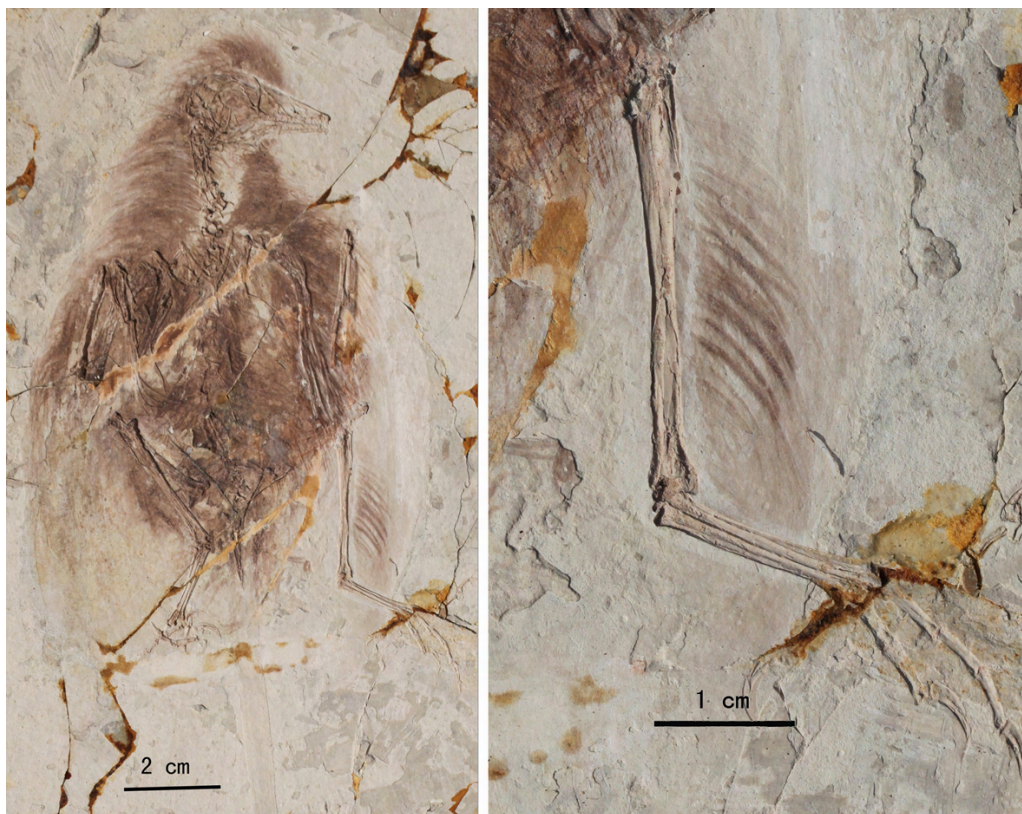


Figure S6 Photographs of enantiornithine (STM 7-50) and its leg feathers



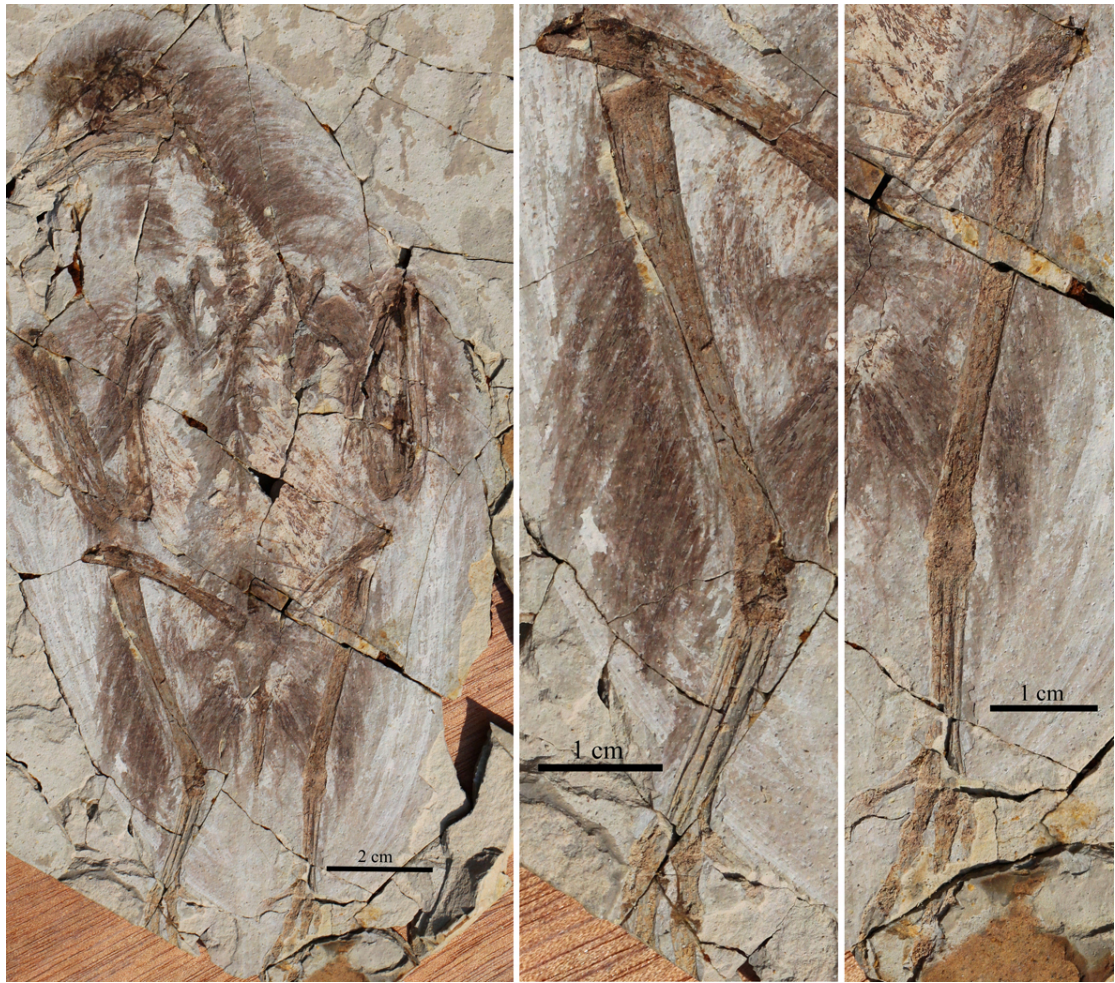


Figure S7 Photographs of enantiornithine (STM 7-161) and its leg feathers

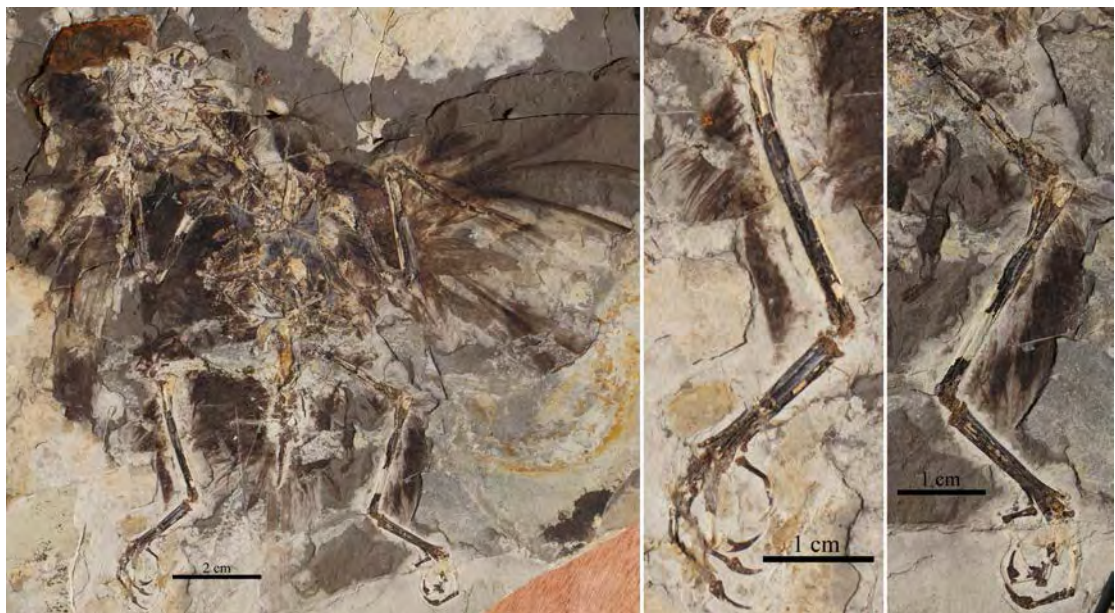


Figure S8 Photographs of enantiornithine (STM 7-215) and its leg feathers



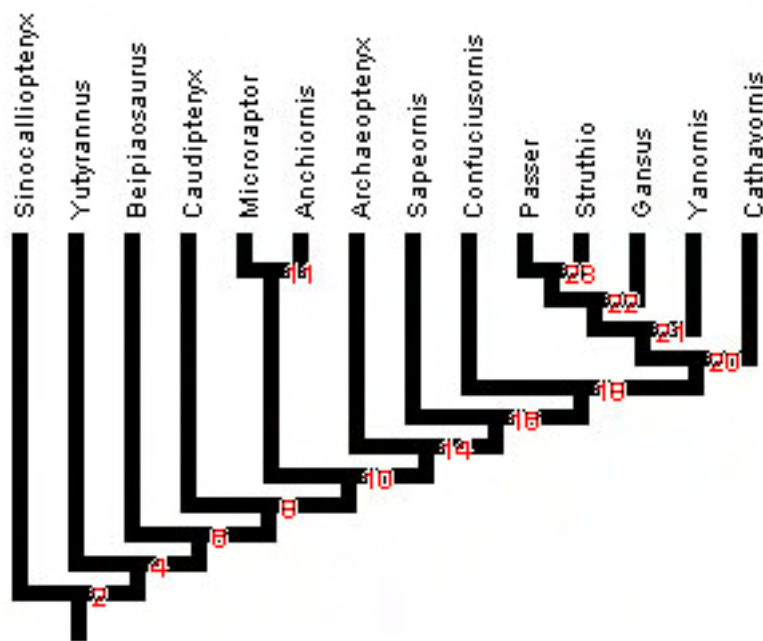


Figure S9 A coelurosaurian phylogeny simplified from an informal consensus of published phylogenetic studies on theropods (refs. 4, 54-60), with *Archaeopteryx* shown as a basal avialan. Numbers identify individual nodes.

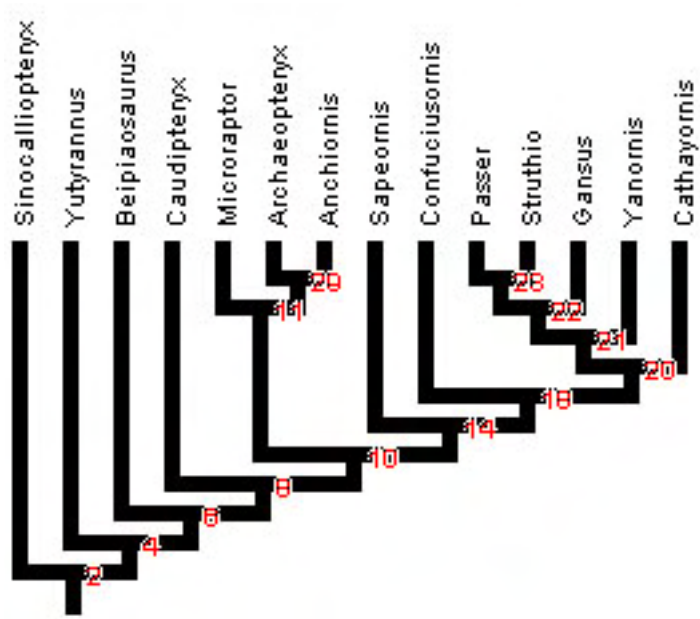


Fig. S10. A coelurosaurian phylogeny simplified from an informal consensus of published phylogenetic studies on theropods (refs. 4, 54-60) with *Archaeopteryx* shown as a basal deinonychosaur. Numbers identify individual nodes.

## Supplementary tables

Table 1. Scorings for two leg integument characters for selected coelurosaurian taxa

<i>Sinocalliopteryx</i>	00
<i>Yutyrannus</i>	0?
<i>Beipiaosaurus</i>	?0
<i>Caudipteryx</i>	?1
<i>Microraptor</i>	12
<i>Anchiornis</i>	12
<i>Archaeopteryx</i>	?2
<i>Sapeornis</i>	12
<i>Cathayornis</i>	?2
<i>Confuciusornis</i>	?2
<i>Yanornis</i>	21
<i>Gansus</i>	2?
<i>Struthio</i>	21
<i>Passer</i>	21

Table 2. Reconstructed ancestral states (min./max.) for various coelurosaurian clades based on figure S9

Node	11	23	22	21	20	18	16	14	10	8	6	4	2
Char													
character 1	1/1	2/2	2/2	2/2	??	??	1/1	??	1/1	??	??	0/0	0/0
character 2	2/2	1/1	??	1/1	2/2	2/2	2/2	2/2	2/2	1/1	0/0	??	0/0

Table 3. Reconstructed ancestral states (min./max.) for various coelurosaurian clades based on figure S10

Node	29	11	23	22	21	20	18	14	10	8	6	4	2
Char													
character 1	??	1/1	2/2	2/2	2/2	??	??	1/1	1/1	??	??	0/0	0/0
character 2	2/2	2/2	1/1	??	1/1	2/2	2/2	2/2	2/2	1/1	0/0	??	0/0



## References

1. X. Xu *et al.*, Four-winged dinosaurs from China. *Nature* **421**, 335 (2003).  
[doi:10.1038/nature01342](https://doi.org/10.1038/nature01342) [Medline](#)
2. X. Xu, F.-C. Zhang, A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* **92**, 173 (2005).  
[doi:10.1007/s00114-004-0604-y](https://doi.org/10.1007/s00114-004-0604-y) [Medline](#)
3. D. Y. Hu, L.-H. Hou, L. J. Zhang, X. Xu, A pre-Archaeopteryx troodontid theropod from China with long feathers on the metatarsus. *Nature* **461**, 640 (2009).  
[doi:10.1038/nature08322](https://doi.org/10.1038/nature08322) [Medline](#)
4. X. Xu, H. You, K. Du, F. Han, An Archaeopteryx-like theropod from China and the origin of Avialae. *Nature* **475**, 465 (2011). [doi:10.1038/nature10288](https://doi.org/10.1038/nature10288) [Medline](#)
5. D. E. Alexander, E. Gong, L. D. Martin, D. A. Burnham, A. R. Falk, Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2972 (2010). [doi:10.1073/pnas.0911852107](https://doi.org/10.1073/pnas.0911852107) [Medline](#)
6. S. Chatterjee, R. J. Templin, Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 1576 (2007). [doi:10.1073/pnas.0609975104](https://doi.org/10.1073/pnas.0609975104) [Medline](#)
7. R. O. Prum, Palaeontology: Dinosaurs take to the air. *Nature* **421**, 323 (2003).  
[doi:10.1038/421323a](https://doi.org/10.1038/421323a) [Medline](#)
8. F. C. Zhang, Z. H. Zhou, Palaeontology: Leg feathers in an Early Cretaceous bird. *Nature* **431**, 925 (2004). [doi:10.1038/431925a](https://doi.org/10.1038/431925a) [Medline](#)
9. N. R. Longrich, Structure and function of hindlimb feathers in *Archaeopteryx lithographica*. *Paleobiology* **32**, 417 (2006). [doi:10.1666/04014.1](https://doi.org/10.1666/04014.1)
10. K. Padian, Four-winged dinosaurs, bird precursors, or neither? *Bioscience* **53**, 451 (2003). [doi:10.1641/0006-3568\(2003\)053\[0451:FDBPON\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0451:FDBPON]2.0.CO;2)
11. K. Padian, K. P. Dial, Origin of flight: Could 'four-winged' dinosaurs fly? *Nature* **438**, E3, discussion E3 (2005). [doi:10.1038/nature04354](https://doi.org/10.1038/nature04354) [Medline](#)
12. See the supplementary materials on *Science* Online.
13. Z. Zhou, P. M. Barrett, J. Hilton, An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**, 807 (2003). [doi:10.1038/nature01420](https://doi.org/10.1038/nature01420) [Medline](#)
14. Z. H. Zhou, F. C. Zhang, Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Can. J. Earth Sci.* **40**, 731 (2003). [doi:10.1139/e03-011](https://doi.org/10.1139/e03-011)
15. L. H. Hou, C. M. Chuong, A. Yang, X. L. Zeng, J. F. Hou, *Fossil Birds of China* (Yunnan Science and Technology Press, Kunming, China, 2003).
16. L. M. Chiappe, S.-A. Ji, Q. Ji, M. A. Norell, *Bull. Am. Mus. Nat. Hist.* **242**, 1 (1999).

17. Z. Zhou, F. C. Zhang, Discovery of an ornithurine bird and its implication for Early Cretaceous avian radiation. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 18998 (2005). [doi:10.1073/pnas.0507106102](https://doi.org/10.1073/pnas.0507106102)
18. H. L. You *et al.*, A nearly modern amphibious bird from the Early Cretaceous of northwestern China. *Science* **312**, 1640 (2006). [doi:10.1126/science.1126377](https://doi.org/10.1126/science.1126377) [Medline](#)
19. F. C. Zhang, Z. H. Zhou, Research highlights. *Nature* **438**, E4 (2005). [doi:10.1038/438004a](https://doi.org/10.1038/438004a)
20. X. Xu, *Deinonychosaurian Fossils from the Jehol Group of Western Liaoning and the Coelurosaurian Evolution* (Chinese Academy of Sciences, Beijing, China, 2002).
21. M. Norell *et al.*, Palaeontology: 'modern' feathers on a non-avian dinosaur. *Nature* **416**, 36 (2002). [doi:10.1038/416036a](https://doi.org/10.1038/416036a) [Medline](#)
22. Q. Ji, M. A. Norell, K.-Q. Gao, S.-A. Ji, D. Ren, The distribution of integumentary structures in a feathered dinosaur. *Nature* **410**, 1084 (2001). [doi:10.1038/35074079](https://doi.org/10.1038/35074079) [Medline](#)
23. X. Xu *et al.*, A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chin. Sci. Bull.* **54**, 430 (2009). [doi:10.1007/s11434-009-0009-6](https://doi.org/10.1007/s11434-009-0009-6)
24. M. A. R. Koehl, D. Evangelista, K. Yang, *Integr. Comp. Biol.* **56**, 1002 (2011).
25. J. Hall, H. J. Habib, M. Hone, L. Chiappe, *J. Vertebr. Paleontol.* **32**, 105B (2012).
26. C. W. Beebe, *Zool. Sci. Contrib. N. Y. Zool. Soc.* **2**, 39 (1915).
27. S. A. Ji, Q. Ji, J. C. Lu, C. X. Yuan, *Acta Geol. Sin.* **81**, 8 (2007).
28. X. Xu *et al.*, A gigantic feathered dinosaur from the lower cretaceous of China. *Nature* **484**, 92 (2012). [doi:10.1038/nature10906](https://doi.org/10.1038/nature10906) [Medline](#)
29. X. Xu, Z.-L. Tang, X.-L. Wang, *Nature* **399**, 350 (1999). [doi:10.1038/20670](https://doi.org/10.1038/20670)
30. Q. Ji, P. J. Currie, M. A. Norell, S.-A. Ji, *Nature* **393**, 753 (1998).
31. A. M. Lucas, P. R. Stettenheim, *Avian Anatomy: Integument* (U.S. Department of Agriculture, Washington, DC, 1972).
32. L. Kelso, E. H. Kelso, The relation of feathering of feet of American owls to humidity of environment and to life zones. *Auk* **53**, 51 (1936). [doi:10.2307/4077355](https://doi.org/10.2307/4077355)
33. W. P. Maddison, D. R. Maddison (2011), <http://mesquiteproject.org>.
34. M. Logan, Finger or toe: The molecular basis of limb identity. *Development* **130**, 6401 (2003). [doi:10.1242/dev.00956](https://doi.org/10.1242/dev.00956) [Medline](#)
35. R. H. Sawyer, L. W. Knapp, Avian skin development and the evolutionary origin of feathers. *J. Exp. Zool.* **298B**, 57 (2003). [doi:10.1002/jez.b.26](https://doi.org/10.1002/jez.b.26)



36. M. P. Harris, B. L. Linkhart, J. F. Fallon, Bmp7 mediates early signaling events during induction of chick epidermal organs. *Dev. Dyn.* **231**, 22 (2004). [doi:10.1002/dvdy.20096](https://doi.org/10.1002/dvdy.20096) [Medline](#)
37. R. B. Widelitz, T.-X. Jiang, J.-F. Lu, C. M. Chuong, Beta-catenin in epithelial morphogenesis: Conversion of part of avian foot scales into feather buds with a mutated beta-catenin. *Dev. Biol.* **219**, 98 (2000). [doi:10.1006/dbio.1999.9580](https://doi.org/10.1006/dbio.1999.9580) [Medline](#)
38. F. Prin, D. Dhouailly, How and when the regional competence of chick epidermis is established: Feathers vs. scutate and reticulate scales, a problem en route to a solution. *Int. J. Dev. Biol.* **48**, 137 (2004). [doi:10.1387/ijdb.15272378](https://doi.org/10.1387/ijdb.15272378) [Medline](#)
39. S. M. Gatesy, K. P. Dial, Locomotor modules and the evolution of avian flight. *Evolution* **50**, 331 (1996). [doi:10.2307/2410804](https://doi.org/10.2307/2410804)
40. Y. Hu *et al.*, Geochemistry of heavy oil in the T block, Oriente Basin and its origin mechanism. *Acta Geol. Sin.* **84**, 406 (2010). [doi:10.1111/j.1755-6724.2010.00143.x](https://doi.org/10.1111/j.1755-6724.2010.00143.x)
41. L. M. Chiappe, C. Walker, in *Mesozoic Birds: Above the Heads of Dinosaurs*, L. M. Chiappe, L. M. Witmer, Eds. (Univ. of California Press, Berkeley, CA, 2002), pp. 240–267.
42. Z. Zhou, J. Clarke, F. Zhang, Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. *J. Anat.* **212**, 565 (2008). [doi:10.1111/j.1469-7580.2008.00880.x](https://doi.org/10.1111/j.1469-7580.2008.00880.x) [Medline](#)
43. J. A. Clarke, Z. Zhou, F. Zhang, Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. *J. Anat.* **208**, 287 (2006). [doi:10.1111/j.1469-7580.2006.00534.x](https://doi.org/10.1111/j.1469-7580.2006.00534.x) [Medline](#)
44. Z. H. Zhou, F. C. Zhang, *China Sci. Bull.* **46**, 1 (2001).
45. X. T. Zheng, *The Origin of Birds* (Shandong Science and Technology Press, Jinan, China, 2009).
46. Q. Ji *et al.*, *Mesozoic Jehol Biota of Western Liaoning, China* (Geological Publishing House, Beijing, China, 2004).
47. P. F. Goetinck, Tissue interactions in the development of ptilopody and brachydactyly in the chick embryo. *J. Exp. Zool.* **165**, 293 (1967). [doi:10.1002/jez.1401650213](https://doi.org/10.1002/jez.1401650213) [Medline](#)
48. F. F. Gander *et al.*, From field and study. *Condor* **32**, 64 (1930). [doi:10.2307/1363640](https://doi.org/10.2307/1363640)
49. J. Brougham, S. Brusatte, Distorted *Microraptor* specimen is not ideal for understanding the origin of avian flight. *Proc. Natl. Acad. Sci. U.S.A.* **107**, E155 (2010). [doi:10.1073/pnas.1004977107](https://doi.org/10.1073/pnas.1004977107)

50. X. Xu, Z.-H. Zhou, F.-C. Zhang, X.-L. Wang, X.-W. Kuang, *J. Vertebr. Paleontol.* **24**, 251A (2004). [doi:10.1671/21](https://doi.org/10.1671/21)
51. A. Feduccia, *The Origin and Evolution of Birds* (Yale Univ. Press, ed, 2, New Haven, CT, 1999).
52. J. R. Speakman, Flight capabilities in Archaeopteryx. *Evolution* **47**, 336 (1993). [doi:10.2307/2410145](https://doi.org/10.2307/2410145)
53. J. R. Speakman, S. C. Thomson, Flight capabilities of Archaeopteryx. *Nature* **370**, 514 (1994). [doi:10.1038/370514a0](https://doi.org/10.1038/370514a0)
54. J. Gauthier, *Mem. Calif. Acad. Sci.* **8**, 1 (1986).
55. P. C. Sereno, The evolution of dinosaurs. *Science* **284**, 2137 (1999). [doi:10.1126/science.284.5423.2137](https://doi.org/10.1126/science.284.5423.2137) [Medline](#)
56. T. Holtz, *Gaia* **15**, 5 (2000).
57. M. A. Norell, J. M. Clark, P. J. Makovicky, in *New Perspectives on the Origin and Evolution of Birds*, J. Gauthier, L. F. Gall, Eds. (Yale Univ. Press, New Haven, CT, 2001) pp. 49–67.
58. A. H. Turner, D. Pol, J. A. Clarke, G. M. Erickson, M. A. Norell, A basal dromaeosaurid and size evolution preceding avian flight. *Science* **317**, 1378 (2007). [doi:10.1126/science.1144066](https://doi.org/10.1126/science.1144066) [Medline](#)
59. J. N. Choiniere *et al.*, A basal alvarezsauroid theropod from the early Late Jurassic of Xinjiang, China. *Science* **327**, 571 (2010). [doi:10.1126/science.1182143](https://doi.org/10.1126/science.1182143) [Medline](#)
60. P. Senter, J. I. Kirkland, D. D. DeBlieux, S. Madsen, N. Toth, New Dromaeosaurids (Dinosauria: Theropoda) from the lower cretaceous of Utah, and the evolution of the Dromaeosaurid tail. *PLoS ONE* **7**, e36790 (2012). [doi:10.1371/journal.pone.0036790](https://doi.org/10.1371/journal.pone.0036790) [Medline](#)