

and the Darwin rise are the sites of most Pacific hotspots over the past 120 Myr (ref. 14) and correspond to a prominent, long-wavelength geoid high¹⁸ and to a zone of low seismic velocities extending to the lower mantle¹⁹. The Superswell may thus be located over a stable, persisting zone of upwelling from the lower mantle^{7,20} which may have been acting as a barrier since at least Cretaceous times, separating two large mantle domains with different convective histories.

We discuss two interpretations of the above three observations. (1) The pollution hypothesis: the data can be interpreted in terms of the southern N-MORB being polluted by sources having a HIMU (that is, high μ , where $\mu = {}^{238}\text{U}/{}^{204}\text{Pb}$) end component affinity (high ${}^{206}\text{Pb}/{}^{204}\text{Pb}$, low ${}^{87}\text{Sr}/{}^{86}\text{Sr}$), where the northern N-MORB would be polluted by sources having an EM (enriched mantle) end component affinity (high ${}^{87}\text{Sr}/{}^{86}\text{Sr}$). This view is supported by the observation that the 25°S boundary coincides with the SOPITA (Fig. 1), which has its northern part dominated by EM (Samoa, Societies and Marquesas) whereas its southern part is dominated by HIMU (Cook-Austral and Foundation chains)^{4,21,22}. An alternative view, based on the observation that the relative slopes are indistinguishable in Pb–Pb plots²³, would be that the northern province has experienced more pollution by EM sources on a time-integrated basis than the southern province.

(2) Melting hypothesis: according to the “plum-pudding” model²⁴, the MORB mantle source is composed of small-scale, uniformly distributed mantle heterogeneities which are expected to have high ${}^{87}\text{Sr}/{}^{86}\text{Sr}$ (relative to ${}^{143}\text{Nd}/{}^{144}\text{Nd}$ or ${}^{206}\text{Pb}/{}^{204}\text{Pb}$). These heterogeneities would be preferentially sampled^{25,26} by the low extents of melting which may prevail beneath the axis of the deeper, northern province. The higher extents of melting expected in the shallower, southern province would average the properties of mantle components, resulting in lower (${}^{87}\text{Sr}/{}^{86}\text{Sr}$)/(${}^{143}\text{Nd}/{}^{144}\text{Nd}$) and (${}^{87}\text{Sr}/{}^{86}\text{Sr}$)/(${}^{206}\text{Pb}/{}^{204}\text{Pb}$). However, the differences of mantle temperatures and melt parameters between the two provinces are not resolved by a petrological model²⁷ based on Na₈ data (Na normalized to 8% MgO).

These two hypotheses may be reconciled by considering the link between the chemical characteristics of the mantle and its physical properties (thermal state) as expressed at the surface by the bathymetry of the ridge. To summarize, the Pacific mantle displays at the same time large-scale variation of composition and temperature.

The rather sharp bathymetric²⁸ and geochemical²⁹ transition at 25°S indicates a superficial origin, whereas the cluster of hotspots constituting the Pacific Superswell suggests the existence of a deep-mantle process. This apparent paradox requires some interactions between the deeper and the shallower layers of the mantle. We propose that the lower-mantle upwelling suspected to be present near 25°S could have contributed to the isolation of two large-scale, deep-mantle domains with their own convective histories, producing slight differences in their chemical properties, thus influencing differently the thermal structure of the overlying MORB mantle source layer. □

Received 22 July 1998; accepted 8 March 1999.

- Dupré, B. & Allègre, C. J. Pb–Sr isotope variation in Indian Ocean basalts and mixing phenomena. *Nature* **303**, 142–143 (1983).
- White, W. M., Hofmann, A. W. & Puchelt, H. Isotope geochemistry of Pacific mid-ocean ridge basalt. *J. Geophys. Res.* **92**, 4881–4893 (1987).
- Cohen, R. S. & O’Nions, R. K. The lead, neodymium and strontium isotopic structure of ocean ridge basalts. *J. Petrol.* **23**, 299–324 (1982).
- Ferguson, E. M. & Klein, E. M. Fresh basalts from the Pacific Antarctic ridge extend the Pacific geochemical province. *Nature* **366**, 330–333 (1993).
- Klein, E. M., Langmuir, C. H., Zindler, A., Staudigel, H. & Hamelin, B. Isotope evidence of a mantle convection boundary at the Australian–Antarctic discordance. *Nature* **333**, 623–629 (1988).
- Davies, G. B. & Pribac, E. in *The Mesozoic Pacific: Geology, Tectonics and Volcanism* (eds Pringle, M. S. et al.) 39–52 (Geophys. Monogr. 77, Am. Geophys. Un., Washington DC, 1995).
- Castillo, P. The Dupal anomaly as a trace of the upwelling lower mantle. *Nature* **336**, 667–670 (1988).
- Castillo, P. R., Natland, J., Niu, Y. & Lonsdale, P. F. Sr, Nd and Pb isotopic variation along the Pacific–Antarctic rise crest, 53–57 degrees S: Implications for the composition and dynamics of the South Pacific upper mantle. *Earth Planet. Sci. Lett.* **154**, 109–125 (1998).
- Macdougall, J. D. & Lugmair, G. W. Extreme isotopic homogeneity among basalts from the southern

- East Pacific Rise: mantle or mixing effect? *Nature* **313**, 209–211 (1985).
- Macdougall, J. D. & Lugmair, G. W. Sr and Nd isotopes in basalts from the East Pacific Rise: significance for mantle heterogeneity. *Earth Planet. Sci. Lett.* **77**, 273–284 (1986).
- Bach, W. et al. Unusually large Nb–Ta depletions in North Chile ridge basalts at 36 degrees 50’ to 38 degrees 56’ S: Major element, trace element, and isotopic data. *Earth Planet. Sci. Lett.* **142**, 223–240 (1996).
- Vlastelic, I. et al. Geochemistry of the Hollister Ridge: Relation with the Louisville hotspot and the Pacific–Antarctic Ridge. *Earth Planet. Sci. Lett.* **160**, 777–793 (1998).
- Klein, E. M. & Karsten, J. L. Ocean-ridge basalts with convergent-margin geochemical affinities from the Chile Ridge. *Nature* **374**, 52–57 (1995).
- Staudigel, H. et al. The longevity of the South Pacific isotopic and thermal anomaly. *Earth Planet. Sci. Lett.* **102**, 24–44 (1991).
- McNutt, M. K. & Fisher, K. M. in *Seamounts, Islands, and Atolls* (eds Keating, B. H., Fryer, P., Batiza, R. & Boehlert, G. W.) 25–34 (Geophys. Monogr. 43, Am. Geophys. Un., Washington DC, 1987).
- McNutt, M. K. & Judge, A. V. The superswell and mantle dynamics beneath the South Pacific. *Science* **248**, 969–975 (1990).
- McNutt, M. K., Winter, E. L., Sager, W. W., Natland, J. H. & Ito, J. The Darwin rise: a Cretaceous superswell. *Geophys. Res. Lett.* **17**, 1101–1104 (1990).
- Hager, B. H., Clayton, R. W., Richards, M. A., Comer, R. P. & Dziewonski, A. M. Lower mantle heterogeneity, dynamic topography, and the geoid. *Nature* **313**, 541–545 (1985).
- Dziewonski, A. & Woodhouse, J. Global images of the Earth’s interior. *Science* **236**, 37–48 (1987).
- Tatsumi, Y., Shinjoe, H., Ishizuka, H., Sager, W. W. & Klaus, A. Geochemical evidence for a mid-Cretaceous superplume. *Geology* **26**, 151–154 (1998).
- Chauvel, C., Hofmann, A. W. & Vidal, P. HIMU EM—The French Polynesian connection. *Earth Planet. Sci. Lett.* **110**, 99–119 (1992).
- Hémond, C. & Devey, C. W. The Foundation seamount chain, southeastern Pacific: first isotopic evidence of a newly discovered hotspot track. *J. Conf. Abs.* **1**, 255 (1996).
- Hanan, B. B. & Graham, D. W. Lead and helium isotope evidence from oceanic basalts for a common deep source of mantle plumes. *Science* **272**, 991–995 (1996).
- Zindler, A., Staudigel, H. & Batiza, R. Isotope and trace element geochemistry of young Pacific seamounts: Implications for the scale of upper mantle heterogeneity. *Earth Planet. Sci. Lett.* **70**, 175–195 (1984).
- Hanson, G. N. Geochemical evolution of the suboceanic mantle. *J. Geol. Soc. Lond.* **134**, 235–253 (1977).
- Sleep, N. Tapping of magmas from ubiquitous mantle heterogeneities: an alternative to mantle plume? *J. Geophys. Res.* **89**, 10029–10041 (1984).
- Klein, E. M. & Langmuir, C. H. Global correlations of ocean ridge basalt chemistry with axial depth and crustal thickness. *J. Geophys. Res.* **92**, 8089–8115 (1987).
- Smith, W. H. F. & Sandwell, D. T. Global sea floor topography from satellite altimetry and ship depth soundings. *Science* **277**, 1956–1962 (1997).
- Bach, W., Hegner, E., Erzinger, J. & Satir, M. Chemical and isotopic variations along the superfast spreading East Pacific Rise from 6 degrees S to 30 degrees S. *Contrib. Mineral. Petrol.* **116**, 365–380 (1994).
- Géll, L. et al. Evolution of the Pacific–Antarctic Ridge south of the U d’ontsev fracture zone. *Science* **278**, 1281–1284 (1997).
- Lonsdale, P. Geomorphology and structural segmentation of the crest of the Southern (Pacific–Antarctic) East Pacific Rise. *J. Geophys. Res.* **99**, 4683–4702 (1994).

Supplementary information is available on Nature’s World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

Acknowledgements. We thank C. Bollinger, and M. Bohn for their help in the laboratory. Captain G. Tredunit and the crew of RV *L’Atalante* for their efforts during the PACANTARCTIC cruise, and P. R. Castillo and B. Hanan for comments. This work was supported by Institut National des Sciences de l’Univers (INSU) and IFREMER.

Correspondence and requests for materials should be addressed to L.D. (e-mail: Laure.Dosso@ifremer.fr).

A therizinosauroid dinosaur with integumentary structures from China

Xing Xu*, Zhi-lu Tang* & Xiao-lin Wang*†

*Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, PO Box 643, Beijing 100044, People’s Republic of China

†Natural History Museum, Changchun University of Science and Technology, No. 6 Ximingzhu Street, Changchun, 130026, People’s Republic of China

Therizinosauroida (‘segnosaurs’) are little-known group of Asian dinosaurs with an unusual combination of features that, until recently, obscured their evolutionary relationships. Suggested affinities include Ornithischia¹, Sauropodomorpha^{2,3}, Theropoda^{4–11} and Saurischia *sedis mutabilis*¹². Here we describe a new therizinosauroid from the Yixian Formation (Early Cretaceous, Liaoning, China)¹³. This new taxon provides fresh evidence that therizinosauroids are nested within the coelurosaurian theropods^{8–11}. Our analysis suggests that several specialized therizinosauroid characters, such as the Sauropodomorpha-like tetradactyl pes^{1,2}, evolved independently within this group. Most interestingly, this new dinosaur has integumentary filaments as in

Sinosauropteryx^{14,15}. This indicates that such feather-like structures may have a broad distribution among non-avian theropods, and supports the hypothesis that the filamentous integumentary structures may be homologous to the feathers of birds^{14,15}.

Dinosauria Owen 1842

Theropoda Marsh 1881

Coelurosauria *sensu* Gauthier 1986

Therizinosauroida Russell and Dong 1993

Beipiaosaurus inexpectus gen. et sp. nov.

Etymology. Beipiao: the city near the locality where the specimen was found; saurus: lizard; inexpectus: referring to the surprising features in this animal.

Holotype. IVPP V11559 (Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China; see Fig. 1).

Locality and horizon. Sihetun locality near Beipiao, Liaoning, China. The lower part of the Yixian Formation, probably from the Lower Cretaceous based on latest radiometric evidence¹³.

Diagnosis. *Beipiaosaurus inexpectus* differs from other therizinosauroids in having shorter and more bulbous tooth crowns, a larger skull, a tridactyl pes with a splint-like proximal first metatarsal, a shallow anterior iliac process, a long manus (10% longer than a femur), a long tibia (275 mm > 265 mm of the femur), an elongated lateral articular surface on the palmar side of manual phalanx I-1, and proximally compressed metatarsals III and IV.

Beipiaosaurus is the largest known theropod from the Yixian Formation, with an estimated length of 2.2 m. It has a relatively large skull compared to other therizinosauroids (preserved dentary is 65% of femur length). The anterior end of its dentary is downturned. The dentary has a lateral shelf, similar to other therizinosauroids and ornithischians¹. *Beipiaosaurus* has a large number of teeth (more than 37, inferred from the preserved alveoli in the broken dentary). They resemble those of *Protarchaeopteryx*¹⁶, but have larger serrations (3 serrations per mm) as in other therizinosauroids and troodontids⁹. Replacement teeth developed in oval resorption pits next to the roots of erupted teeth (Fig. 2a), as in *Archaeopteryx*¹⁷. Dorsally pointed, triangular interdental plates are present.

The cervical vertebrae bear low, anteroposteriorly short neural spines. Lateral depressions are present on the lateral sides of the centra of the fused posterior dorsals.

The coracoid is subrectangular, as in some maniraptoran theropods, with a pronounced coracoid tubercle. Exquisite impressions show that the furcula is a widely arched bone, oblate-shaped in cross section, without a hypocleidium. Compared to the short and stout hindlimb, the forelimbs are relatively long. The elongate hand is longer than the foot, as in dromaeosaurids and primitive *Avialae*¹⁸. As in other therizinosauroids, the humerus has a pointed internal tuberosity on its proximal end, and anteriorly positioned radial and ulnar condyles on its distal end. A depression on the proximal surface of the humerus separates the head and internal tuberosity, as in other therizinosauroids and *Mononykus*¹⁹. Five carpals are preserved. The largest distal carpal, the semilunate (Fig. 2c, d), is smaller than but otherwise identical to that of *Deinonychus*²⁰. It primarily contacts metacarpal II but also touches metacarpal I (Fig. 2d), unlike the condition in *Alxasaurus*, in which the largest carpal is the distal carpal I⁹. Distal carpal I is large and oval (Fig. 2c). The proximal carpals are represented by a V-shaped radiale in close contact with the radius, and a small rounded carpal between the distal ends of the radius and ulna (Fig. 2c, d). The manus is slender and elongate, proportionally similar to that of *Deinonychus*²⁰. Metacarpal I has a pronounced distal flange, as in *Deinonychus*. The proximal parts of metacarpals I and II are closely appressed. Metacarpal III is slender and slightly bowed. The combined lengths of phalanges III-1 and III-2 are equal to the length of phalanx III-3, as in advanced theropods². There are well developed ligament pits on the lateral sides of the distal ends of the phalanges. The manual unguals are laterally compressed and strongly curved. As in other

therizinosauroids⁸, their proximal ends are deep but taper to needle-sharp points. The second manual claw is slightly longer than the first, resembling those of *Archaeopteryx* and *Protarchaeopteryx*²¹.

The ilium is shaped like a parallelogram, similar to those of dromaeosaurids and basal birds, but unlike the sauropod-like ilia of derived therizinosauroids^{1,22}. The posterodorsal margin of the ilium curves ventrally in lateral view. The anterior and posterior processes are almost the same length. The posteroventral margin of the ilium is deflected laterally at a right angle to the vertical ramus, and has a shallow brevis fossa similar to those of other coelurosaurians²³. The partial pubic peduncle of the ilium is longer than the ischiadic peduncle, similar to those of therizinosauroids, dromaeosaurids and *Archaeopteryx*²³. Both the pubic and the ischial shafts are more rounded than flattened, unlike those of *Alxasaurus* and *Segnosaurus*. As in some theropods, the pubic apron is compressed and positioned more distally. The femur of *Beipiaosaurus* has a wing-like lesser trochanter, a cleft between the greater trochanter and the lesser trochanter, and a crest-like fourth trochanter. The tibia has a fibular crest, a feature of theropods². The fibula is very slender compared to the tibia, especially the distal half. As in *Alxasaurus*⁸ and the *Avialae*²⁴, the medial surface of the fibula is flat, lacking the medial fossa of some theropods. As in other therizinosauroids, the astragalus has a tall ascending process and reduced condyles that only partly cover the distal end of the tibia. The calcaneum is sub-oval and disk-shaped. The metatarsus is 39% of the length of the tibia, larger than in known therizinosauroids but less than in other theropods (>45%)⁸. The proximal end of metatarsal I is flattened and tapered and, as in most maniraptorans, does not contact the tarsus (Fig. 2e, f). The proximal ends of both metatarsals III and IV are compressed, especially on the medial side. Metatarsal V is slender and strap-like, being only half the length of the other metatarsals. One pedal ungual is preserved, and is shorter than any manual unguals.

Large patches of integumentary structures were found in close association with the ulna, radius, femur and tibia, as well as with pectoral elements. The filamentous structures are best preserved near the ulna, almost perpendicular to the bone (Fig. 3). They are similar to the integumentary structures of *Sinosauropteryx*¹⁵ in their parallel arrangement. Unlike those of *Sinosauropteryx*, the integumentary structures of *Beipiaosaurus* contact the ulna. They are densest close to the bone. Most of the integumentary filaments are about 50 mm long, although the longest is up to 70 mm. Some filaments have shallow and faint median grooves, possibly indicating hollow cores that had collapsed, and have indications of branching distal ends as in *Sinosauropteryx*¹⁵. As in *Sinosauropteryx*¹⁵ and birds from the same locality, it is difficult to isolate a single filament and thus difficult to describe the branching pattern of the integumentary filaments.

Therizinosauroida has many perplexing features for a theropod, such as a very small head, a sauropod-like ilium and a short and broad tetradactyl pes with rudimentary metatarsal V^{1,2,12,22}. Until now, no cladogram has been proposed for the relationships and morphological evolution of therizinosauroids. We ran a phylogenetic analysis with an 84-character dataset (see Supplementary Information for the character list and matrix). We left out the unnamed 'segnosaur' from the Early Jurassic Lower Lufeng Formation²⁵ as it is too incomplete. Using PAUP (3.1.1. Exhaustive search, Deltran optimization; Swofford, 1993), we obtained a single most parsimonious tree (tree length, 133; consistency index, 0.707; retention index, 0.645; rescaled consistency index, 0.456). Our analysis (Fig. 4) places *Beipiaosaurus* as a basal taxon within Therizinosauroida. *Beipiaosaurus* has a relatively large skull (1.0) among therizinosauroids, a tridactyl pes (79.0) and a fibular crest on the tibia, all of which are primitive theropod features. The pelvic elements are also very similar to those of other coelurosaurians. These characteristics support the hypothesis that therizinosauroids (including *Beipiaosaurus*) are nested within the coelurosaurian

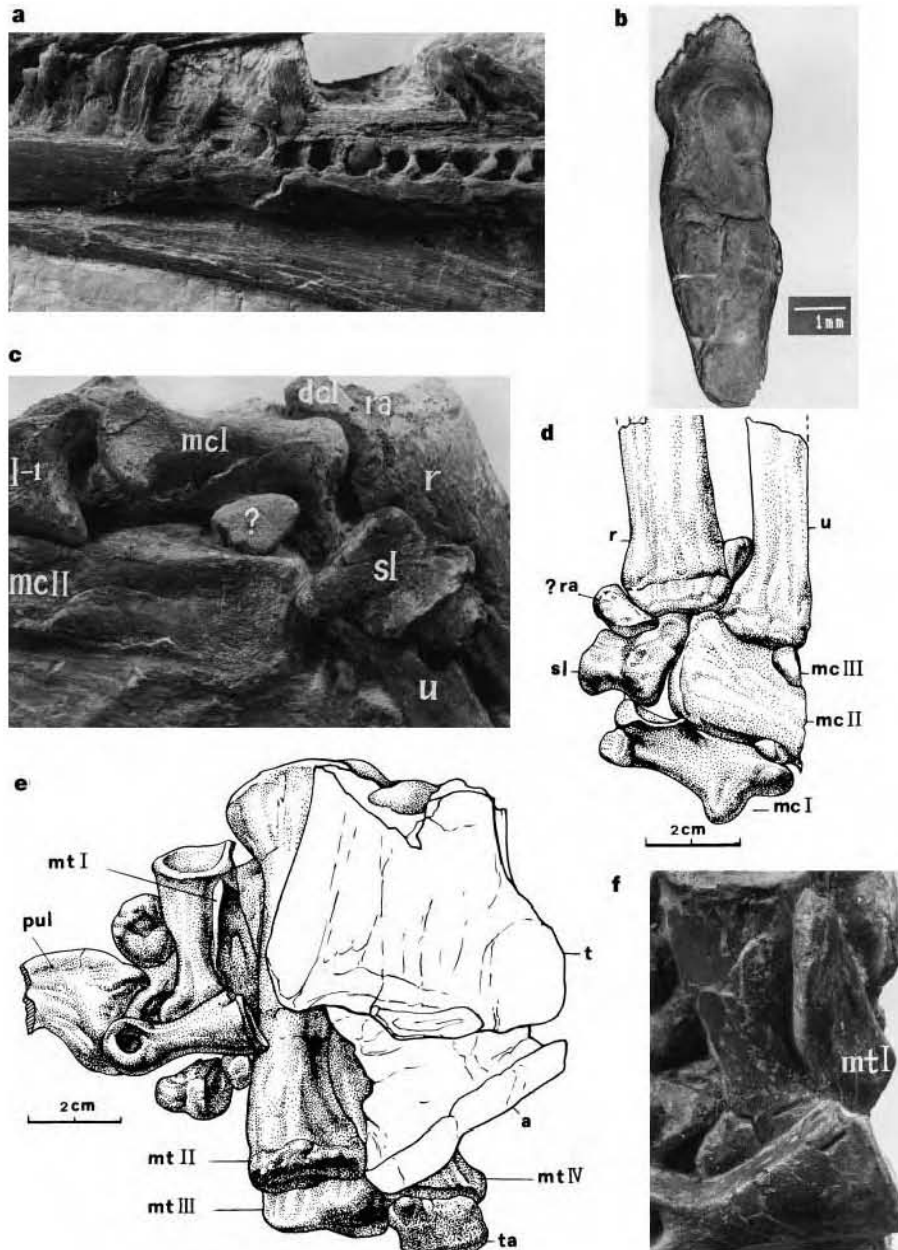


Figure 2 *Beipiaosaurus inexpectus*. **a**, Nine right dentary teeth in medial view. Note the resorption pits and replacement teeth. **b**, A dentary tooth in lateral view. **c**, Close-up of the left semilunate carpal of V11559. **d**, Drawing of part of the right manus of V11559. Note the shape and position of the semilunate, which is very similar to that of birds¹⁷. **e**, Drawing of the partially preserved right pes of V11559.

f, Close-up of the first metatarsal of V11559. Note the proximally pinched theropod first metatarsal. The theropod first metatarsal is absent in other therizinosaurs, which has been argued as being strong evidence against the theropod affinities of therizinosaurs¹. Additional abbreviations: mc I-III, metacarpals I-III; mt I-IV, metatarsals I-IV; pul, pedal ungual; r, radius; ra, radiale; ta, tarsal; u, ulna.

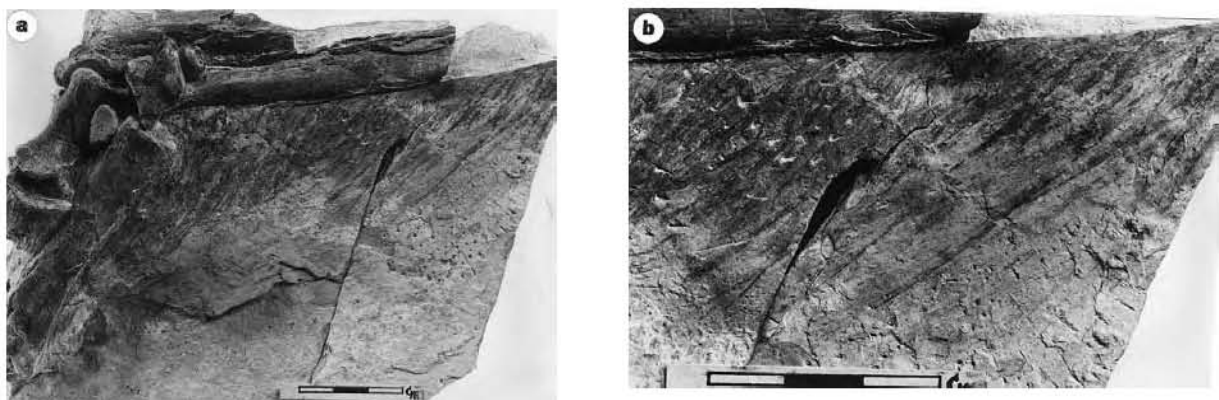


Figure 3 *Beipiaosaurus inexpectus*. **a**, Partially preserved forelimb with unusual integumentary impression. **b**, Close-up of the integumentary impression.

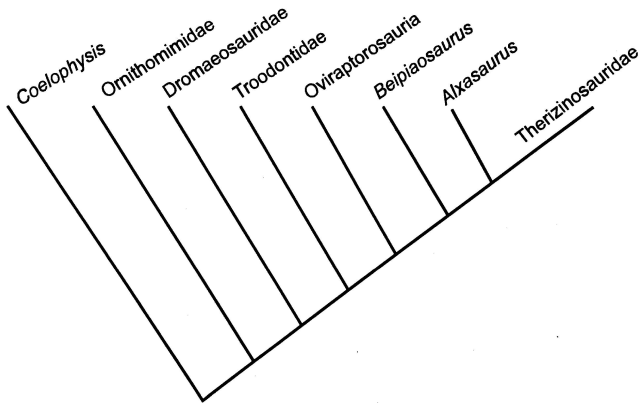


Figure 4 Phylogenetic relationships of *Beipiaosaurus inexpectus*. *Beipiaosaurus* and other therizinosaurids share 18 synapomorphies, including the following unique characters: a prominent dorsolateral shelf on the dentary (21.1), teeth that increase in size anteriorly (25.1), tooth crowns with sub-circular basal cross-sections that lack mediolateral compression (27.1), anteroposteriorly narrow and dorsoventrally deep pubic peduncle of ilium (46.1 and 47.1), very deep proximal end of manual unguals (70.1), short metatarsus (78.1) and reduced main body of astragalus (82.1). It is less derived than other therizinosaurids because it lacks 13 characters of Therizinosaurioidea (1.1, 36.1, 38.0, 43.0, 48.1, 49.1, 51.1, 52.1, 58.1, 60.0, 66.0, 77.1, 79.1), including the following unusual characters: a very small head (1.1), the long and deep preacetabular portion of ilium (48.1 and 49.1) and absence of the theropod first metatarsal (79.1).

theropods^{8–11}. Given this phylogeny (Fig. 4), some derived characters of therizinosaurids other than *Beipiaosaurus* are most parsimoniously interpreted as having evolved convergently with some other dinosaur groups, sauropodomorphs in particular. Thus, therizinosaurids re-evolved a robust first digit in which the proximal end of metatarsal I articulates with the tarsals (79.1).

Feathers are complex structures. Their abrupt appearance in the bird fossil record has been difficult to explain, mainly because no intermediate structures are preserved in the related theropod taxa. The integumentary filaments of *Sinosauropteryx* have been considered to be 'proto-feathers' by some, but this idea has been rejected by others²⁶. Such structures have not been preserved with any other theropods²⁶ until the discovery of *Beipiaosaurus*. The filamentous structures in *Beipiaosaurus* are similar to, but longer than, those of the compsognathid *Sinosauropteryx*. They are perpendicular to the limb bones, and are unlikely to be muscle fibres or frayed collagen²⁷. Their presence in both therizinosaurids and compsognathids indicates that there may be a broader distribution of similar structures in theropod dinosaurs. This supports the idea that these simple integumentary filaments may represent an intermediate evolutionary stage to the more complex feathers of *Protarchaeopteryx*, *Caudipteryx*¹⁶ and more derived Avialae. The absence of such structures in most theropod fossils is probably attributable to the lack of such ideal preservation as is found in the Yixian Formation. This again indicates that feathers preceded flight¹⁶, because both therizinosaurids and compsognathids apparently could not fly and did not descend from flying animals. □

Received 4 November 1998; accepted 31 March 1999.

1. Paul, G. S. The segnosaurian dinosaurs: relics of the prosauropod-ornithischian transition. *J. Vert. Paleontol.* **4**, 507–515 (1984).
2. Gauthier, J. A. Saurischian monophyly and the origin of birds. *Mem. Calif. Acad. Sci.* **8**, 1–55 (1986).
3. Sereno, P. C. Prosauropod monophyly and basal sauropodomorph phylogeny. *J. Vert. Paleontol.* (suppl.) **9**, 38A (1989).
4. Perle, A. Segnosauridae—a new family of theropods from the Late Cretaceous of Mongolia. *Trans. Joint Soviet–Mongolian Palaeontological Expedition* **8**, 45–55 (1979).
5. Perle, A. A new segnosaurid from the Upper Cretaceous of Mongolia. *Trans. Joint Soviet–Mongolian Palaeontological Expedition* **15**, 28–39 (1981).
6. Barsbold, R. & Perle, A. Segnosauria, a new infraorder of carnivorous dinosaurs. *Acta Palaeontol. Pol.* **25**(2), 187–195 (1980).
7. Barsbold, R. Carnivorous dinosaurs from the Cretaceous of Mongolia. *Trans. Joint Soviet–Mongolian Palaeontological Expedition* **19**, 1–116 (1983).

8. Russell, D. A. & Dong, Z. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, China. *Can. J. Earth Sci.* **30**, 2107–2127 (1993).
9. Clark, J. M., Perle, A. & Norell, M. A. The skull of *Ericosaurus andrewsi*, a Late Cretaceous "Segnosaur" (Theropod: Therizinosauridae) from Mongolia. *Am. Mus. Novit.* **3115**, 1–39 (1994).
10. Sues, H.-D. On *Chirostenotes*, a Late Cretaceous Oviraptorosaur (Dinosauria: Theropod) from Western North America. *J. Vert. Paleontol.* **17**, 498–716 (1997).
11. Makovicky, P. & Sues, H.-D. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *Am. Mus. Novit.* **3240**, 1–27 (1998).
12. Barsbold, R. & Maryanska, T. in *The Dinosauria* (eds Weishampel, D. B., Dodson, P. & Osmolska, H.) 408–415 (Univ. California Press, Berkeley, 1990).
13. Swisher, C. C., Wang, Y.-q., Wang, X.-l., Xu, X. & Wang, Y. ⁴⁰Ar/³⁹Ar dating of the lower Yixian Fm., Liaoning Province, northeastern China. *Chinese Sci. Bull.* (suppl.) **43**, 125 (1998).
14. Ji, Q. & Ji, S. A. On discovery of the earliest bird fossil in China and the origin of birds. *Chinese Geol.* **233**, 30–33 (1996).
15. Chen, P.-j., Dong, Z.-m. & Zhen, S.-A. An exceptionally well preserved theropod dinosaur from the Yixian Formation of China. *Nature* **391**, 147–152 (1998).
16. Ji, Q., Currie, P. J., Norell, M. A. & Ji, S.-A. Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761 (1998).
17. Martin, L. D. in *Origins of Higher Groups of Tetrapods* (eds Schultz, H.-P. & Treube, L.) 485–540 (Cornell Univ. Press, Ithaca, N. Y., 1991).
18. Bellairs, A. D'A. & Jenkin, C. R. in *Biology and Comparative Physiology of Birds* Vol. 9 (ed. Marshall, A.) 241–300 (Academic, New York, 1960).
19. Perle, A., Chiappe, L. M., Barsbold, R., Clark, J. M. & Norell, M. A. Skeletal morphology of *Mononykus olecranus* (Theropod, Avialae) from the Late Cretaceous of Mongolia. *Am. Mus. Novit.* **3105**, 1–29 (1994).
20. Ostrom, J. H. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist., Yale Univ.* **30**, 1–165 (1969).
21. Ji, Q. & Ji, S. A. Protarchaeopterygid bird (*Protarchaeopteryx* gen. nov.)-fossil remains of archaeropterygids from China. *Chinese Geol.* **238**, 38–41 (1997).
22. Russell, D. A. in *Encyclopedia of Dinosaurs* (eds Currie, P. J. & Padian, K.) 729–730 (Academic, San Diego, 1997).
23. Norell, M. & Makovicky, P. J. Important features of the *Dromaeosaur* skeleton: information from a new specimen. *Am. Mus. Novit.* **3215**, 1–28 (1997).
24. Chiappe, L., Norell, M. A. & Clark, J. Phylogenetic position of *Mononykus* (Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. *Mem. Queensland Mus.* **39**, 557–582 (1996).
25. Zhao, X. & Xu, X. The oldest coelurosaurian. *Nature* **394**, 234–235 (1998).
26. Unwin, D. M. Feathers, filaments and theropod dinosaurs. *Nature* **391**, 119–120 (1998).
27. Gibbons, A. Plucking the feathered dinosaur. *Science* **278**, 1229 (1997).

Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

Acknowledgements. We thank J. Clark for advice and reviewing the manuscript; Z.-X. Luo for improving the organization and language of the manuscript as well as the use of PAUP 3.11; Z.-H. Zhou and O. Rauhut for discussions; P. Currie, M. Norell, P. Sereno, X.-C. Wu and H. Osmolska for reviews and comments; and the Liaoxi expedition members of the IVPP. Photographs were taken by J. Zhang, electronic photography by L. Oyang, and line drawings are by R.-S. Li, Y.-T. Li, H.-J. Wang and J.-Z. Ding prepared the specimen. This study was supported by research grants from the Chinese Academy of Sciences and the National Natural Science Foundation of China.

Correspondence and requests for materials should be addressed to X.X. (e-mail: xxu@sun.midwest.com.cn).

Complex dynamics and phase synchronization in spatially extended ecological systems

Bernd Blasius, Amit Huppert & Lewi Stone

The Porter Super-Center for Ecological and Environmental Studies & Department of Zoology, Tel Aviv University, Ramat Aviv, Tel Aviv 69978, Israel

Population cycles that persist in time and are synchronized over space pervade ecological systems, but their underlying causes remain a long-standing enigma^{1–11}. Here we examine the synchronization of complex population oscillations in networks of model communities and in natural systems, where phenomena such as unusual '4- and 10-year cycle' of wildlife are often found. In the proposed spatial model, each local patch sustains a three-level trophic system composed of interacting predators, consumers and vegetation. Populations oscillate regularly and periodically in phase, but with irregular and chaotic peaks together in abundance—twin realistic features that are not found in standard ecological models. In a spatial lattice of patches, only small amounts of local migration are required to induce broad-scale 'phase synchronization'^{12,13}, with all populations in the lattice phase-locking to the same collective rhythm. Peak population abundances, however, remain chaotic and largely uncorrelated. Although synchronization is often perceived as being detrimental

Four-winged dinosaurs from China

Xing Xu*, Zhonghe Zhou*, Xiaolin Wang*, Xuewen Kuang†, Fucheng Zhang* & Xiangke Du‡

* Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, China

† Tianjin Museum of Natural History, Tianjin 300074, China

‡ Radiological Department, People's Hospital, Beijing University, Beijing 100044, China

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}.

Microaptor 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 *Microaptor* 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

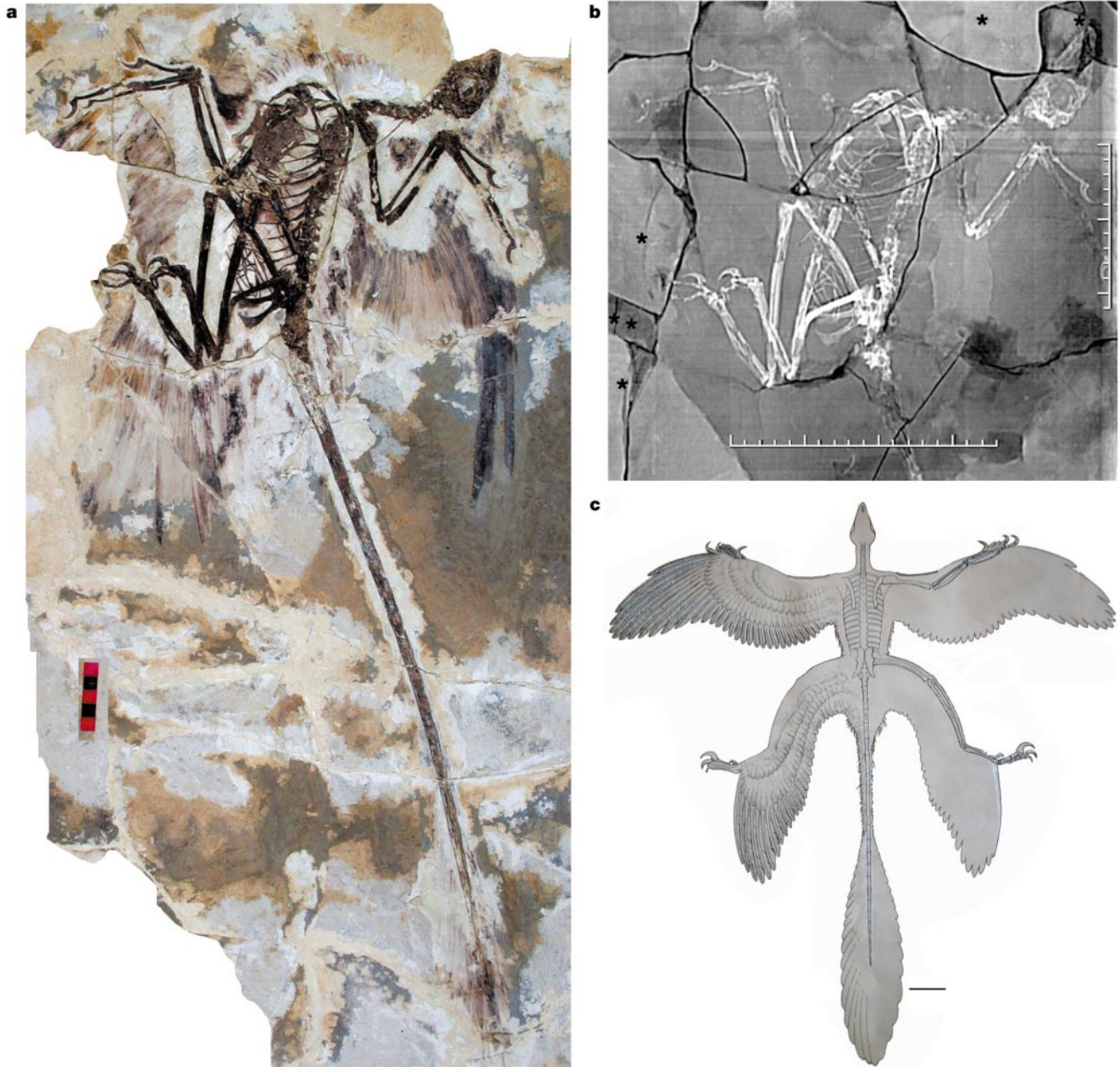


Figure 1 *Microaptor gui*. **a**, Skeleton of *Microaptor gui* (IVPP V13352). Scale bar, 5 cm. **b**, A computerized tomography (CT) image of the major part of the IVPP V13352. Scale bar, 13 cm. Scanning was performed using a CT machine (LightSpeed Qx/i) at an energy level of 140 kV and 250 mA. The images 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.

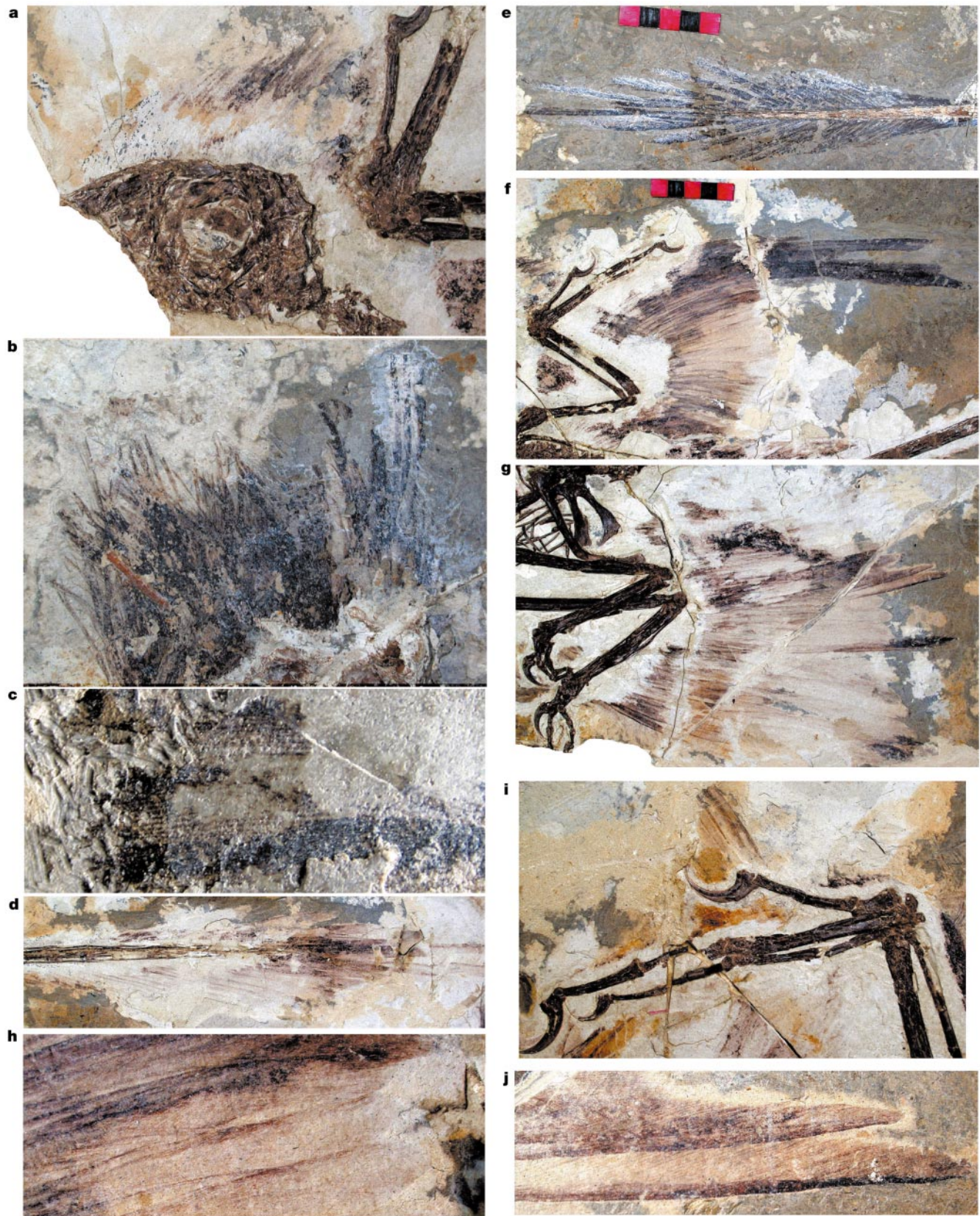


Figure 2 Feathers of IVPP V13352 and TNP00996. Feathers attached to the skull (a), the tail (d), the forelimb (f), the manual digit I (i), and the hindlimb (g) of IVPP V13352, and to the skull (b) and the tail (e) of TNP00996; close-up of the skull feathers of TNP 00996 (c), and of secondaries (h) and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

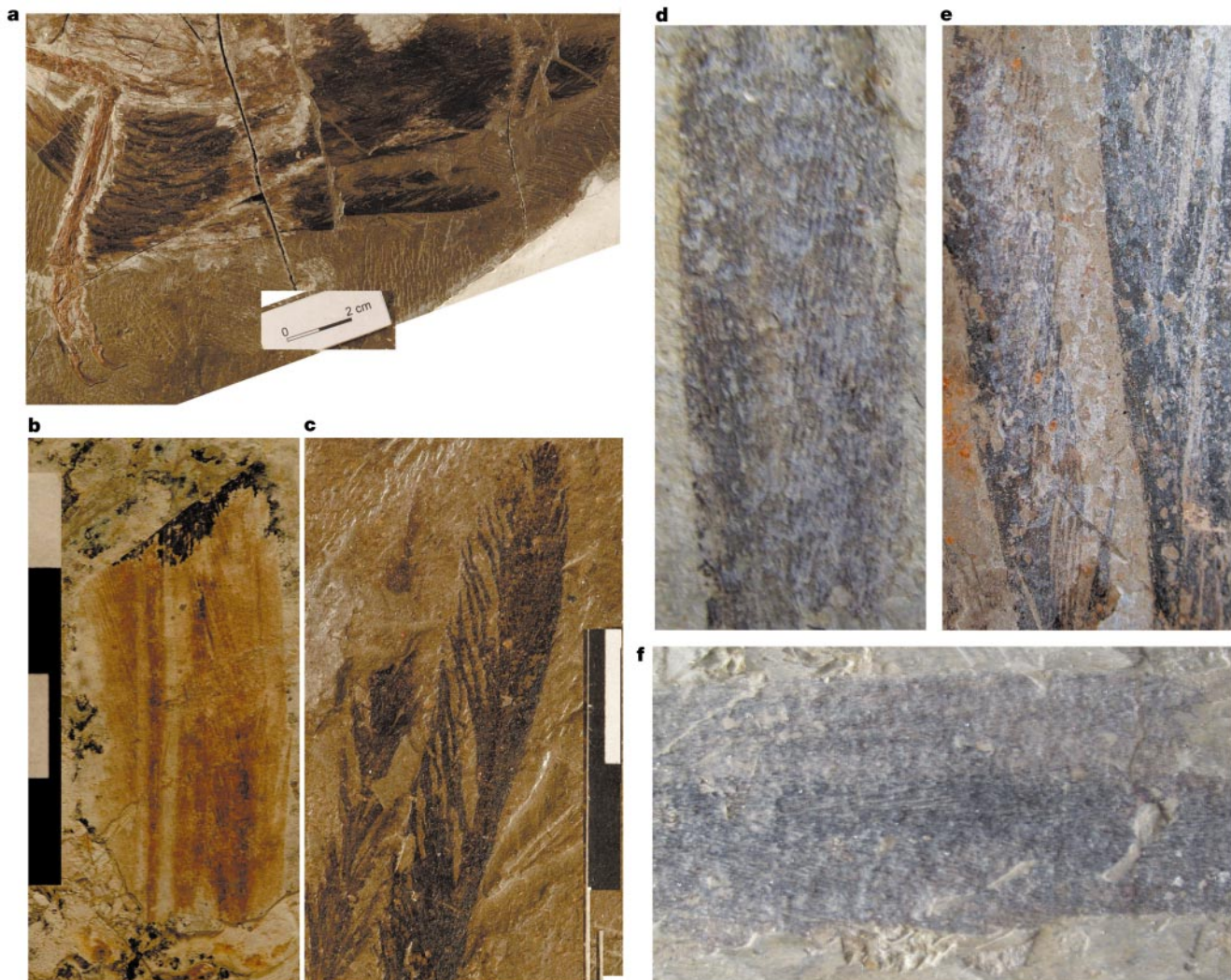


Figure 3 Feathers showing the asymmetrical vanes. Pennaceous feathers attached to the left metatarsus of IVPP V13477 (a) and right metatarsus of IVPP V13320 (b). c, Close-up of a distal pennaceous feather on the left metatarsus of IVPP V13477. d, Close-up of a

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. □

Received 5 August; accepted 29 November 2002; doi:10.1038/nature01342.

- Ostrom, J. H. Osteology of *Deinonychus antirrhopus*, an unusual theropod dinosaur from the Lower Cretaceous of Montana. *Peabody Mus. Nat. Hist. Bull.* **30**, 1–165 (1969).
- Currie, P. J. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. *Can. J. Earth Sci.* **22**, 1643–1658 (1985).
- Norell, M. A., Clark, J. M., Chiappe, L. M. & Dashzeveg, D. A nesting dinosaur. *Nature* **378**, 774–776 (1995).
- Novas, F. E. & Puerta, P. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* **387**, 390–392 (1998).
- Forster, C. A., Sampson, S. D., Chiappe, L. M. & Krause, D. W. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* **279**, 1915–1919 (1998).
- Ji, Q., Currie, P. J., Norell, M. A. & Ji, S.-A. Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761 (1998).
- Xu, X., Wang, X.-L. & Wu, X.-C. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* **401**, 262–266 (1999).
- Xu, X., Zhou, Z.-H. & Wang, X.-L. The smallest known non-avian theropod dinosaur. *Nature* **408**, 705–708 (2000).
- Zhou, Z.-H. & Zhang, F.-C. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* **418**, 405–409 (2002).
- Gauthier, J. A. Saurischian monophyly and the origin of birds. *Mem. Calif. Acad. Sci.* **8**, 1–55 (1986).
- Holtz, T. R. Jr The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *J. Paleontol.* **68**, 1100–1117 (1994).
- Holtz, T. R. Jr A new phylogeny of the carnivorous dinosaurs. *Gaia* **15**, 5–61 (2000).
- Sereno, P. C. The evolution of dinosaurs. *Science* **284**, 2137–2147 (1999).
- Norell, M. A., Clark, J. M. & Makovicky, P. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. & Gall, L. F.) 49–67 (Peabody Mus. Nat. Hist., Yale Univ., New Haven, 2001).
- Xu, X., Norell, M. A., Wang, X.-L., Makovicky, P. & Wu, X.-C. A basal troodontid from the Early Cretaceous of China. *Nature* **415**, 780–784 (2002).
- Makovicky, P. & Sues, H.-D. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *Am. Mus. Novit.* **3240**, 1–27 (1998).
- Norell, M. A. *et al.* 'Modern' feathers on a non-avian dinosaur. *Nature* **416**, 36–37 (2002).
- Smith, P. E. *et al.* Dates and rates in ancient lakes: ⁴⁰Ar–³⁹Ar evidence for an early Cretaceous for the Jehol Group, northeast China. *Can. J. Earth Sci.* **32**, 1426–1431 (1995).
- Jones, T. D., Farlow, J. O., Ruben, J. A., Henderson, D. M. & Hillenius, W. J. Cursoriality in bipedal archosaurs. *Nature* **406**, 716–718 (2000).
- Xu, X. *Deinonychosaurian Fossils from the Jehol Group of Western Liaoning and the Coelurosaurian Evolution*. PhD dissertation, Chinese Academy of Sciences (2002).
- Norell, M. A. & Makovicky, P. J. Important features of the dromaeosaur skeleton: information from a new specimen. *Am. Mus. Novit.* **3215**, 1–28 (1997).
- Zhang, X.-H. *et al.* A long-necked therizinosauroid dinosaur from the Upper Cretaceous Iren Dabusu Formation of Nei Mongol, People's Republic of China. *Vertebrata Palasiatica* **39**, 282–290 (2001).
- Sanz, J. L. *et al.* An Early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature* **382**, 442–445 (1996).
- Zhang, F.-C. & Zhou, Z.-H. A primitive enantiornithine bird and the origin of feathers. *Science* **290**, 1955–1959 (2000).
- Beebe, C. W. *A Tetrapteryx Stage in the Ancestry of Birds* (Zoologica, New York, 1915).
- Heilmann, G. *The Origin of Birds* (Witherby, London, 1927).
- Burnham, D. A. *et al.* Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. *Univ. Kansas Paleont. Contri. (new series)* **13**, 1–14 (2000).
- Feduccia, A. & Tordoff, H. B. Feathers of *Archaeopteryx*: asymmetric vanes indicate aerodynamic function. *Science* **203**, 1021–1022 (1979).
- Ostrom, J. H. The cursorial origin of avian flight. *Mem. Calif. Acad. Sci.* **8**, 73–81 (1986).
- Padian, K. & Chiappe, L. M. The origin and early evolution of birds. *Biol. Rev.* **73**, 1–42 (1998).
- Burgers, P. & Chiappe, L. M. The wing of *Archaeopteryx* as a primary thrust generator. *Nature* **399**, 60–62 (1999).
- Chatterjee, S. *The Rise of Birds* (Johns Hopkins Univ. Press, Baltimore, 1997).
- Yalden, D. W. Climbing *Archaeopteryx*. *Archaeopteryx* **15**, 107–108 (1997).
- Chiappe, L. M., Ji, S.-A., Ji, Q. & Norell, M. A. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the late Mesozoic of Northeastern China. *Bull. Am. Mus. Nat. Hist.* **242**, 1–89 (1999).
- Hopson, J. A. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. & Gall, L. F.) 211–236 (Peabody Mus. Nat. Hist., Yale Univ., New Haven, 2001).
- Zhou, Z.-H. & Farlow, J. O. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. & Gall, L. F.) 237–254 (Peabody Mus. Nat. Hist., Yale Univ., New Haven, 2001).
- Sereno, P. & Rao, C. Early evolution of avian flight and perching: new evidence from the Early Cretaceous of China. *Science* **255**, 845–848 (1992).
- Arnold, E. N. in *New Perspectives on the Origin and Early Evolution of Birds* (eds Gauthier, J. & Gall,

- L. F.) 195–210 (Peabody Mus. Nat. Hist., Yale Univ., New Haven, 2001).
39. Norberg, U. M. Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. *Am. Nat.* **126**, 303–327 (1985).
40. Norberg, U. M. in *The Beginnings of Birds* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 293–302 (Freunde des Jura-Museums Eichstatt, Eichstatt, 1985).
41. Norberg, U. M. *Vertebrate Flight* (Springer, Berlin, 1990).
42. Rayner, J. M. V. in *The Beginnings of Birds* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 279–288 (Freunde des Jura-Museums Eichstatt, Eichstatt, 1985).
43. Rayner, J. M. V. in *The Beginnings of Birds* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 289–292 (Freunde des Jura-Museums Eichstatt, Eichstatt, 1985).
44. Bock, W. J. The arboreal origin of avian flight. *Mem. Calif. Acad. Sci.* **8**, 57–72 (1986).
45. Rowe, T. *et al.* The Archaeoraptor forgery. *Nature* **410**, 539–540 (2001).
46. Speakman, J. R. & Thomson, S. C. Flight capabilities of *Archaeopteryx*. *Nature* **370**, 524 (1994).

Acknowledgements We thank L. Witmer and A. Milner for their suggestions and comments, M. Norell, X.-J. Ni, J. Liu, J. Clarke and P. Sereno for discussions, Y.-L. Huo, Y.-T. Li and H.-J. Wang for preparing the specimens, R.-S. Li for drawings, and Z.-G. Sun and B. An for help with CT scanning. Thanks also go to members of the Liaoxi expedition team of the IVPP for fieldwork. This work was supported by grants from the National Natural Science Foundation of China, the National Geographic Society, Special Funds for Major State Basic Research Projects of China, and the Chinese Academy of Sciences.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to X.X. (e-mail: xing_xu@sina.com).