

# The smallest known non-avian theropod dinosaur

Xing Xu\*, Zhonghe Zhou\* & Xiaolin Wang\*†

\* The Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, People's Republic of China

† College of Earth Science and Resources, China University of Geosciences, Beijing 100083, People's Republic of China

Non-avian dinosaurs are mostly medium to large-sized animals, and to date all known mature specimens are larger than the most primitive bird, *Archaeopteryx*<sup>1</sup>. Here we report on a new dromaeosaurid dinosaur, *Microraptor zhaoianus* gen. et sp. nov., from the Early Cretaceous Jiufotang Formation of Liaoning, China<sup>2</sup>. This is the first mature non-avian dinosaur to be found that is smaller than *Archaeopteryx*<sup>1</sup>, and it eliminates the size disparity between the earliest birds and their closest non-avian theropod relatives. The more bird-like teeth, the *Rahonavis*-like ischium and the small number of caudal vertebrae of *Microraptor* are unique among dromaeosaurids and improve our understanding of the morphological transition to birds. The nearly completely articulated foot shows features, such as distally positioned digit I, slender and recurved pedal claws, and elongated penultimate phalanges, that are comparable to those of arboreal birds<sup>3–6</sup>. The discovery of these in non-avian theropods provides new insights for studying the palaeoecology of some bird-like theropod dinosaurs.

Theropoda Marsh 1881

Maniraptora Gauthier 1986

Dromaeosauridae Matthew & Brown 1922

*Microraptor zhaoianus* gen. et sp. nov.

**Etymology.** The generic name refers to the small size of this new dromaeosaurid dinosaur; the specific name is in honour of Zhao Xijin, a distinguished dinosaurologist who introduced the first author to the field of vertebrate paleontology.

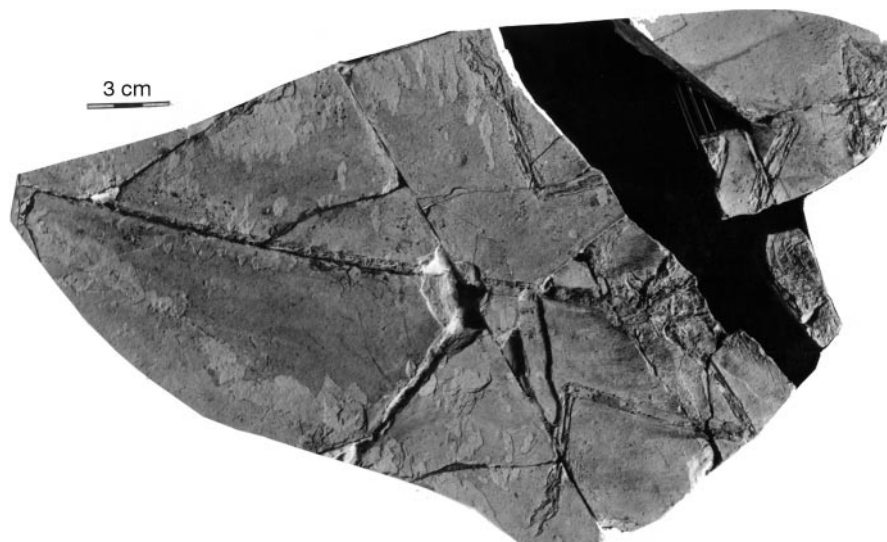
**Holotype.** IVPP (The Institute of Vertebrate Paleontology and Paleoanthropology) V 12330, a partial skeleton preserved in main (Fig. 1) and counter slabs.

**Locality and horizon.** Xiasanjiazi, Chaoyang County, western Liaoning; Jiufotang Formation (Early Cretaceous<sup>2</sup>), underlain by the famous Yixian Formation which has yielded more than 1,000 specimens of early birds and feathered dinosaurs<sup>7</sup>.

**Diagnosis.** Distinguishable from other dromaeosaurids in anterior serrations are absent on all of the teeth; posterior teeth have a basal constriction between crown and root; middle caudals are about 3–4 times as long as the anterior dorsals; accessory crest of femur at the base of the lesser trochanter; the tail has less than 26 vertebrae; and it has strongly recurved and slender pedal unguals with a prominent flexor tubercle.

**Description.** The holotype of *M. zhaoianus* is an articulated skeleton missing the middle portion of the body (Figs 1 and 2). The premaxilla is similar to that of *Archaeopteryx*<sup>8</sup> and *Sinornithosaurus*<sup>9</sup> in that it has a sloping anterior margin. As in *Archaeopteryx* and troodontids<sup>10</sup>, the maxilla contributes to the border of the external naris (Fig. 2b). There are at least 15 dentary teeth, which are closely packed as in troodontids<sup>11</sup>. The anterior teeth, including premaxillary teeth, are more recurved and laterally compressed than the posterior teeth as in most theropods, but they lack serrations on both the anterior and the posterior carinae as seen in some non-avian theropods and birds (Fig. 2c). The posterior teeth have posterior serrations; however, they are bird-like in having a less compressed crown and a constriction between the root and crown (Fig. 2d). These 'waisted' teeth are reported here for the first time in a dromaeosaurid, although among non-avian theropods<sup>12</sup> they have already been reported in therizinosaurs, troodontids and ornithomimosaurs. The heterodont dentition provides information on the transition from the non-avian theropod type of dentition to that of the typical avian type. It seems that the reduction of serrations begins in the anterior teeth and with the anterior margins of the teeth, however, the basal constriction of the tooth crown first appears in the posterior teeth.

The body is extremely short, with an estimated trunk length of about 47 mm (this length is inferred from the presumption that *Microraptor* had 13 dorsal bones and that its cervicodorsals are relatively long as compared with the remaining dorsals, as in other dromaeosaurids<sup>13</sup>). Five fused sacral bones are preserved and the anterior three are transversely enlarged, although the sacrals of the holotype are slightly crushed and flattened (Fig. 3a). The tail is almost complete and articulated with the sacrum. There are 24 or 25



**Figure 1** Main slab (V 12330, holotype) containing *M. zhaoianus*. V 12330 includes a partial skull, complete mandible, right radius, right ulna, partial right manus, incomplete right hindlimb and nearly complete left hindlimb, dorsals, sacrals, nearly complete tail, and ribs, and nearly complete pelvic girdle. Examination of the preservation and

proportions of the elements indicate that the material represents a single individual. The tail portion of the single known specimen of '*Archaeopteryx*' forms the counterpart of the tail of V 12330 and therefore represents part of the holotype of *Microraptor zhaoianus*.

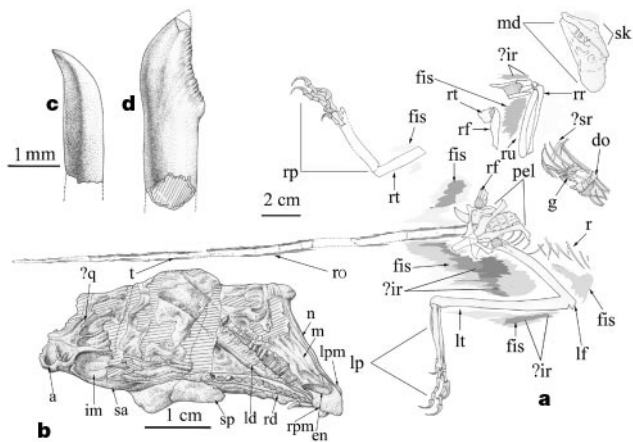
caudals, which is close to the caudal number of *Archaeopteryx*<sup>14</sup>. The articulated tail has elongate rod-like extensions of the prezygapophyses and chevrons characteristic of dromaeosaurid dinosaurs<sup>13,15</sup>. These rod-like extensions reach almost to the sacrum (Fig. 3a). The caudals are significantly elongated. Gastralia and what appear to be sternal ribs and uncinata processes are preserved.

The ulna is bowed posteriorly and when compared with the femur<sup>9</sup> it is proportionately shorter than in other dromaeosaurids; the radius is much thinner than the ulna. There are at least three carpals and an additional one may be present (Fig. 3b), a pattern that is similar to that of *Archaeopteryx*. The semilunate carpal is relatively small as in *Sinornithosaurus* (IVPP, V 12811) and in *Archaeopteryx*<sup>16,17</sup>, and has more contact with the proximal end of

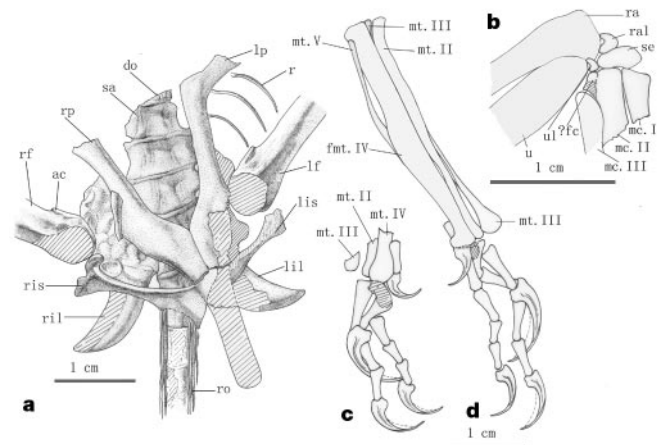
metacarpal II than with metacarpal I (Fig. 3b).

The pubis is probably retroverted as in other dromaeosaurids and birds (Fig. 3a), and its symphysis is about 49% the length of the pubis. The ischium is plate-like and less than half the length of the pubis; it has a posterior process as in *Sinornithosaurus*<sup>9</sup>, *Unenlagia*, *Archaeopteryx* and *Rahonavis*<sup>18</sup>. A large distally positioned obturator process is present as in *Rahonavis*<sup>18</sup> and *Sinornithosaurus* (IVPP, V 12811).

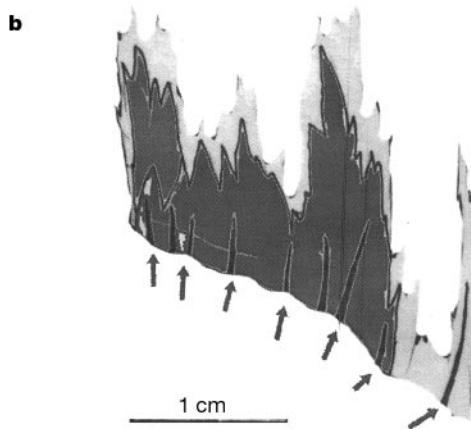
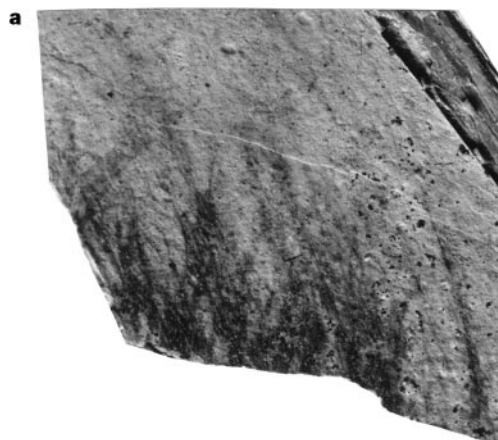
The femur of *M. zhaoianus* has an accessory crest pendent at the base of the lesser trochanter, as in the basal oviraptorosaurian *Microvenator*<sup>19</sup>. The tibia is about 128% the length of the femur. The fibula is slender and reaches the calcaneum. Pedal digit I is preserved on the posterior surface of metatarsals II–IV in both of the hindlimbs and has a more distal position than in other known non-avian theropods. Metatarsals II, III and IV are subequal in length. The proximal end of metatarsal III is significantly compressed in posterior view, which suggests an arctometatarsalian condition<sup>20</sup>. Metatarsal IV is much more robust than metatarsals II and III, which is also the case in troodontids. Metatarsal V is long and bowed laterally and its mid-shaft is expanded. Metatarsal IV bears a pronounced flange on the posteromedial surface as in other dromaeosaurids<sup>9,21</sup>. The second pedal digit is a specialized raptorial tool<sup>13</sup> as in other dromaeosaurids, troodontids and *Rahonavis*. Like other dromaeosaurids<sup>22</sup>, the ungual is more than one and a half times longer than phalanx II-1. All of the pedal unguals are sharp and strongly recurved, similar to those of trunk-climbing birds<sup>4–6</sup>. The horny sheath is well preserved, with a columnar dorsal margin



**Figure 2** Outline of skeleton and identification of the skull with lower jaws and an anterior and posterior dentary tooth of *M. zhaoianus* (V 12330). **a**, Outline of the skeleton (broken lines indicate bones preserved only as impressions; stippled line indicates damaged bone). **b**, Skull with lower jaws. **c**, An anterior dentary tooth in medial view. **d**, A posterior dentary tooth in lateral view. a, articular; do, dorsal vertebra; en, external naris; fis, feather-like integumentary structures; g, gastralia; im, internal mandibular fossa; ir, impression of rachis; lf, left femur; lp, left pes; lpm, left premaxilla; lt, left tibia; m, maxilla; md, mandible; n, nasal; pel, pelvis; q, quadrate; r, rib; rd, right dentary; rf, right femur; ro, rod-like extensions; rp, right pes; rpm, right premaxilla; rr, right radius; rt, right tibia; ru, right ulna; sp, splenial; sa, surangular; sk, skull; sr, sternal rib; and t, tail. Question mark indicates uncertain identification.



**Figure 3** Identification of pelvic girdle, right forelimb and pes of *M. zhaoianus* (V 12330). **a**, Pelvic girdle in ventral view. **b**, Right forelimb in ventral view. **c**, Right pes in posterior view. **d**, Left pes in posterior view. Additional abbreviations: ac, accessory crest; fc, fourth carpal; fmt. IV, flange on metatarsal IV; lil, left ilium; lis, left ischium; lp, left pubis; mc. I–III, metacarpals I–III; mt. II–V, metatarsals II–V; ra, radius; ral, radiale; ril, right ilium; ris, right ischium; rp, right pubis; sa, sacrum; se, semilunate distal carpal; and u, ulna. See also Fig. 3 for abbreviations. Question mark indicates uncertain identification.



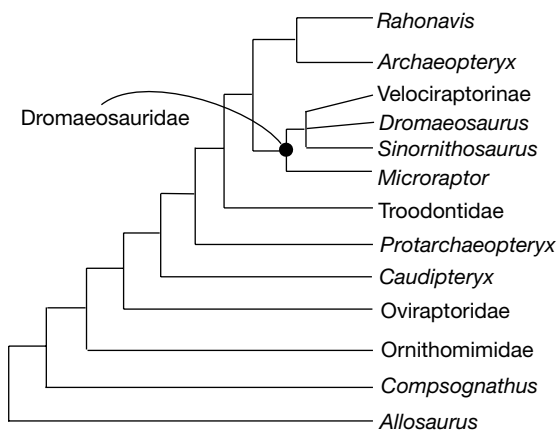
**Figure 4** Integument of *M. zhaoianus* (V 12330). Photograph (**a**), and line drawing (**b**), of parts of the integument preserved adjacent to the femur. Shaded areas represent the carbonized integument, and arrows point to the median depression that was probably made by the rachis.

and a thin ventral margin.

Large patches of integuments are preserved *in situ* around the skeleton (Figs 1 and 2a), and the pattern of preservation is similar to that of early birds from the same locality (IVPP, V 12325). Integumentary structures are best preserved near the femur, where they run almost perpendicular to the bone (Fig. 4). They are long (average 25–30 mm), narrow, and have a feather-like contour, whereas those along the tibia and in the hip area are shorter. Some impressions of the integuments contain a structure similar to that of a rachis (Fig. 4b), suggesting that true feathers may have been present among dromaeosaurids.

**Discussion.** We investigated the phylogenetic relationship of *Microraptor* by means of a cladistic analysis of a data set comprising 13 taxa and 89 characters (see Supplementary Information). Our analysis suggests that *Microraptor* is a basal dromaeosaurid (Fig. 5). Notable in this new dromaeosaurid is the presence of some salient similarities to those of troodontids, such as troodontid-like posterior teeth and arctometatarsalian metatarsals. The discovery of *Microraptor* completes some morphological gaps between dromaeosaurid dinosaurs and birds; for example, it has more bird-like teeth than do other dromaeosaurids, a *Rahonavis*-like ischium, enlarged sacrals and fewer caudal vertebrae. These bird-like characteristics were more widespread and retained in the lineage leading to the birds and in the basal dromaeosaur *Microraptor*, but were lost (by means of reversal to a more primitive state) in more derived dromaeosaurids.

There are a few notable features of *Microraptor*, one of which is its small size. The holotype of *Microraptor* is a mature animal, as indicated by the fusion of the sacral vertebrae, the pubic symphysis and the partial fusion of the last dorsal to the synsacrum. The fine serrations on the tooth crown, the well-developed accessory crest on the femur and the well-ossified cortical bone provide further



**Figure 5** Phylogenetic relationships of *M. zhaoianus*. Shown is a strict consensus tree of the two most parsimonious trees (tree length = 170; consistency index = 0.594; retention index = 0.667). Characters 1–3 are ordered. The tree was produced using the branch-and-bound option of PAUP. Synapomorphies for each node were determined by accelerated transformation (ACCTRAN). *M. zhaoianus* was referred to Dromaeosauridae on the basis of the following unique dromaeosaurid features: ossified caudal rods extending the length of prezygapophyses and chevrons present (80.1); a longitudinal ridge along the posteromedial surface of metatarsal IV present (87.1); second pedal claw apparently larger than the pedal phalanx II-1 (89.1). Additional synapomorphies: 2.1, 3.1, 10.1, 66.1, 68.1, 70.1, 74.1, 76.1, 79.1, 63.1, 64.1, 65.1, 67.1, 69.1 and 75.1.

*M. zhaoianus* is less derived than other dromaeosaurids and lacks the following synapomorphies: denticles present on anterior and posterior carinae of teeth (1.0); all teeth laterally compressed and recurved (2.0); constriction between crown and root absent on all teeth (3.0); maxilla contribution to naris absent (4.0); number of caudal vertebrae more than 30 (20.0), femoral neck present (53.0), tibia less than 115% length of femur (53.0); and internal mandibular fenestra triangular and relatively large (78.1). The monophyletic Dromaeosauridae tree did not collapse until four more steps had been added by re-analysing the data matrix and sequentially adding steps.

evidence of its maturity<sup>19,23</sup>. Additional evidence includes its relatively small skull (skull/femur length ratio is 0.85) and sacrum (sacrum/femur length ratio is 0.36, compared with 0.44 in *Sinornithosaurus*; in *Archaeopteryx* the larger individuals have a smaller sacrum/femur length ratio than in *Microraptor*).

Although a number of non-avian theropods of small size have been reported previously, all are larger than the most primitive bird *Archaeopteryx*<sup>1</sup> (see Supplementary Information). The trunk of *Microraptor* is shorter than in all but the smallest individual of *Archaeopteryx*<sup>24</sup>; the sacrum is as long as in the smallest individual of *Archaeopteryx*; and the femur is as long as that of the Berlin specimen<sup>24</sup>, which is the third smallest specimen of *Archaeopteryx* found (see Supplementary Information). These comparisons indicate that *Microraptor* has the smallest adult size of any non-avian dinosaur found to date. Decrease of body size is an evolutionary trend among coelurosaurians<sup>1</sup> and had an important role in the origin of bird flight<sup>25</sup>. The small size of *Microraptor* suggests that non-avian theropods were pre-adapted for the origin of flight. In contrast, a trend of increasing body size is evident among dromaeosaurids, and is also found in many other coelurosaurian lineages including tyrannosaurids<sup>26</sup>, therizinosauroids<sup>27</sup> and oviraptorosaurians<sup>1</sup>.

Some pedal features of *Microraptor* are consistent with an arboreal habit. Pedal digit I is relatively distal in position, as indicated by its first phalanx extending distally almost to the distal end of metatarsal III. This is similar to the situation in *Archaeopteryx* (see ref. 24), *Confuciusornis* (IVPP, V 11370) and arboreal birds, but is different from that of most non-avian theropods and ground birds in which pedal digit I is more proximally positioned. All pedal unguals of *Microraptor* are slender, with a curvature of more than 155° (calculated by the method of ref. 6) and a prominent flexor tubercle (Fig. 3c, d). They are different from all known non-avian theropods, but comparable to those of climbing birds<sup>4–6</sup> (see Supplementary Information). The penultimate pedal phalanges of *Microraptor* and, to a lesser degree, other dromaeosaurids are elongated relative to those of most cursorial theropods (see Supplementary Information). The ratios of pedal phalanx II-2/II-1 are larger than 1 in dromaeosaurids and early birds but smaller than 1 in other non-avian maniraptorans. The elongation of the distal pedal phalanges has been suggested to be indicative of an arboreal habit<sup>25,28</sup>. The available evidence indicates that *Microraptor* may have been able to climb trees, although this dinosaur is apparently derived from a cursorial ancestor as it retained an arctometatarsalian foot.

Non-avian theropods are usually regarded as being terrestrial cursors<sup>29</sup>. The discovery of *Microraptor* provides the first evidence to suggest that some non-avian theropods had arboreal habits, indicating that the palaeoecology of non-avian theropods may be more diverse than previously thought. The evidence for arboreality in non-avian theropods is an important discovery as it could be used to test the ‘tree-down’ hypothesis for the origin of bird flight<sup>30</sup>. The theropod ancestors of birds may have passed through an arboreal phase, although more evidence is needed to confirm this hypothesis. □

Received 24 March; accepted 29 September 2000.

- Sereno, P. C. The evolution of dinosaurs. *Science* **284**, 2137–2147 (1999).
- Jin, F. New advances in the late Mesozoic stratigraphic research of western Liaoning, China. *Vertebrata Palasiatica* **34**, 102–122 (1996).
- Yaden, D. W. in *The Beginnings of Birds* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 91–97 (Freunde des Jura-Museums Eichstatt, Eichstatt, 1985).
- Yalden, D. W. Climbing *Archaeopteryx*. *Archaeopteryx* **15**, 107–108 (1997).
- Ostrom, J. H. The cursorial origin of avian flight. *Mem. Calif. Acad. Sci.* **8**, 73–81 (1986).
- Feduccia, A. Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. *Science* **259**, 790–793 (1993).
- Xu, X. & Wang, X.-L. New psittacosaur (Ornithischia, Ceratopsia) occurrence from the Yixian Formation of Liaoning, China and its stratigraphical significance. *Vertebrata Palasiatica* **36**, 147–158 (1998).
- Wellnhofer, P. Ein neues Exemplar von *Archaeopteryx*. *Archaeopteryx* **6**, 1–30 (1988).
- 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).



10. Russell, D. A. & Dong, Z.-M. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. *Can. J. Earth Sci.* **30**, 2163–2173 (1994).
11. Currie, P. J. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *J. Vert. Paleont.* **7**, 72–81 (1987).
12. Clark, J. M., Perle, M. & Norell, M. A. The skull of *Erlicosaurus andrewsi*, a Late Cretaceous "Segnosaur" (Theropoda: Therizinosauridae from Mongolia). *Am. Mus. Novit.* **3115**, 1–39 (1994).
13. 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).
14. Wellnhofer, P. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. *Archaeopteryx* **11**, 1–47 (1993).
15. Currie, P. J. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *J. Vert. Paleont.* **15**, 576–591 (1995).
16. Martin, L. D. in *Origins of the Higher Groups of Tetrapods* (eds Schultze, H.-P. & Trueb, L.) 485–540 (Comstock, Ithaca and London, 1991).
17. Zhou, Z. & Martin, L. D. Feathered dinosaur or bird?—a new look at the hand of *Archaeopteryx*. *Smithson. Contrib. Paleobiol.* **89**, 289–293 (1999).
18. 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).
19. 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).
20. Holtz, T. R. Jr. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *J. Paleont.* **68**, 1100–1117 (1994).
21. Norell, M. A. & Makovicky, P. J. Important features of the dromaeosaur skeleton: information from a new specimen. *Am. Mus. Novit.* **3215**, 1–28 (1997).
22. Currie, P. J. & Peng, J.-H. A juvenile specimen of *Saurornithoides mongoliensis* from the Upper Cretaceous of northern China. *Can. J. Earth Sci.* **30**, 2224–2230 (1994).
23. Currie, P. J., Rigby, J. K. & Sloan, R. E. in *Dinosaur Systematics: Perspectives and Approaches* (eds Carpenter, K. & Currie, P. J.) 108–125 (Cambridge Univ. Press, Cambridge, 1990).
24. Wellnhofer, P. A. A new specimen of *Archaeopteryx* from the Solnhofen Limestone. *Nat. Hist. Mus. Los Angeles County Sci. Ser.* **36**, 3–23 (1992).
25. Zhou, Z.-H. & Hou, L.-H. *Confuciusornis* and the early evolution of birds. *Vertebrata Palasiatica* **36**(2), 136–146 (1998).
26. Buffetaut, E., Suteethorn, V. & Tong, H.-Y. The earliest known tyrannosaur from the Lower Cretaceous of Thailand. *Nature* **381**, 689–691 (1996).
27. Xu, X., Tang, Z.-L. & Wang, X.-L. A therizinosaurid dinosaur with integumentary structures from China. *Nature* **399**, 350–354 (1999).
28. Clark, J. M., Hopson, J. A., Hernandez, R., Fastovsky, D. E. & Montellano, M. Foot posture in a primitive pterosaur. *Nature* **391**, 886–889 (1998).
29. Chiappe, L. M. Climbing *Archaeopteryx*? A response to Yalden. *Archaeopteryx* **15**, 109–112 (1997).
30. Chatterjee, S. *The Rise of Birds* (John Hopkins Univ. Press, Baltimore, 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 D. Unwin, L. Chiappe, X.-C. Wu, J. Clark and L. Witmer for comments; M.-M. Chang and Y.-Q. Wang for assistance during the course of the work; H.-J. Wang for preparing the specimen; R.-S. Li for making the drawings; and J. Zhang and H.-L. You for taking the photographs. This work was supported by the Special Funds for Major State Basic Research Projects of China, and research grants from the National Geographic Society of the United States, Chinese Natural Science Foundation, and the Chinese Academy of Sciences.

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

## Mitochondrial genome variation and the origin of modern humans

Max Ingman\*, Henrik Kaessmann†, Svante Pääbo† & Ulf Gyllenstein\*

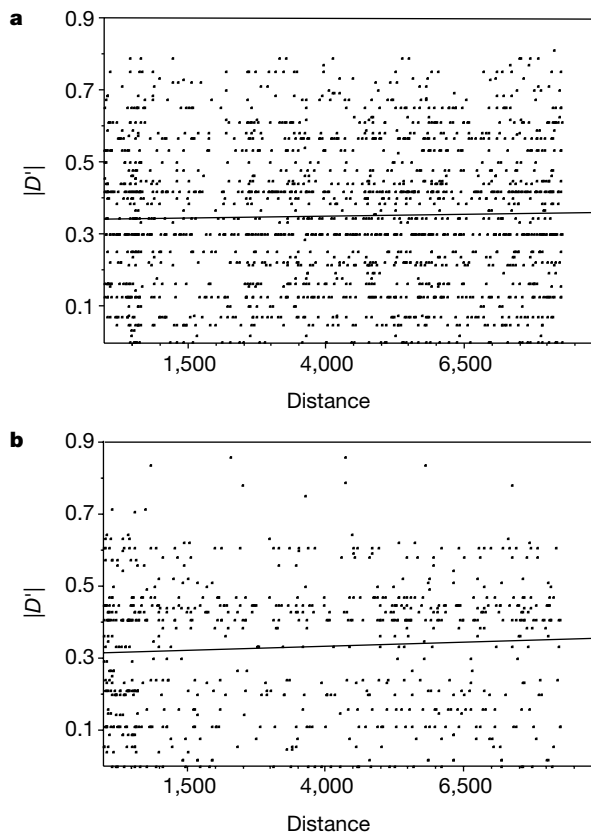
\* Department of Genetics and Pathology, Section of Medical Genetics, Rudbeck Laboratory, University of Uppsala, S-751 85 Uppsala, Sweden

† Max Planck Institute for Evolutionary Anthropology, Inselstrasse 22, D-04103 Leipzig, Germany

The analysis of mitochondrial DNA (mtDNA) has been a potent tool in our understanding of human evolution, owing to characteristics such as high copy number, apparent lack of recombination<sup>1</sup>, high substitution rate<sup>2</sup> and maternal mode of inheritance<sup>3</sup>. However, almost all studies of human evolution based on mtDNA sequencing have been confined to the control region, which constitutes less than 7% of the mitochondrial

genome. These studies are complicated by the extreme variation in substitution rate between sites, and the consequence of parallel mutations<sup>4</sup> causing difficulties in the estimation of genetic distance and making phylogenetic inferences questionable<sup>5</sup>. Most comprehensive studies of the human mitochondrial molecule have been carried out through restriction-fragment length polymorphism analysis<sup>6</sup>, providing data that are ill suited to estimations of mutation rate and therefore the timing of evolutionary events. Here, to improve the information obtained from the mitochondrial molecule for studies of human evolution, we describe the global mtDNA diversity in humans based on analyses of the complete mtDNA sequence of 53 humans of diverse origins. Our mtDNA data, in comparison with those of a parallel study of the Xq13.3 region<sup>7</sup> in the same individuals, provide a concurrent view on human evolution with respect to the age of modern humans.

The molecular clock hypothesis postulates that DNA sequence evolution is roughly constant over time in all evolutionary lineages. We used a test<sup>8</sup> that compares the log likelihoods of trees reconstructed with and without the molecular clock assumption to examine the supposition that the mtDNA lineages evolve at 'clock-like' rates. The human mtDNA sequences, excluding the D-loop, have evolved at roughly constant rates ( $P = 0.094$ ), and a relative rates test<sup>9</sup>, using a gorilla sequence as an outgroup, demonstrates that there is also no significant difference between the evolutionary rate of human and chimpanzee mtDNAs ( $P = 0.123$ ), excluding the D-loop. In contrast, the D-loop has not evolved at a constant rate across all human lineages ( $P < 0.001$ ), and is consequently less suitable for dating evolutionary events. Therefore, unless specifically mentioned, we have excluded the D-loop from the analyses that follow.



**Figure 1** The relationship between linkage disequilibrium, measured by  $|D'|$  versus distance between nucleotide sites for all 53 complete human mtDNA genomes. Values of  $\pm 1.0$  have been removed. **a**, Individuals of African descent ( $n = 1,719$  comparisons),  $R^2 = 0.001$ ; **b**, only non-African individuals ( $n = 741$  comparisons),  $R^2 = 0.005$ .