

An Early Cretaceous heterodontosaurid dinosaur with filamentous integumentary structures

Xiao-Ting Zheng¹, Hai-Lu You², Xing Xu³ & Zhi-Ming Dong³

Ornithischia is one of the two major groups of dinosaurs, with heterodontosauridae as one of its major clades. Heterodontosauridae is characterized by small, gracile bodies and a problematic phylogenetic position^{1,2}. Recent phylogenetic work indicates that it represents the most basal group of all well-known ornithischians³. Previous heterodontosaurid records are mainly from the Early Jurassic period (205–190 million years ago) of Africa^{1,3}. Here we report a new heterodontosaurid, *Tianyulong confuciusi* gen. et sp. nov., from the Early Cretaceous period (144–99 million years ago) of western Liaoning Province, China. *Tianyulong* extends the geographical distribution of heterodontosaurids to Asia and confirms the clade's previously questionable temporal range extension into the Early Cretaceous period. More surprisingly, *Tianyulong* bears long, singular and unbranched filamentous integumentary (outer skin) structures. This represents the first confirmed report, to our knowledge, of filamentous integumentary structures in an ornithischian dinosaur.

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Heterodontosauridae Kuhn, 1966

Tianyulong confuciusi gen. et sp. nov.

Etymology. The generic name refers to Shandong Tianyu Museum of Nature (STMN; Pingyi, Shandong Province, China), where the specimen is housed; the specific name is dedicated to Confucius, the founder of Confucianism.

Holotype. STMN 26-3 is an incomplete skeleton preserving a partial skull and mandible, partial presacral vertebrae, proximal–middle caudal vertebrae, nearly complete right scapula, both humeri, the proximal end of the left ulna, partial pubes, both ischia, both femora, the right tibia and fibula and pes, and filamentous integumentary structures.

Locality and horizon. Jianchang County, Liaoning Province, China. Jehol Group, Early Cretaceous^{4,5}.

Diagnosis. A heterodontosaurid dinosaur distinguishable from other species in having a semi-circular diastema, a barely developed buccal emargination, a dorsally placed mandibular jaw joint well above the level of the dentary tooth row, only one premaxillary tooth (which is caniniform), a distinct gap between the dentary teeth and coronoid process, caudally increasing tooth sizes, and adjacent maxillary and dentary tooth crowns distinctly separate and lacking mesial and distal marginal denticles and ridges on the buccal surfaces.

Description. The *T. confuciusi* holotype is estimated to be 70 cm long, with a cranium that is 6 cm long and tail that is 44 cm long based on the proportions of *Heterodontosaurus tucki*^{1,6} (Fig. 1a, b; also see Supplementary Information for measurements). The holotype probably represents a subadult individual because the sutural lines between the neural arches and the centra are still visible, whereas the ends of the preserved long bones are all ossified.

The partial skull, exposed in right lateral view, is missing most of its caudodorsal portion, including the braincase (Fig. 1c, d). A relatively long preorbital portion occupies about 46% of the basal skull length. The ventral edge of the premaxilla lies well below the maxillary tooth row, whereas its dorsal (nasal) process contacts the nasal. A distinct semi-circular diastema is demarcated on the lateral surface across the junction between the premaxilla and the maxilla. Caudal to the diastema, a large, triangular antorbital fossa occupies almost the entire caudal half of the lateral facial area. The long rostradorsal (maxillary) process of the jugal tapers towards its rostral end and inserts between the maxilla and the lacrimal. The lateral mandibular articular condyle of the quadrate is slightly larger than the medial one. The prementary has a smooth, horizontal oral margin of equal length as the oral margin of the premaxilla. The dentary has roughly parallel dorsal and ventral margins, and its horizontal tooth row occupies its rostral two-thirds. A slender external mandibular fenestra is surrounded by the dentary, surangular and angular. The ventral margin of the angular tilts caudodorsally, positioning the jaw joint well above the level of the dentary tooth row. Only one large, caniniform premaxillary tooth exists and protrudes from the caudal end of the oral margin of the premaxilla. The maxillary tooth crowns are triangular in lateral view and lack both denticles along the mesial and distal edges and ridges on the buccal surface. Adjacent crowns are clearly separate from each other. Compared to the maxillary crowns, individual dentary teeth are relatively small and have more pointed apical ends.

The cervical vertebrae are slightly downturned, whereas the dorsals are arched dorsally. Most of the 22 proximal–middle caudals are tightly bound by longitudinally arranged ossified epaxial and hypaxial tendons. The relatively long, straight humerus has a prominent deltopectoral crest. The ischium is straight, compressed mediolaterally, and does not possess tab-shaped obturator process. The postpubis is about half the length of the ischium. The distal end of the femur has an intercondylar extensor groove and an open flexor intercondylar groove. The four preserved metatarsals are closely appressed to each other; metatarsal I is reduced, and its first phalanx does not extend beyond the proximal end of metatarsal II.

Three patches of filamentous integumentary structures are preserved: one ventral to the cervical vertebrae (Fig. 2a), one dorsal to the dorsal vertebrae (Fig. 2b), and the largest dorsal to the proximal caudal vertebrae (Fig. 2c). The filaments in each patch largely parallel each other; those ventral to the body angle about 45° caudally, whereas those dorsal to the body lie almost perpendicular to the long axes of their respective parts of the vertebral column but curve gently. We interpret these as integumentary structures based on their general morphology and distribution along the fossil body. The elongation and hollow nature of these filaments argues against them being subdermal structures, such as collagen fibres^{7,8}.

The tail filaments are especially long, with estimated overall lengths of 60 mm (seven times the lengths of the underlying caudal centra) and

¹Shandong Tianyu Museum of Nature, Lianhuashan Road West, Pingyi, Shandong, 273300, China. ²Institute of Geology, Chinese Academy of Geological Sciences, 26 Baiwanzhuang Road, Beijing 100037, China. ³Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xiwai Street, Beijing 100044, China.

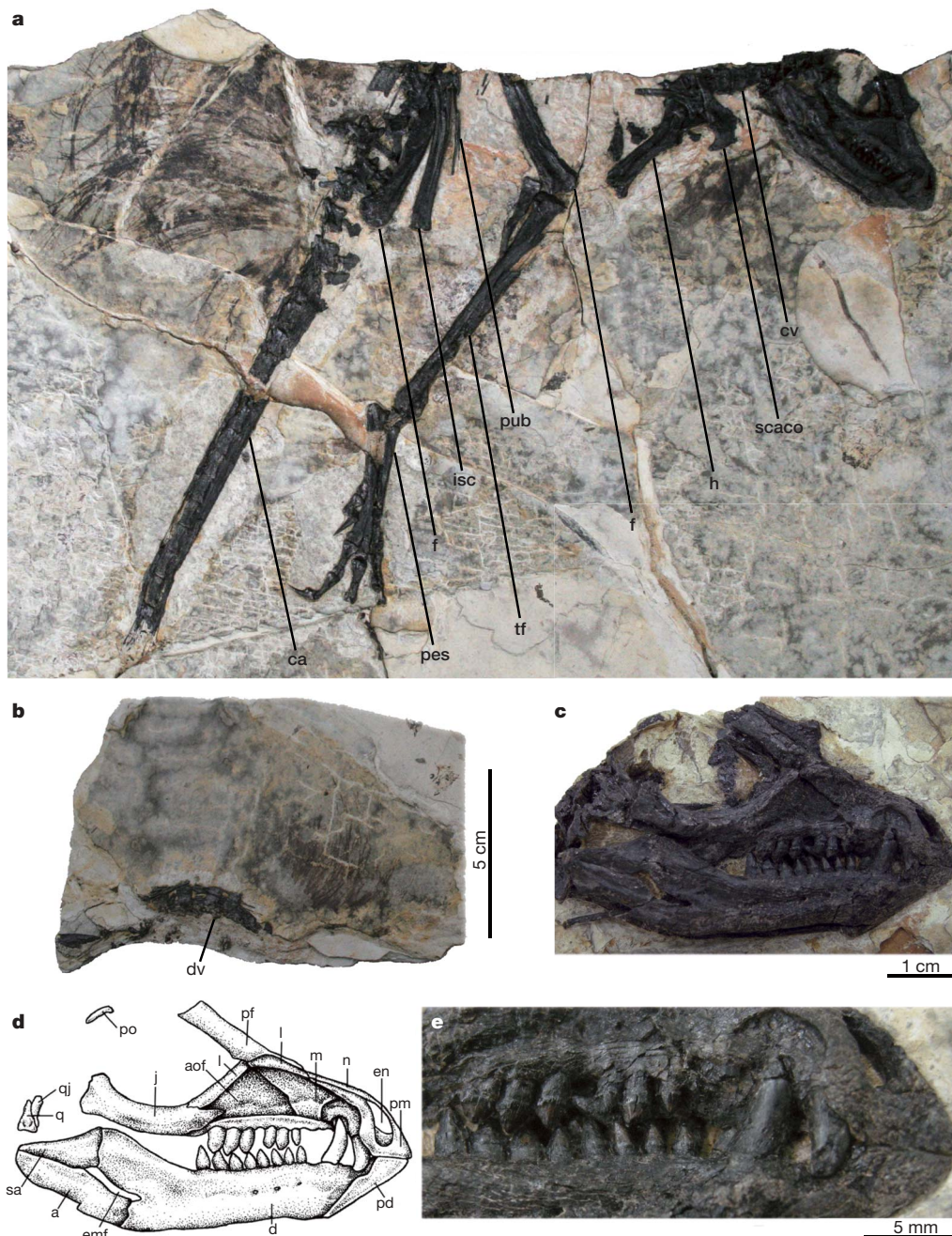


Figure 1 | New heterodontosaurid ornithischian dinosaur *T. confuciusi*. **a**, Main slab of the holotype (STMN 26-3). **b**, Broken slab. The scale bar in **b** refers also to **a**. **c**, Close-up of skull and mandible. **d**, Interpretive drawing of skull and mandible. **e**, Close-up of dentition. Abbreviations: a, angular; aof, antorbital fossa; ca, caudal vertebrae; cv, cervical vertebrae; d, dentary;

dv, dorsal vertebrae; emf, external mandibular fenestra; en, external naris; f, femur; h, humerus; isc, ischium; j, jugal; l, lacrimal; m, maxilla; n, nasal; pd, premandible; pf, prefrontal; pm, premaxilla; po, postorbital; pub, pubis; q, quadrate; qj, quadratojugal; scaco, scapulocoracoid; sa, surangular; tf, tibia and fibula.

widths of 0.4 mm. Although their bases are not clearly preserved, all the filaments seem to be singular, showing no evidence of branching. The filaments appear to have been relatively rigid because none are wavy or bent and they do not deviate along their lengths from otherwise gentle curvatures. The widths of all filaments appear similar in each patch, which strongly suggests that they have roughly constant radial dimensions and therefore circular cross sections. Although largely overlapping, several isolated, partial filaments on the tail also display dark, longitudinal 'stripes', implying that each had a tubular structure (Fig. 2d).

Given the stronger evidence for a tubular structure and their apparent rigidity, the filamentous integumentary structures of *Tianyulong* are more similar to those preserved on the tail of a specimen of *Psittacosaurus*⁹ than to the 'protofeather' structures in both

avian and non-avian theropods^{10,11}. However, the integumentary structures in *Psittacosaurus* are preserved only on the tail, and not distributed more widely along the body as in *Tianyulong*. Also, those in *Psittacosaurus* are more rigid and more widely separated from each other than in *Tianyulong*. The central tail feathers of the basal avialan *Epidipteryx*¹² (Fig. 2e), the basal pygostylian (all birds with shortened tails) *Confuciusornis*¹³ and some enantiornithean (one of the two major clades of early birds, which became extinct by the end of Cretaceous period) birds^{14,15} are also elongate, and represent a feather type unknown in extant birds. Unlike the structures in *Tianyulong*, however, they are ribbon-like and branch at their distal ends¹⁰.

Among the 'protofeathers' of theropods, the integumentary growths of *Tianyulong* are more similar to those of *Sinosauropteryx*¹⁶ than to

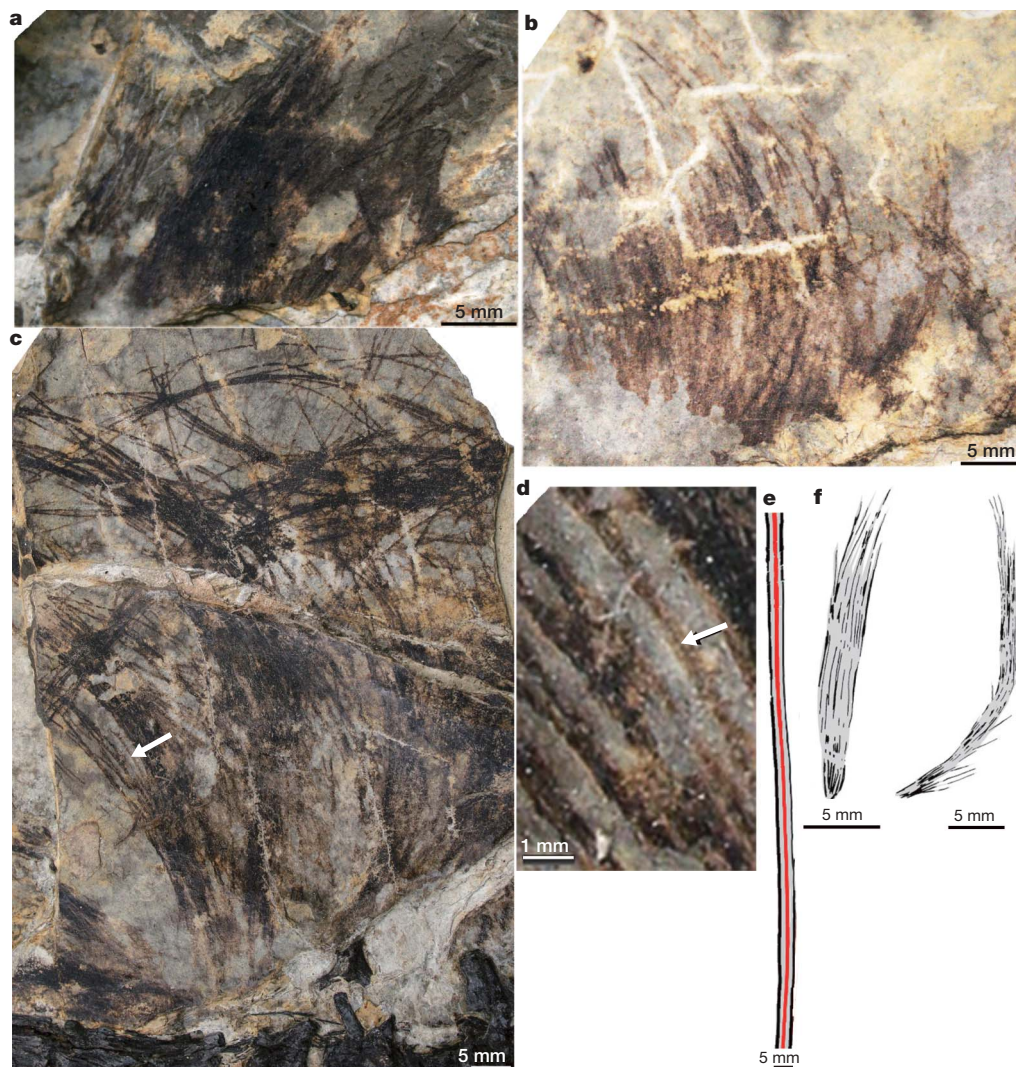


Figure 2 | Integumentary structures of *T. confuciusi* holotype (STMN 26-3) and others for comparison. a, Ventral to the cervical vertebral series. b, Dorsal to the dorsal vertebral series. c, Dorsal to the proximal–middle caudal vertebral series. d, Close-up of c. Arrows in c and d point to single filament exhibiting a clear, dark, midline ‘stripe’. e, Schematic of long, central tail feather of *Epidexipteryx* (after ref. 12). f, Two types of integumentary filaments of *Sinornithosaurus* (after ref. 17).

those of *Sinornithosaurus*¹⁷ (Fig. 2f) and others. In both *Tianyulong* and *Sinosauropteryx*, the filamentous structures are singular and unbranched, although the ‘protofeathers’ in the similar-sized *Sinosauropteryx* are much shorter and more slender than the caudal structures in *Tianyulong*, with lengths of less than 30 mm and widths of less than 0.2 mm¹⁶. In many of the theropods, the ‘protofeathers’ are more or less bundled together (Fig. 2f, left); in others, they exhibit a clear branching pattern (Fig. 2f, right). Overall, they appear to have been much more pliable^{10,11,16}.

Phylogenetic analysis recovers *Tianyulong* as a member of Heterodontosauridae, which, in turn, is the basalmost coherent group among all well-known ornithischians³ (Fig. 3; also see Supplementary Information). Shared derived features of heterodontosaurids include: ventral deflection of the oral margin of the premaxilla ventral to the maxillary tooth row, a large premaxilla–maxilla diastema at least one crown in length, quadrate with larger lateral than medial mandibular condyle, and a large, caudally placed caniniform premaxillary tooth; all these features are present in *Tianyulong*. Besides three heterodontosaurid genera from the Early Jurassic of southern Africa^{1,18}, other reports include one genus from the Early Cretaceous of England¹⁹, as well as fragmentary Middle and Late Jurassic–Early Cretaceous material from Europe^{19,20} and the Late Jurassic of North America²¹. Thus, *Tianyulong* expands the distribution of heterodontosaurids into Asia and confirms a long temporal extension for the clade into the Early Cretaceous, bolstering a heterodontosaurid interpretation for the European and North American reports.

The discovery of filamentous integumentary structures in *Tianyulong* provides an unprecedented phylogenetic extension of archosaurian dermal structures, previously reported only in derived theropodan saurischian dinosaurs, to Ornithischia. It also expands the known diversity of elaborate integumentary structures in Mesozoic reptiles, such as those in the diapsid *Longisquama*^{22,23}, pterosaurs^{24,25}, non-avian coelurosaurian theropods^{10,11} and birds^{10,11}, to ornithischians. However, the homology of these structures across taxa remains poorly understood. In terms of their relationships to feathers, both convergence^{23,24,26} and homology^{4,11,27} have been proposed to explain the elongate dorsal projections of *Longisquama* and the short, hair-like structures of pterosaurs; homology is favoured for the structures of theropods^{4,11,28} because they share features (such as branching) known elsewhere only in feathers. The unique filaments of *Tianyulong* add more complexity to the issue of feather origins. Homology of the structures in *Tianyulong* and theropods is far from obvious with present data, but cannot be precluded. Although based on negative evidence, the derived position within the Theropoda for the known appearance of ‘protofeathers’ indicates that earlier theropods lacked integumentary structures, implying in turn that the common ancestor of theropods and ornithischians also lacked such structures and that their appearances in each clade were convergent.

When homology with ‘protofeathers’ is hypothesized, a possible scenario is that the elongate, singular, cylindrical filaments of *Tianyulong* represent elaborations of the initial stage in development models of the origin and evolution of feathers^{28,29}. The basal position

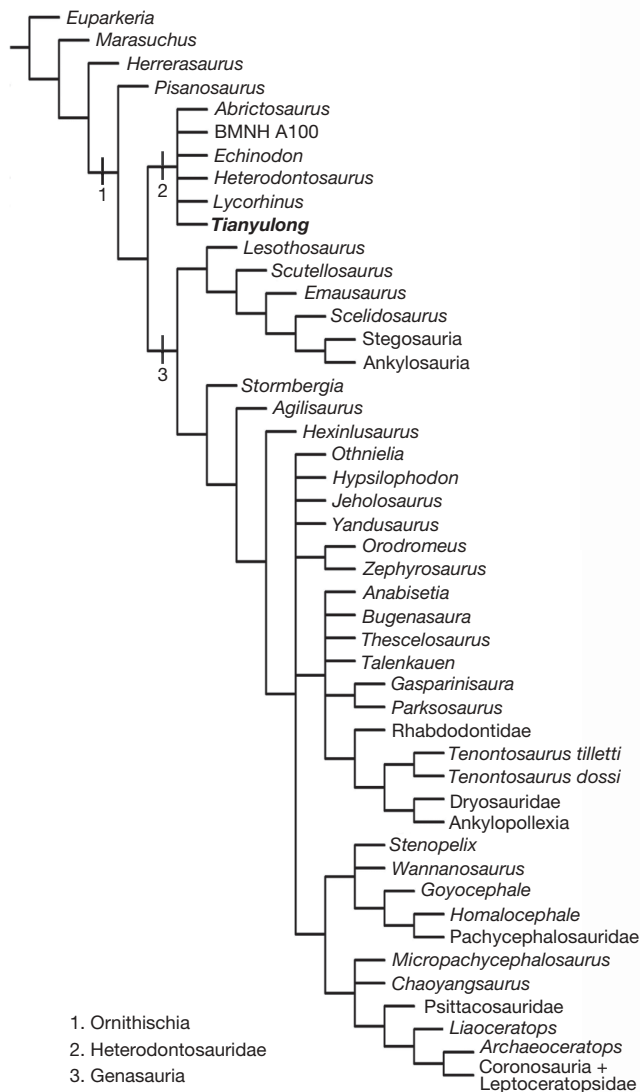


Figure 3 | Phylogenetic relationships of *T. confuciusi* and Heterodontosauridae. Cladistic analysis recovers *Tianyulong* as a member of Heterodontosauridae, which is itself a basal clade of ornithischian dinosaurs. This is based on a strict consensus of 8 most parsimonious trees with a tree length of 485, consistency index of 0.501 and retention index of 0.730. This analysis was performed by a sectorial search of TNT (tree analysis using new technology)³⁰ (see Supplementary Information).

of Heterodontosauridae within Ornithischia then suggests that such early-stage structures were present in the earliest dinosaurs (before or at the Saurischia–Ornithischia split) and inherited by basal members of each group. Later ornithischians and non-theropod saurischians for which skin impressions are known would therefore represent secondary losses of these structures at as-yet undetermined systematic positions. The structures in *Tianyulong*, as well as the bristle-like structures of the basal ceratopsian *Psittacosaurus*⁹, which have frequently been perceived as nonhomologous with the filamentous structures of theropods, may truly be homologous, albeit derived in structure compared to those of theropods.

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1. Norman, D. B., Sues, H.-D., Witmer, L. M. & Coria, R. A. in *The Dinosauria* 2nd edn (eds Weishampel, D. B., Dodson, P. and Osmólska, H.) 393–412 (Univ. California Press, 2004).
2. Xu, X., Forster, C. A., Clark, J. M. & Mo, J. A basal ceratopsian with transitional features from the Late Jurassic of northwestern China. *Proc. R. Soc. Lond. B* **273**, 2135–2140 (2006).

3. Butler, R. J., Upchurch, P. & Norman, D. B. The phylogeny of the ornithischian dinosaurs. *J. Syst. Palaeontol.* **6**, 1–40 (2008).
4. Zhou, Z., Barrett, P. M. & Hilton, J. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**, 807–814 (2003).
5. Ji, Q. et al. *Mesozoic Jehol Biota of Western Liaoning, China* (Geological Publishing House, 2004).
6. Weishampel, D. B. & Witmer, L. M. in *The Dinosauria* 1st edn (eds Weishampel, D. B., Dodson, P. & Osmólska, H.) 486–497 (Univ. California Press, 1990).
7. Lingham-Soliar, T., Feduccia, A. & Wang, X. A new Chinese specimen indicates that ‘protofeathers’ in the Early Cretaceous theropod dinosaur *Sinosauropteryx* are degraded collagen fibres. *Proc. R. Soc. Lond. B* **274**, 1823–1829 (2007).
8. Feduccia, A., Lingham-Soliar, T. & Hinchliffe, J. R. Do feathered dinosaurs exist? Testing the hypothesis on neontological and paleontological evidence. *J. Morphol.* **266**, 125–166 (2005).
9. Mayr, G., Peters, D. S., Plodowski, G. & Vogel, O. Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften* **89**, 361–365 (2002).
10. Zhang, F., Zhou, Z. & Dyke, G. J. Feathers and ‘feather-like’ integumentary structures in Liaoning birds and dinosaurs. *Geol. J.* **41**, 395–404 (2006).
11. Xu, X. Feathered dinosaurs from China and the evolution of major avian characters. *Integ. Zool.* **1**, 4–11 (2006).
12. Zhang, F. et al. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* **455**, 1105–1108 (2008).
13. Zhang, F., Zhou, Z. & Benton, M. J. A primitive confuciosornithid bird from China and its implications for early avian flight. *Sci. China Ser. D* **51**, 625–639 (2008).
14. Zhang, F. & Zhou, Z. A primitive enantiornithine bird and the origin of feathers. *Science* **290**, 1955–1960 (2000).
15. Zheng, X., Zhang, X. & Hou, L. A new enantiornithine bird with four long rectrices from the Early Cretaceous of northern Hebei, China. *Acta Geol. Sin.-Engl.* **81**, 703–708 (2007).
16. Currie, P. J. & Chen, P. J. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Can. J. Earth Sci.* **38**, 1705–1727 (2001).
17. Xu, X., Zhou, Z.-H. & Prum, R. O. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* **410**, 200–204 (2001).
18. Butler, R. J., Porro, L. B. & Norman, D. B. A juvenile skull of the primitive ornithischian dinosaur *Heterodontosaurus tucki* from the ‘Stormberg’ of southern Africa. *J. Vertebr. Paleontol.* **28**, 702–711 (2008).
19. Naish, D. & Martill, D. M. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: Ornithischia. *J. Geol. Soc. Lond.* **165**, 613–623 (2008).
20. Sánchez-Hernández, B., Benton, M. J. & Naish, D. Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **249**, 180–215 (2007).
21. Norman, D. B. & Barrett, P. M. Ornithischian dinosaurs from the Lower Cretaceous (Berriasian) of England. *Spec. Pap. Palaeontol.* **68**, 161–189 (2002).
22. Sharov, A. G. An unusual reptile from the Lower Triassic of Fergana. *Paleontol. J.* **1970**, 112–116 (1970).
23. Voigt, S. et al. Feather-like development of Triassic diapsid skin appendages. *Naturwissenschaften* **96**, 81–86 (2009).
24. Wang, X., Zhou, Z., Zhang, F. & Xu, X. A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and ‘hairs’ from Inner Mongolia, northeast China. *Chin. Sci. Bull.* **47**, 226–230 (2002).
25. Ji, Q. & Yuan, C.-X. Discovery of two kinds of protofeathered pterosaurs in the Mesozoic Daohugou Biota in the Ningcheng region and its stratigraphic and biologic significances. *Geol. Rev.* **48**, 221–224 (2002).
26. Reisz, R. R. & Sues, H. D. The ‘feathers’ of *Longisquama*. *Nature* **408**, 428 (2000).
27. Jones, T. D. et al. Nonavian feathers in a late Triassic archosaur. *Science* **288**, 2202–2205 (2000).
28. Prum, R. O. & Brush, A. H. The evolutionary origin and diversification of feathers. *Q. Rev. Biol.* **77**, 261–295 (2002).
29. Yu, M., Wu, P., Wideltz, R. B. & Chuong, C.-M. The morphogenesis of feathers. *Nature* **420**, 308–312 (2002).
30. Goloboff, P. A., Farris, J. S. & Nixon, K. C. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786 (2008).

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

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