

Four-winged dinosaurs from China

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Although the dinosaurian hypothesis of bird origins is widely accepted, debate remains about how the ancestor of birds first learned to fly. Here we provide new evidence suggesting that basal dromaeosaurid dinosaurs were four-winged animals and probably could glide, representing an intermediate stage towards the active, flapping-flight stage. The new discovery conforms to the predictions of early hypotheses that proavians passed through a tetrapteryx stage.

For the past few decades, the theropod hypothesis of bird origin has been strongly corroborated by fossil evidence^{1–9} and systematic work^{10–15}. Dromaeosaurids, one of the most distinctive theropod groups, have attracted particular attention since the description of *Deinonychus*¹, owing to its pivotal role in supporting a theropod origin of birds. They, either by themselves or with troodontids^{7,10,11,13–16}, have been regarded as most closely related to birds. A better understanding of these animals is therefore crucial in reconstructing the evolutionary transition towards birds. Recent discoveries from the Jehol Group of western Liaoning, China, suggest that basal dromaeosaurs are small, feathered animals with forelimbs similar to those of *Archaeopteryx*, and feet showing features comparable to those of arboreal birds^{7,8,17}. In 2001 and 2002, we obtained six new basal dromaeosaurid specimens from the Lower Cretaceous Jehol Group at a few localities in Chaoyang Basin, western Liaoning, China. IVPP (The Institute of Vertebrate Paleontology and Paleoanthropology) V13352 and V13320 were identified as a new species of *Microraptor*, TNP00996 (Tianjin Museum of Natural History), IVPP V13351 and IVPP V13476 as *Microraptor* sp., and IVPP V13477 as Dromaeosauridae gen. et sp. indet. These specimens provide new information on the morphology and distribution of feathers on non-avian dromaeosaurids. Here we describe the new dromaeosaurid species and in particular the morphology and distribution of feathers on the newly collected dromaeosaurid specimens.

Theropoda Marsh, 1881
 Maniraptora Gauthier, 1986
 Dromaeosauridae Matthew & Brown, 1922
Microraptor Xu, Zhou & Wang, 2000
Microraptor gui sp. nov.

Etymology. The specific name is in honour of Gu Zhiwei, a distinguished palaeontologist who contributed greatly to the study of Jehol biota.

Material. IVPP V13352 (holotype) and V13320 (referred specimen), both represented by an almost complete skeleton.

Locality and horizon. Dapingfang, Chaoyang County, western Liaoning (30 km southwest of Chaoyang City); Jiufotang Formation¹⁸ (Early Cretaceous).

Diagnosis. Distinguishable from *Microraptor zhaoianus* in having prominent biceps tubercosity on radius, much shorter manual digit I, strongly curved pubis, and bowed tibia.

Description. *Microraptor gui* is a small animal, the holotype being approximately 77 cm in total length (Fig. 1a). Little can be said about the cranial morphology but a tri-radiate postorbital is identifiable. As in *M. zhaoianus*⁸, the basal troodontid *Sinovenator*¹⁵, and the basal oviraptorosaur *Caudipteryx*¹⁹, *M. gui* has a relatively short trunk length, which is 44–50% of hindlimb length (according to the method of ref. 19). The tail is long (Fig. 1a) but has relatively few vertebrae (approximately 26). The middle and posterior caudals are significantly elongate as in other basal dromaeosaurs, basal troodontids and *Archaeopteryx*²⁰. The sternum is a single, flat and large bone (Fig. 1a), different from the condition in other dromaeosaurids^{7,21} where two unfused sternal plates are present. At least seven pairs of slender uncinat processes are present. The anterior uncinat processes cover three ribs and the posteriormost one is short and does not reach the succeeding rib. The fused scapula and coracoid are similar to those of *Sinornithosaurus* and *M. zhaoianus* in the following features: scapula shorter than humerus; glenoid fossa laterally faced; angle between scapula and coracoid less than 90°; and large supracoracoid fenestra present on coracoid²⁰. The forelimb is approximately 2.7 times the femoral length. The ulna is bowed and the radius is much thinner than the ulna (Fig. 1). Metacarpal I is about one-quarter of metacarpal II in length and metacarpal III is slender and bowed laterally. Manual digit II, particularly phalanx II-1, is thick. The pelvis displays the following derived features as in *M. zhaoianus*, *Sinornithosaurus*, *Sinovenator* and basal birds^{5,7,15}: postacetabular process of the ilium tapered; pubis retroverted; and ischium short, with a distally located obturator process and two dorsal processes. The tibia is variably bowed, more so in the referred specimen than the holotype. The pes is similar to that of *M. zhaoianus* in showing a sub-arcotometatarsalian

Table 1 Measurements of femoral length and the length and asymmetry ratio of feathers from the forelimb, hindlimb and tail

Specimen	Femoral length	A distal primary feather	A middle secondary feather	A proximal secondary feather	A distal metatarsus feather	A proximal metatarsus feather	A distal tail feather
IVPP V13352	97	222/1.94* (7)†	95*/1.52 (10)†	81/1.0 (15)†	194/? (2)†	104/1.33 (13)†	120/? (2)†
TNP00996	63	??	??	??	121/1.56* (1)†	72/1.1 (13)†	100/2.1* (1)†
IVPP V13477	72	??	??	??	113/3.08 (2)†	??	??
IVPP V13351	81	??	??	??	190/? (4)†	??	185/? (1)†
IVPP V13320	61	186/1.5* (10)†	??	??	??/2.4 (1)†	130/? (10)†	??
IVPP V13476	94*	??	??	??	175/? (1)†	??	??

Length measurements are given in millimetres. Asymmetry ratio is measured based on the method of ref. 46. Numbers in parentheses indicate the anatomical positions of the feathers (the metatarsal feathers are numbered from distal).

* Incomplete measurements.

† Estimation.

condition and in having slender, strongly curved claws^{8,20}.

Microraptor gui can be unequivocally referred to Dromaeosauridae based on the following derived characters²⁰: extremely elongate prezygapophyses and chevrons; manual phalanges III-1 significantly longer than III-2; specialized pedal digit II; and long metatarsal V. Furthermore it can be referred to *Microraptor* on the basis of the following features²⁰: metacarpal III subequal to metacarpal II in length; extremely short manual phalanx III-2 that is less than one-quarter of manual III-1 length; manual III-3 extremely slender and shorter than III-1 in length, and small distal articulation

of manual III-3 skewed ventrally. However, a few features distinguish it from *M. zhaoianus*. A prominent biceps tuberosity is present close to the proximal end of the radius and this feature has not been reported in most other non-avian theropods except a recently described therizinosauroid²². As in most birds, *M. gui* has a proportionately very short manual digit I (metacarpal I + phalanx I-1/metacarpal II length ratio is 0.80–0.84). For comparison, this ratio is 0.97 in *M. zhaoianus* and more than 1.0 in most other non-avian theropods and the basal birds *Archaeopteryx* and *Confuciusornis*. The pubis of *M. gui* is strongly curved (120°), whereas the

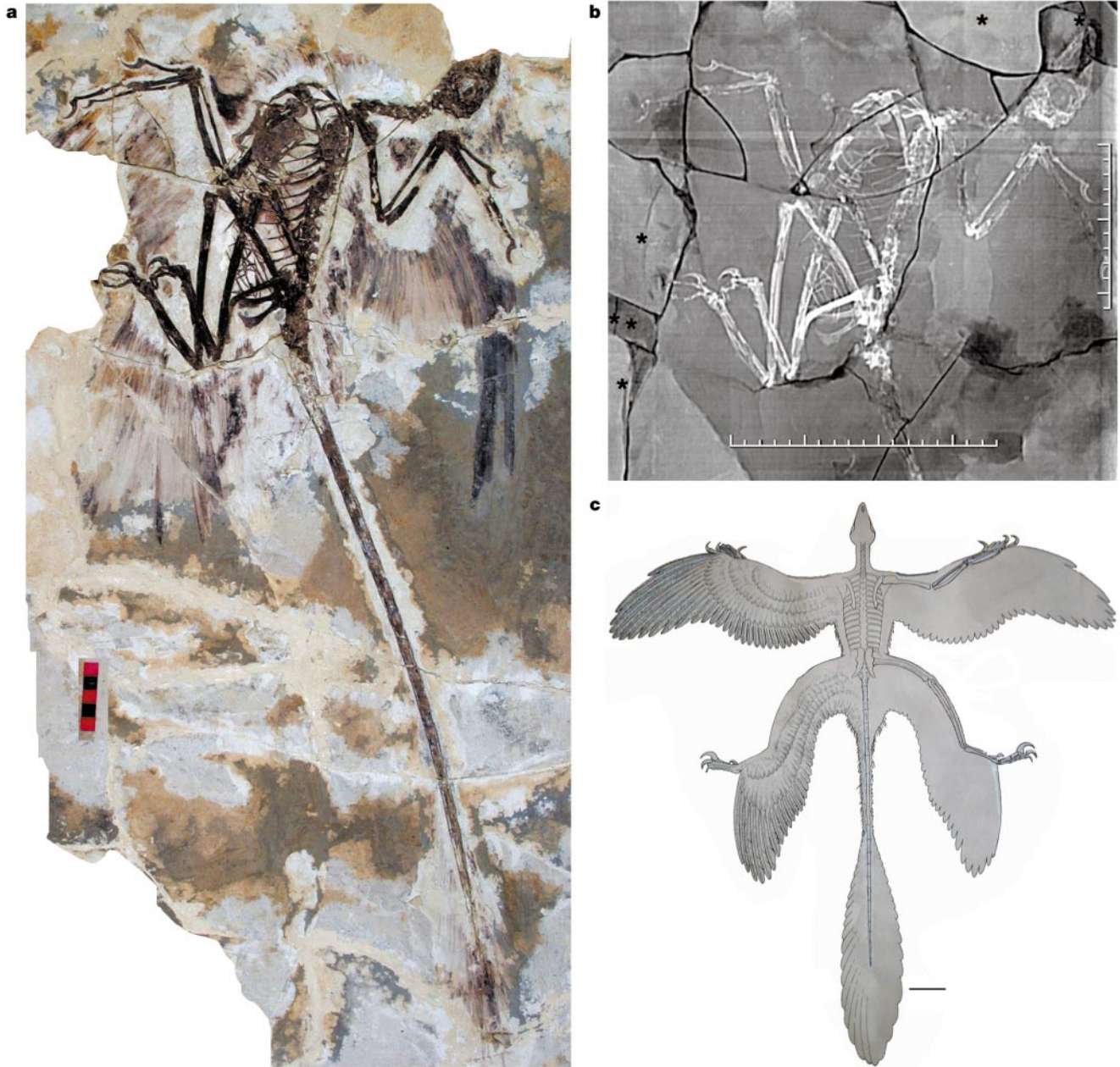


Figure 1 *Microraptor gui*. **a**, Skeleton of *Microraptor gui* (IVPP V13352). Scale bar, 5 cm. **b**, A computerized tomography (CT) image of the major part of the IVPP V13352. Scale bar, 13 cm. Scanning was performed using a CT machine (LightSpeed Qx/i) at an energy level of 140 kV and 250 mA. The images were collected at a size of 800 × 600 pixels. On the basis of comparison of adjacent fracture-face geometries, density of adjacent pieces, and continuity across fractures of bones (see ref. 45), we find a few pieces are unverified or assembled in the wrong position (marked by asterisks). For

example, one small piece containing the anterior end of the skull and a medium-sized piece near the right forelimb preserving some arm feathers are dubious. The latter is actually from the counter slab. However, the CT information suggests that most pieces lie together in their natural relationships, including pieces containing the forelimb, hindlimb and associated feather impressions. This is concordant with microscopic observations. **c**, A reconstruction of *M. gui* showing the morphology and distribution of the pennaceous feathers. Scale bar, 6 cm.

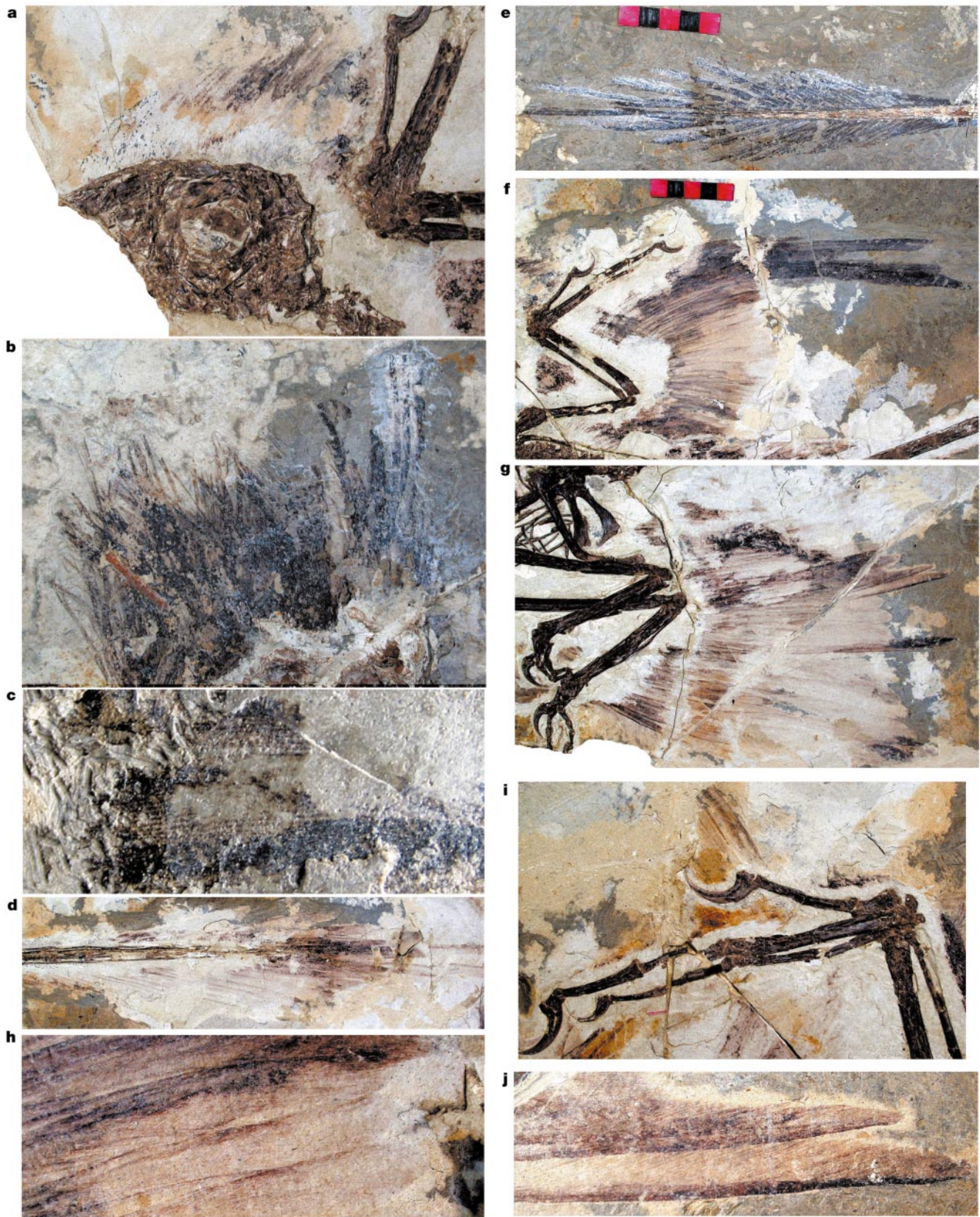


Figure 2 Feathers of IVPP V13352 and TNP00996. Feathers attached to the skull (a), the tail (d), the forelimb (f), the manual digit I (i), and the hindlimb (g) of IVPP V13352, and to the skull (b) and the tail (e) of TNP00996; close-up of the skull feathers of TNP 00996 (c), and of secondaries (h) and large pennaceous feathers on distal metatarsus (j) of IVPP

V13352. Note the pennaceous feathers attached to the digit (i) that might be a precursor to the alula. This is concordant with the fact that *M. gui* has a short manual digit I, because the alula is often associated with a reduced alular digit except in *Protopteryx*²⁴. Scale bar, 5 cm.

pubis is relatively straight in most other non-avian theropods, including *M. zhaoianus*. The other distinctive feature of *M. gui* is the bowed tibia whereas in most other theropods, it is straight. These features suggest that *M. gui* is a new species.

Integument. Information on the integument is based on the holotype (IVPP V13352) and referred specimen (V13320) of *M. gui* as well as TNP00996, IVPP V13351, IVPP V13476 and IVPP V13477 (Table 1). IVPP V13476 and IVPP V13477 were collected from Shangheshou (3 km northwest of Chaoyang City, Liaoning) and the other specimens are from Dapingfang. The integumentary remains are best preserved in IVPP V13352 and TNP00996, in which they are well preserved around the whole skeleton. The integument displays two types: plumulaceous and pennaceous feathers. The body is covered by plumulaceous feathers that are about 25–30 mm long. The feathers attached to the skull roof are up to 40 mm long in IVPP V13352 (Fig. 2a), and in TNP00996 they are proportionately even longer (Fig. 2b). Some feathers on the head display well-organized pennaceous vanes (Fig. 2c). These feathers are most probably functionally related to display, as in some modern birds such as *Pithecophaga jefferyi*. Large pennaceous feathers are attached to the distal tail, forelimb and hindlimb (Figs 1a, c and 2d–g). The remiges (wing feathers) are preserved in a pattern similar to those of modern birds (Fig. 2f). The

primaries (approximately 12 in number) are significantly longer than the secondaries (approximately 18 in number); the most distal primaries are more or less parallel to the manus, and the others are at angle to the manus, with the angle increasing from distal to proximal. The longest primaries (incompletely preserved) are 2.7 times as long as the humerus or 2.3 times as long as the femur. Some primaries on the holotype display asymmetry, with the leading vane much narrower than the trailing vane. The secondaries are longer than the humerus and more or less perpendicular to the ulna. The proximal ones have symmetrical vanes and the distal ones display weak asymmetry (Fig. 2h). The presence of a few relatively small feathers attached to the manual digit I (Fig. 2i) on the holotype is noteworthy. These display well-organized pennaceous vanes, and might be the precursor to the alula, which is associated with flight control and which is present in most birds other than *Archaeopteryx* and *Confuciusornis*^{23,24}. Coverts are present and appear to be variable in size. Some coverts can be identified as under-wing coverts. The presence of remex-like feathers along the hindlimbs is most unusual. The leg feathers are arranged in a pattern similar to the arm feathers (Fig. 2g). There are at least 14 large pennaceous feathers attached to the metatarsus; different from the primaries, they are more or less perpendicular to the metatarsus. The distal feathers have asymmetrical vanes (Fig. 2j) and the proximal feathers

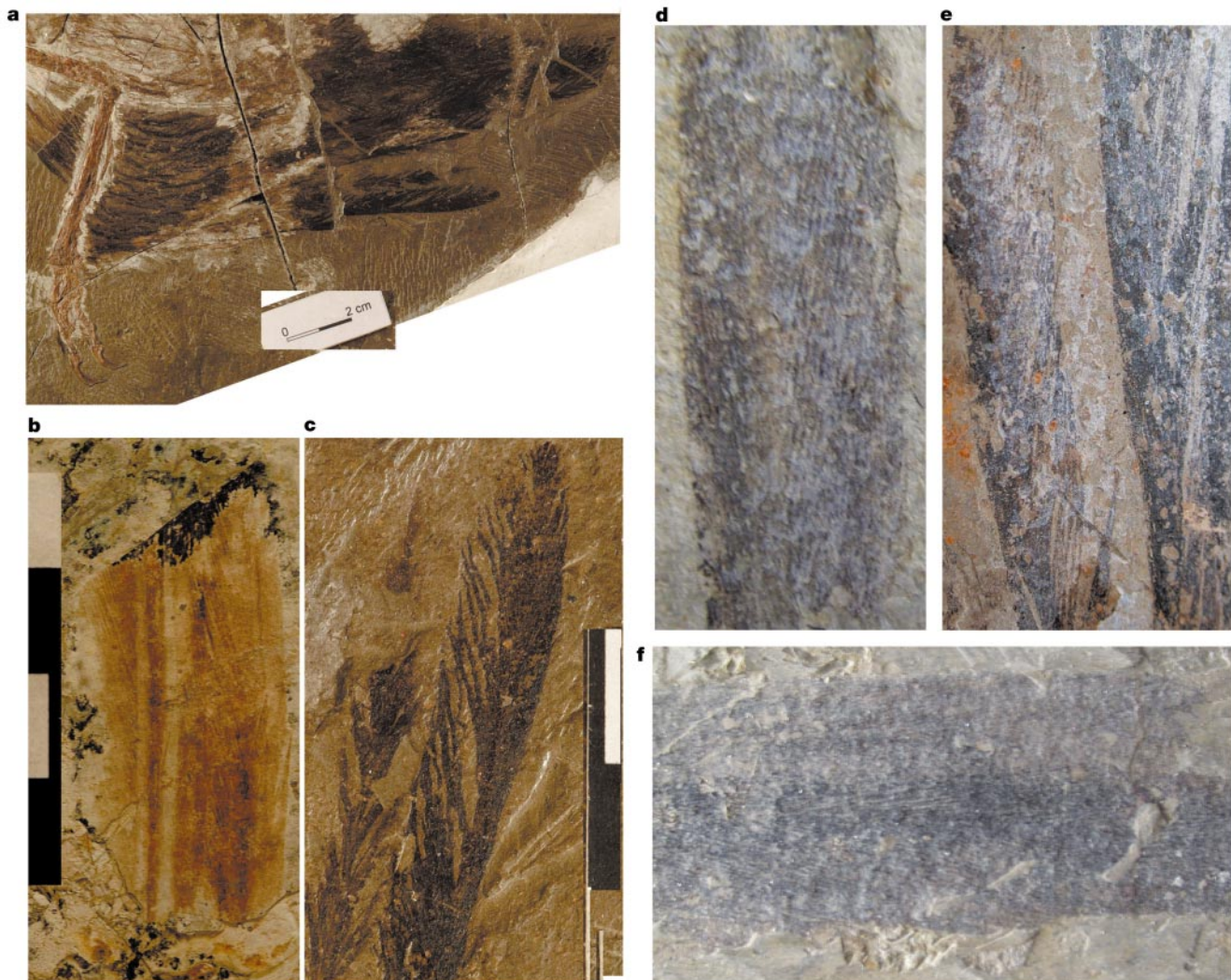


Figure 3 Feathers showing the asymmetrical vanes. Pennaceous feathers attached to the left metatarsus of IVPP V13477 (a) and right metatarsus of IVPP V13320 (b). c, Close-up of a distal pennaceous feather on the left metatarsus of IVPP V13477. d, Close-up of a

distal pennaceous feather on the left metatarsus of TNP00996. e, Close-up of some tail feathers of TNP00996. f, Close-up of some distal primaries of IVPP V13352.

are shorter in length and have symmetrical vanes. Coverts are also seen attached to the metatarsus and seem to be denser than those on the forelimb. Pennaceous feathers are also present on the tibia, and they appear to be shorter than the feathers on the metatarsus. The longest leg feathers (incompletely preserved) are more than twice femoral length and located close to the distal end of the metatarsus. The rectrices (tail feathers) begin with the 15th to 18th caudal through the end of the tail. The rectrices in basal dromaeosaurs extend less proximally (Figs 1c and 2d, e) on the tail than in *Archaeopteryx* but more proximally than in *Caudipteryx*⁶. The most distal rectrices are more than 120 mm in length on the holotype, and in TNP00996 the longest rectrices are about 105 mm relative to a 290-mm-long tail.

Discussion. Recent discoveries suggest that pennaceous feathers are present on Dromaeosauridae¹⁷, a non-avian theropod group, and our observations on the newly collected specimens provide new information that is important for understanding the transition towards birds.

The most unusual feature is the attachment of pennaceous feathers to the whole length of the metatarsus (Figs 1a, c, 2g and 3a). They are long and some have asymmetrical vanes like flight feathers (Fig. 3a–d). We exclude the possibility that these are preservation artefacts because we observed this feature in all six specimens in the present study, most of which are represented by well-articulated skeletons. Pennaceous feathers are also associated with the tibia and femur¹⁹ and they display symmetrical vanes. In general, the leg feathers are arranged in a pattern similar to wing feathers in modern birds, suggesting the presence of a hindlimb wing. Although there is no modern analogue, our observations are concordant with some early hypotheses^{25,26} that there is a tetrapteryx stage in bird evolution.

Recent work shows that basal dromaeosaurs closely resemble *Archaeopteryx* in flight apparatus^{7,8,20,27} (except for some differences in limb proportion, such as the longer arm in the latter taxon), and thus dromaeosaurs were pre-adapted for flight. The new discoveries provide further information on soft tissues and greatly improve our knowledge of these close relatives of birds. Asymmetrical pennaceous feathers are suggested to have the aerodynamic function necessary for flight²⁸. The asymmetry is present not only on the forelimb and tail feathers, but also the hindlimb feathers of basal dromaeosaurs (Fig. 3c–f). The forelimb and the leg feathers would make a perfect aerofoil together, analogous to the patagium in bats or gliding animals. These features together suggest that basal dromaeosaurids probably could glide, representing an intermediate stage between the flightless non-avian theropods and the volant avialans. Apparently some non-avian theropods evolved large and highly specialized pennaceous feathers on the leg for aerodynamic function; these features were later reduced and lost in birds, which depend completely on forewings for flight.

The metatarsus feathers are inconsistent with the suggestions that basal dromaeosaurs are cursorial animals^{1,29} because such long feathers on the feet would be a hindrance for a small cursorial animal. It is unlikely that a small dromaeosaur could run fast with such an unusual integument and this provides negative evidence for the ground-up hypothesis for the origin of avian flight^{29–31}. Some recent osteological studies suggested that non-avian theropods^{8,20,32} and basal birds^{33–36} acquired arboreal capabilities, which were later improved in more derived birds^{20,37,38}. Combined with the new information from the integument, we suggest that basal dromaeosaurs were arboreal animals, and that the ancestor of birds first learned to glide by taking advantage of gravity before flapping flight was acquired in birds^{32,39–44}.

Notes on the specimens. Of the six specimens in the present study, IVPP V13476 was collected by the Liaoxi expedition team of the IVPP in 2001, IVPP V13352, V13320, V13477 and V13351 were purchased by the IVPP during the field seasons of 2001 and 2002, and TNP00996 was purchased by Tianjin Museum of Natural

History in 2002. Some counter slabs of IVPP V13352 and V13477 are available. IVPP V13476 has been prepared at the IVPP. Although much of the preparation was done before we obtained the other specimens, some preparation of IVPP V13352 and V13477 was done at the IVPP. The preparation at the IVPP exposed some parts of the integument, including hindlimb feathers that were covered by the matrix. We observed that there are some pieces of blocks mistakenly glued to the specimens; however, we excluded all the dubious parts from the study (Fig. 1b). We carefully examined the specimens under the microscope and with high-resolution X-ray computerized tomography (CT) to test the authenticity of one of the studied specimens⁴⁵ (IVPP V13352) and can guarantee the accuracy of the information that we provide in this study. □

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