A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings

Xing Xu^{1,2}*, Xiaoting Zheng^{1,3}*, Corwin Sullivan², Xiaoli Wang¹, Lida Xing⁴, Yan Wang¹, Xiaomei Zhang³, Jingmai K. O'Connor², Fucheng Zhang² & Yanhong Pan⁵

The wings of birds and their closest theropod relatives share a uniform fundamental architecture, with pinnate flight feathers as the key component¹⁻³. Here we report a new scansoriopterygid theropod, Yi qi gen. et sp. nov., based on a new specimen from the Middle-Upper Jurassic period Tiaojishan Formation of Hebei Province, China⁴. Yi is nested phylogenetically among winged theropods but has large stiff filamentous feathers of an unusual type on both the forelimb and hindlimb. However, the filamentous feathers of Yi resemble pinnate feathers in bearing morphologically diverse melanosomes⁵. Most surprisingly, Yi has a long rod-like bone extending from each wrist, and patches of membranous tissue preserved between the rod-like bones and the manual digits. Analogous features are unknown in any dinosaur but occur in various flying and gliding tetrapods⁶⁻¹⁰, suggesting the intriguing possibility that Yi had membranous aerodynamic surfaces totally different from the archetypal feathered wings of birds and their closest relatives. Documentation of the unique forelimbs of Yi greatly increases the morphological disparity known to exist among dinosaurs, and highlights the extraordinary breadth and richness of the evolutionary experimentation that took place close to the origin of birds.

> Theropoda Marsh, 1881 Maniraptora Gauthier, 1986 Scansoriopterygidae Czerkas et Yuan, 2002 *Yi qi* gen. et sp. nov.

Etymology. The generic and specific names are derived from Mandarin Yi (wing) and qi (strange), respectively, referring to the bizarre wings of this animal. The intended pronunciation of the name is roughly "ee chee".

Holotype. STM 31-2 (housed at the Shandong Tianyu Museum of Nature), an articulated partial skeleton with associated soft tissue preserved on a slab and counter slab. The specimen was collected by a local farmer, but its provenance and authenticity have been confirmed by multiple lines of evidence including sedimentology, taphonomy and computed tomography (CT) data (Extended Data Figs 1–4; see also Supplementary Information).

Locality and horizon. Mutoudeng, Qinglong County, Hebei Province, China. Tiaojishan Formation, Callovian–Oxfordian stage^{4,11}. On the basis of the provenance of the specimen, *Yi qi* is a member of the Daohugou (or Yanliao) Biota¹².

Diagnosis. A scansoriopterygid theropod distinguishable from other scansoriopterygids in having a low midline crest along the nasals, a relatively small and posteriorly located external mandibular fenestra, tooth crowns that are symmetrical in lateral view and considerably wider mesiodistally than their corresponding roots, a humerus and ulna that are long relative to the tibiotarsus (length ratios are 1.16 and 1.08, respectively, compared to 0.96 and 0.78 in *Epidendrosaurus* and 0.79 and 0.66 in *Epidexipteryx*), an extremely short humeral deltopectoral crest, and a long rod-like bone articulating with the wrist.

Key osteological features are as follows. STM 31-2 (Fig. 1) is inferred to be an adult on the basis of the closed neurocentral sutures of the visible vertebrae, although this is not a universal criterion for maturity across archosaurian taxa¹². Its body mass is estimated to be approximately 380 g, using an empirical equation¹³.

The skull and mandible are similar to those of other scansoriopterygids, and to a lesser degree to those of oviraptorosaurs and some basal birds such as *Sapeornis* and *Jeholornis*^{11,14–17}: the skull is relatively robust, the snout is short (approximately 40% of skull length), the large premaxilla bears a well-developed subnarial process and extends further ventrally than the small maxilla, the parietal is anteroposteriorly long, the antorbital fossa is much smaller than the orbit, the infratemporal fenestra is large, the anterior end of the robust mandible is downturned, four slightly procumbent premaxillary teeth are located anterior to the external naris, the first premaxillary tooth is larger than the more posterior ones, and the anterior dentary teeth are strongly procumbent (Fig. 1a-d). The thoracic appendage resembles that of other paravians in that the scapula is proportionally short and the humerus is long and robust, and further resembles that of other scansoriopterygids¹⁴⁻¹⁶ in having a robust scapular blade, a short humeral deltopectoral crest, a straight ulna that is only slightly more robust than the radius, a metacarpal IV that is longer and more robust than metacarpal III (we identify the three manual digits of Yi and other maniraptorans as II-III-IV, following the position-based numbering used in most ornithological literature, although we acknowledge that an anatomy-based I-II-III numbering convention is preferred by most dinosaur workers), and non-ungual phalanges of digit IV that are all greatly elongated (Fig. 1a, b, e).

The most striking feature of Yi is the presence of an anomalous, slightly curved, distally tapered, rod-like structure (see Supplementary Information for further description), whose length considerably exceeds that of the ulna, associated with each wrist and apparently extending from the ulnar side of the carpus (Fig. 1a, b, f and Extended Data Fig. 5). These structures resemble the preserved bones on the slab in colour, and in displaying a granular texture under magnification. Energy dispersive spectrometry (EDS) analysis of the elemental composition of the rod extending from the right wrist confirms that it is a bone (or possibly a skeletal element composed of calcified cartilage) and not a soft-tissue structure (Extended Data Fig. 6; see also Supplementary Information). However, the rod-like bone of the forelimb of Yi is morphologically unlike any normal theropod skeletal element. Indeed, no equivalent of the rod-like bone is known in any other dinosaur even outside Theropoda, but similar structures are present in a diverse array of extant and extinct flying or gliding

¹Institute of Geology and Paleontology, Linyi University, Linyi City, Shandong 276005, China. ²Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China. ³Shandong Tianyu Museum of Nature, Pingyi, Shandong 273300, China. ⁴School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China. ⁵Key Laboratory of Economic Stratigraphy and Palaeogeography of Chinese Academy of Sciences, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. ^{*}Key Laboratory of Economic Stratigraphy and Palaeogeography of Chinese Academy of Sciences, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. ^{*}These authors contributed equally to this work.



Figure 1 | *Yi qi* holotype (STM 31-2). a, b, Photograph (a) and line drawing (b) of specimen; c, skull and mandible in lateral view; d, premaxillary tooth in lateral view; e, left manus; f, styliform elements (the distally unexposed left styliform element articulates with the wrist, and the orientation of the right styliform element implies a similar relationship to the carpus even though its proximal part is missing). Light and dark grey shading indicates feathers and membranous tissues, respectively. an, angular, cv, cervical vertebrae; d, dentary; dr, dorsal ribs; emf, external mandibular fenestra; en, external naris; f, frontal; lf, left femur; lh, left humerus; lmd2–4, left manual digits 2–4; lmt, left metatarsals; lr, left radius; ls, left scapula; lse, left styliform element; lu, left ulna; mb, mandible; mcII–IV, metacarpals II–IV; n, nasal; or, orbit; p, parietal; phII1 to IV-4; pma, premaxilla; rmd2–4, right manual digits 2–4; rf, right femur; rf, right radius; rse, right styliform element; rt, right tibiotarsus; ru, right ulna; sk, skull. Scale bar, 2 cm.

tetrapod groups^{6–10}. For example, a rod of bone or cartilage is attached to the wrists of petauristine squirrels¹⁸; the elbows of anomalurid squirrels¹⁹, the gliding marsupial *Petauroides volans*¹⁹ and the Oligocene epoch eomyid rodent *Eomys quercyt*⁹; the ankles of many bats, including some early ones^{9,10}; and the wrists of all pterosaurs⁸ (that is, the pteroid). In particular, the rod-like bone of *Yi* is strikingly similar to the enlarged carpally situated element seen in some petauristines⁷, including the Japanese giant flying squirrel *Petaurista leucogenys* (Extended Data Fig. 7; see also Supplementary Information). For convenience, we adopt 'styliform element' as a general term for unjointed, rod-like bony or cartilaginous structures that extend from distal limb joints in tetrapods.

Integumentary structures and preserved melanosomes are as follows. Two major types of integumentary structure are preserved (see Supplementary Information for further description): feathers and membranous soft tissue (Figs 1a, b, 2 and Extended Data Fig. 5). Thin stiff filamentous feathers are distributed around the skull (15-20 mm long; Fig. 2a), and both above and below the neck (about 30 mm long; Extended Data Fig. 5a). The feathers attached to the forelimb (35-60 mm long; Fig. 2b and Extended Data Fig. 5b, c), and to the hindlimb including the metatarsus (up to 60 mm long; Fig. 2c and Extended Data Fig. 5e), are much larger than the skull and neck feathers. Some of the filamentous feathers, including those on the skull and neck, appear to exhibit a simple branching pattern, but their dense preservation makes morphological details difficult to observe. Nevertheless, some isolated feathers clearly comprise multiple radiating filaments (Fig. 2d and Extended Data Fig. 5d), and the majority of the limb feathers have a unique paintbrush-like morphology (Fig. 2e): the proximal three-fourths of each feather is a wide (about 1.2 mm), undifferentiated shaft-like structure, whereas the distal part is composed of numerous near-parallel filaments.

Several patches of membranous soft tissue are exposed around the styliform element and digits in both hands (Figs 1a, b, 2f and Extended Data Fig. 5f, g). Additional patches appear to exist, but cannot be easily exposed (see Supplementary Information). The tissue has a sheet-like appearance, making it clearly distinguishable from the individual filaments or small groups of filaments that represent feathers (Fig. 2g), and in some areas displays prominent ripple-like striations that may represent either fibres or closely spaced folds. The membranous tissue does not closely resemble any type of integumentary structure previously reported in theropods from the Mesozoic era deposits of north-eastern China.

We examined the integumentary structures using scanning electron microscopy (Extended Data Fig. 8), revealing what we interpret as preserved melanosomes on both feathers and membranous tissue patches (although several studies have questioned the identification of melanosomes in theropod fossils^{20,21}). The melanosomes are highly variable in size (long axis 300–2,100 nm), shape (aspect ratio of 1.0 to 3.6) and density (Extended Data Fig. 9). It is noteworthy that some of the preserved melanosomes are among the largest known from either fossil or modern feathers⁵. The membranous tissue contains only small phaeomelanosomes (long axis 300–400 nm), unlike the filamentous feathers in which eumelanosomes predominate and relatively few phaeomelanosomes are present (see Supplementary Information for details).

A numerical phylogenetic analysis places Yi within the enigmatic Scansoriopterygidae family^{14–17}, which in turn is posited as the sister taxon to other paravians (Fig. 3 and Extended Data Fig. 10). Scansoriopterygids including Yi have numerous unusual skeletal features, including a highly elongated third finger and a highly modified pelvis^{14,16,17}. They also display unusual integumentary features: despite being basal paravians, they lack pinnate feathers, but their filamentous feathers resemble the pinnate feathers of other pennaraptorans in having morphologically diverse melanosomes⁵. Given that scansoriopterygids are phylogenetically nested within Pennaraptora, they appear to represent a case of extreme morphological divergence near the origin of birds, involving not only extensive modification of the skeleton but also secondary loss of normal pennaraptoran pinnate feathers.

Large flight feathers and even propatagia are present in the basal oviraptorosaur *Caudipteryx* and the basal deinonychosaurs *Anchiornis* and *Microraptor*¹⁻³ (and a propatagium has been identified in the scansoriopterygid *Epidendrosaurus*²²), indicating that the feathered wing is a primitive feature of the Pennaraptora even though basal members of this group are flightless²³. Both phylogenetic bracketing²⁴







Figure 3 Simplified coelurosaurian phylogeny showing the recovered position of *Yi*. The skeletal silhouette and two possible alternative planform reconstructions of *Yi* highlight the proportionally long and robust forelimbs and large leg feathers that *Yi* shares with other basal paravian theropods, indicating the presence of aerial capability, and the inferred membranous wings, a feature unique among known paravians but seen in most other gliding or flying tetrapods. Various uncertainties, such as how the styliform element is oriented and whether membranous tissue is present lateral to the trunk as in most volant tetrapods, imply that a variety of reconstructions of the aerodynamic apparatus of *Yi* are currently plausible (see Supplementary Information for additional possible reconstructions).

Figure 2 | Soft tissues preserved in *Yi qi* holotype (STM 31-2). a–e, Feathers above the skull (a), along the humerus (b) and along the tibiotarsus (c); isolated basally converging (d) and brush-like (e) feathers; f, sheet-like soft tissue associated with the right forelimb (yellow arrows point to patches of sheet-like soft tissue); g, comparison of sheet-like soft tissue (above digit II) and individual feathers (below digit II).

and the preserved morphology of the shoulder girdle and forelimb suggest that Yi resembles other basal paravians in the overall skeletal structure of its thoracic girdle and appendages. In Yi, however, the large flight feathers present in other pennaraptorans appear to be at least partly replaced by membranes supported by the styliform element and manual digits, in stark contrast to the archetypal wings that are universal in birds and their closest relatives. The highly elongated manual digit IV of Yi and other scansoriopterygids is unique among theropods but superficially similar to the long manual digits II–V of bats and the highly elongated fourth finger in pterosaurs. Furthermore, some major components of the wing of Yi, such as the membrane and styliform element, are not known in other winged theropods. The discovery of Yi thus adds considerably to the known diversity of thoracic appendage morphologies present near the transition to birds.

Because other amniotes that possess a styliform element invariably utilize this structure to support an aerodynamic membrane that contributes to gliding or powered flight⁶⁻¹⁰, and alternative functions for a long, unjointed rod of bone or cartilage extending from a distal limb joint are difficult to imagine (see Supplementary Information), the occurrence of a styliform element in Yi is a strong indication that membranous aerodynamic surfaces and some degree of aerial capability were present in this taxon. Further evidence that Yi was volant comes from the preserved patches of membranous tissue associated with the styliform element and digits, and from the proportions of the appendicular skeleton (see Supplementary Information). It is worth emphasizing that, even if our inference that Yi was an aerially adapted taxon with membranous wings proves incorrect, the styliform element and membranous tissue patches will stand as highly unusual features that imply some kind of equally distinctive forelimb function in this peculiar theropod.

Even under our preferred interpretation, the flight apparatus of Yi cannot be confidently reconstructed due to the incomplete preservation of the wing membrane in the only known specimen, combined with uncertainties regarding the styliform element's orientation and connection to the wrist. However, the range of possible flight apparatus configurations can be explored by considering different reconstructions (Fig. 3 and Extended Data Fig. 7) that are supported to varying degrees by morphological and taphonomic information from the specimen, fundamental aerodynamic principles, and the aerial locomotion of other volant tetrapods. Preliminary analysis of the wing loadings and other properties of some of these configurations supports the plausibility of Yi as a volant taxon (see Supplementary Information). In having wings with a well-developed membranous component, Yi would differ from other volant paravians but resemble

distantly related groups including pterosaurs, bats and many gliding mammals, representing a striking case of convergent evolution of the aerodynamic apparatus among tetrapods^{6–10}.

The mode of aerial locomotion that might have been used by Yi is difficult to reconstruct on the basis of present evidence. Yi may have been capable of flapping flight or only of gliding, or may have combined the two locomotor styles as in many extant birds and some bats (see Supplementary Information). There are some indications that Yi may have relied more on gliding than on flapping, including the lack of strongly expanded muscle attachment surfaces on the forelimb bones and the possibility that the unwieldy styliform element would have interfered with the rapid oscillations and rotations of the distal part of the forelimb needed for efficient flapping flight, but the mode of aerial locomotion that is most likely for Yi remains uncertain. Regardless, the evident occurrence in this taxon of a membranous wing supported by a styliform element represents an unexpected aerodynamic innovation close to the origin of birds, and highlights the breadth of flight-related morphological experimentation that took place in the early stages of paravian history.

Received 11 February; accepted 20 March 2015. Published online 29 April 2015.

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Supplementary Information is available in the online version of the paper.

Acknowledgements We thank Z. Zhou, R. Dudley, J. Clarke and T. Stidham for discussion, X. Ding for specimen preparation, Y. Liu and Y. Han for providing illustrations, Z. Zhang for assistance with the EDS analysis, and Y. Hou for CT scanning the specimen. This research was funded by the National Natural Science Foundation of China (41372014, 41472023, 41120124002 and 41125008) and Major Basic Research Projects of the Ministry of Science and Technology, China (2012CB821900).

Author Contributions X.X., X. Zheng and C.S. designed the project, X.X., X. Zheng, C.S., X.W., Y.W., L.X., X. Zhang, J.K.O'C., F.Z. and Y.P. performed the research, and X.X. and C.S. wrote the manuscript.

Author Information Data have been deposited in ZooBank under Life Science Identifier (LSID) urn:Isid:zoobank.org:pub:5B765FD5-A534-45D5-AE14-62C25EADDD2D. The raw CT data have been deposited in the Dryad Digital Repository (http:// dx.doi.org/10.5061/dryad.fp060). Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to X.X. (xingxu@vip.sina.com) or X. Zheng (ty4291666@163.com).



Extended Data Figure 1 Fossil-bearing beds of the Middle-Upper Jurassic Tiaojishan Formation in Qinglong County, Hebei. The Mutoudeng Locality (top) and Gangou Locality (bottom) are geographically close to each other

(approximately 20 km apart) and very similar in their sedimentology and fossil content. The bottom image shows an excavation we organized at the Gangou Locality.



Extended Data Figure 2 | Photograph of the slab and counter slab of STM 31-2.

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Extended Data Figure 3 | Close-ups of the three counter slab fragments and corresponding slab regions of STM 31-2. Top row: isolated piece from counter slab preserving cranial region (left), and corresponding region of slab (right); middle row: isolated piece from counter slab preserving forelimb region

(left), and corresponding region of slab (right); bottom row: isolated piece from counter slab preserving hindlimb region (left), and corresponding region of slab (right).



Extended Data Figure 4 | Volumetric model generated from superimposed CT slices. Because there is little density contrast between the fossil and the matrix, the outline of the fossil is somewhat vague.

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Extended Data Figure 5 | Photographs of preserved integumentary features of STM 31-2. a–c, Feathers over the neck (a), along the humerus (b) and along the humerus and ulna (c); d, isolated basally converging feathers; e, sheet-like

soft tissue and feathers associated with the right forelimb and feathers along the right hindlimb; \mathbf{f} , \mathbf{g} , close-ups of sheet-like soft tissue associated with the right forelimb (\mathbf{f}) and distal phalanges of manual digit IV (\mathbf{g}).



Extended Data Figure 6 | **Elemental compositions of the styliform element and comparison samples based on EDS analyses.** EDS spectra derived from: **a**, right manual phalanx II-1; **b**, right styliform element; **c**, feathers associated with right tibia; and **d**, sedimentary matrix.



Extended Data Figure 7 Aerodynamic apparatuses in *Yi* and other tetrapods. a–c, Wing of *Yi*, Bat Model (a), Maniraptoran Model (b), and Frog Model (c); d, bat wing; e, pigeon wing; f, pterosaur wing; g, giant Japanese flying squirrel wing. Yellow colour indicates styliform element in a, b, c, d, f, and g.



Extended Data Figure 8 | Scanning electron microscopy sample locations. Numbered circles indicate the locations of samples from the slab and counter slab. 1, distal part of cranial feathers; 2, middle part of tibial feathers; 3, distal part of humeral feathers; 4, distal part of ulnar feathers; 5, proximal part of

cranial feathers; 6, proximal part of neck feathers; 7, distal part of humeral feathers; 8, distal part of humeral feathers; 9 and 10, membranous soft tissue near digit II; 11, membranous soft tissue near digit IV; 12, middle part of tibial feathers.



Extended Data Figure 9 | Scanning electron microscopy images of melanosomes and melanosome impressions preserved in *Yi qi* holotype (STM 31-2). a–m, Note the high morphological diversity of the preserved melanosomes in the feathers, which include: densely distributed, small round phaeomelanosomes and sparsely distributed, medium-sized oval eumelanosomes in the feathers near the skull (a); medium-sized elongate

elliptical eumelanosomes in the feathers near the skull (\mathbf{b}, \mathbf{c}) , neck (\mathbf{d}, \mathbf{e}) , humerus (\mathbf{f}, \mathbf{g}) , and ulna $(\mathbf{h}, \mathbf{i}, \mathbf{j})$; and large oval and elliptical eumelanosomes in the feathers near the tibiotarsus (\mathbf{k}, \mathbf{l}) . The subspherical phaeomelanosomes in the sheet-like soft tissue (\mathbf{m}) appear to be less densely distributed than the melanosomes in the feathers.



Extended Data Figure 10 | Strict consensus of the 96 trees that resulted from analysis of a phylogenetic data matrix for coelurosaurs.