with Sanderson's[26] method of non-parametric rate smoothing (NPRS) implemented in TreeEdit version 1.0 alpha 4-61 (ref. 27). In the absence of reliable fossil data[28,29], all trees were calibrated using an estimated age of 26 Myr for the split between Aizoaceae + Phytolaccaceae and its nearest relative, the Nyctaginaceae. We took this date from a DNA-sequence-based angiosperm phylogeny using ML branch lengths[30]. In addition, to account for the error in the calibration, we recalculated the age of the core Ruschioideae and diversification rate using the most conservative date estimated for the split between Aizoaceae + Phytolaccaceae and Nyctaginaceae (that is, 30 Myr using parsimony branch lengths and DELTRAN optimization)[30]. The standard error in age estimates for each data set with ML branch lengths was also estimated using 100 bootstrap matrices and one of the most equally parsimonious trees found from the initial heuristic searches (*Tetragonia* and *Dorotheanthus* + *Cleretum* once again constrained for the ITS analysis). With a calibration age of 26 Myr, the estimated age of the core Ruschioideae radiation from the plastid data set was 6.2 Myr with ML branch length (mode of bootstrap distribution 8.7 ± 0.7 Myr; Fig. 1) and 6.4 Myr with parsimony branch lengths; and from the ITS data set 3.1 Myr with ML branch lengths (mode of bootstrap distribution 3.8 ± 3.2 Myr; Fig. 1) and 6.6 Myr with parsimony branch lengths. With a calibration age of 30 Myr, the mode of the bootstrap distribution was slightly higher (plastid data 9.5 ± 0.8 Myr and ITS data 4.4 ± 3.7 Myr with ML branch lengths).

We estimated the per-lineage rate of diversification per million years for the core Ruschioideae radiation from both plastid and ITS data sets as $(\ln N - \ln N_0)/T$ (ref. 7), where initial diversity $N_0 = 2$, N is existing diversity and T is estimated clade age (we used the mode of the bootstrap distribution of age estimates as T). Thus, with a calibration of 26 Myr the estimated per-lineage diversification rate per million years based on the plastid data was 0.77 and for ITS 1.75 (0.70 and 1.5 respectively for the plastid and ITS data with a calibration point of 30 Myr). Taking extinction into account with a high value of $\epsilon = 0.9$ (ref. 13), we recalculated diversification rates as 0.58 lineages per million years for the plastid data and 1.32 lineages per million years for the ITS data.

Received 5 August; accepted 11 November 2003; doi:10.1038/nature02243.

1. Jürgens, N. A new approach to the Namib region. Part 1: phytogeographic subdivision. *Vegetatio* **97**, 21–38 (1991).
2. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
3. Jürgens, N. Untersuchungen zur Ökologie sukkulenter Pflanzen des südlichen Afrika. *Mitt. Inst. Allg. Bot. Hamburg* **21**, 139–365 (1986).
4. Ihlenfeldt, H.-D. Diversification in an arid world: The Mesembryanthemaceae. *Annu. Rev. Ecol. Syst.* **25**, 521–546 (1994).
5. Richardson, J. E. *et al.* Rapid and recent origin of species richness in the Cape flora of South Africa. *Nature* **412**, 181–183 (2001).
6. Richardson, J. E., Pennington, R. T., Pennington, T. D. & Hollongsworth, P. M. Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science* **293**, 2242–2245 (2001).
7. Baldwin, B. G. & Sanderson, M. J. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proc. Natl Acad. Sci. USA* **95**, 9402–9406 (1998).
8. Schmiedel, U. & Jürgens, N. Community structure on unusual islands: quartz-fields in the Succulent Karoo, South Africa. *Plant Ecol.* **142**, 57–69 (1999).
9. Hendey, Q. B. *Langebaanweg. A Record of Past Life* (South African Museum, Cape Town, 1982).
10. Axelrod, D. I. & Raven, P. H. in *Biology and Ecology of Southern Africa* (ed. Werger, M. J. A.) 77–130 (The Hague, Junk, 1978).
11. Ward, J. D., Seely, M. K. & Lancaster, N. On the antiquity of the Namib. *S. Afr. J. Sci.* **79**, 175–183 (1983).
12. Ward, J. D. & Corbett, I. Towards an age of the Namib. *Transvaal Mus. Monogr.* **7**, 17–26 (1990).
13. Magallón, S. & Sanderson, M. J. Absolute diversification rates in Angiosperm clades. *Evolution* **55**, 1762–1780 (2001).
14. Eriksson, O. & Bremer, B. Pollination systems, disperal modes, lifeforms, and diversification rates in Angiosperm families. *Evolution* **46**, 258–266 (1992).
15. Mayhew, P. J. Shifts in hexapod diversification and what Haldane could have said. *Proc. R. Soc. Lond. B* **269**, 969–974 (2002).
16. Hulbert, R. C. Jr The rise and fall of an adaptive radiation. *Paleobiology* **19**, 216–234 (1993).
17. McCune, A. R. in *Molecular Evolution and Adaptive Radiation* (eds Givnish, T. J. & Sytsma, K. J.) 585–610 (Cambridge Univ. Press, 1997).
18. Scott, L., Steenkamp, M. & Beaumont, P. B. Palaeoenvironments in South Africa at the Pleistocene–Holocene transition. *Quat. Sci. Rev.* **14**, 937–947 (1995).
19. Landrum, J. V. Wide-band tracheids in leaves of genera in Aizoaceae: the systematic occurrence of a novel cell type and its implications for the monophyly of the subfamily Ruschioideae. *Pl. Syst. Evol.* **227**, 49–61 (2001).
20. Mauseth, J. D., Uosumi, Y., Plemons, B. J. & Landrum, J. V. Structural and systematic study of an unusual tracheid type in cacti. *J. Plant Res.* **108**, 517–526 (1995).
21. Parolin, P. Seed expulsion in fruits of Mesembryanthema (Aizoaceae): a mechanistic approach to study the effect of fruit morphological structures on seed dispersal. *Flora* **196**, 313–322 (2001).
22. Klak, C., Khunou, A., Reeves, G. & Hedderson, T. A phylogenetic hypothesis for the Aiozoaceae (Caryophyllales) based on four plastid DNA regions. *Am. J. Bot.* **90**, 1433–1445 (2003).
23. Swofford, D. L. *PAUP*4.0b2: Phylogenetic Analysis Using Parsimony* (Sinauer Associates, Sunderland, Massachusetts, 1998).
24. Fitch, W. M. Toward defining the course of evolution: minimum change for a specified tree topology. *Syst. Zool.* **20**, 406–416 (1971).
25. Felsenstein, J. Confidence limits on phylogenies: an approach using bootstrap. *Evolution* **39**, 783–791 (1985).
26. Sanderson, M. J. A non parametric approach to estimating divergence times in the absence of rate constancy. *Mol. Biol. Evol.* **14**, 1218–1232 (1997).
27. Rambaut, A. & Charleston, M. *TreeEdit version 1.0 alpha 4–61* [online] ⟨http://evolve.zoo.ox.ac.uk/software/TreeEdit.html⟩ (2000).
28. Scott, L., Anderson, H. M. & Anderson, J. M. in *Vegetation of Southern Africa* (eds Cowling, R. M., Richardson, D. M. & Pierce, S. M.) 62–84 (Cambridge Univ. Press, 1997).
29. Tankard, A. J. & Rogers, J. Late Cenozoic palaeoenvironments on the west coast of Southern Africa. *J. Biogeogr.* **5**, 319–337 (1978).
30. Wikström, N., Savolainen, V. & Chase, M. Evolution of the angiosperms: calibrating the family tree. *Proc. R. Soc. Lond. B* **268**, 1–10 (2001).

A euprimate skull from the early Eocene of China

Xijun Ni[1], Yuanqing Wang[1], Yaoming Hu[1,2,3] & Chuankui Li[1]

[1]*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China*
[2]*Division of Paleontology, American Museum of Natural History, New York 10024, USA*
[3]*Biology Program (Ecology, Evolutionary Biology, and Behavior), Graduate School and City College, City University of New York, New York 10016, USA*

The debut of undoubted euprimates (primates of modern aspect[1,2]) was in the early Eocene, about 55 Myr ago. Since their first appearance, the earliest euprimates can be distinguished as *Cantius*, *Donrussellia* and *Teilhardina*[2–4]. Nonetheless, the earliest euprimates are primarily known from isolated teeth or fragmentary jaws. Here we describe a partially preserved euprimate skull with nearly complete upper and lower dentition, which represents a new species of *Teilhardina* and constitutes the first discovery of the genus in Asia. The new species is from the upper section of Lingcha Formation, Hunan Province, China, with an estimated age of 54.97 Myr ago[5]. Morphology and phylogeny analyses reveal that the new species is the most primitive species of *Teilhardina*, positioned near the root of euprimate radiation. This discovery of the earliest euprimate skull known to date casts new light on the debate[6–12] concerning the adaptive origin of euprimates, and suggests that the last common ancestor of euprimates was probably a small, diurnal, visually oriented predator.

Primates Linnaeus, 1758
Omomyidae Trouessart, 1879
Teilhardina Simpson, 1940
Teilhardina asiatica sp. nov.

Holotype. A partial skull with associated lower jaws (IVPP V12357, Figs 1, 2).
Included material. An isolated lower incisor (IVPP V12357-4) and two additional partial lower jaws (IVPP V12060, V13762).
Horizon and locality. Upper part of the Lingcha Formation, Hengyang Basin, China; earliest Eocene[5].
Diagnosis. Differs from *T. belgica* and *T. americana* in having a

less-reduced lower premolar P_1, which is loosely spaced and aligned in line with P_2.

The braincase of *T. asiatica* is rounded and large (Fig. 1), in sharp contrast to the low and small braincase in plesiadapiforms, such as *Ignacius*, *Palaechthon* and *Plesiadapis*. The skull roof of the new species is smooth and bears no sagittal crest, as on other Eocene omomyids, such as *Tetonius homunculus* and *Shoshonius cooperi*. The infraorbital foramen is relatively large (1 mm in height, 0.83 mm in breadth) and situated above upper premolar P^2, indicating a significantly shortened snout. The relative size of this foramen resembles those in insectivores or plesiadapiforms, and is greater than in extant and known fossil euprimates. Animals with greater infraorbital foramina are expected to have better-developed vibrissae[13]. The orbits are relatively well-preserved, although their zygomatic margins are broken and the frontal bone is slightly distorted dorsoventrally. The zygomatic process of the frontal is long, flat and narrow. Its irregular broken surface suggests that a postorbital bar was present. The preserved portion of the orbital margin is a well-defined, smoothly curved edge, demonstrating that the compression of the frontal bone caused little distortion of the orbit.

Relative to the skull length, the orbital size (mean = 6.92 mm) is much larger than those of plesiadapiforms, but is moderate within euprimates. Also different from plesiadapiforms, the orbits of the new species are significantly convergent with narrow interorbital breadth (3.97 mm). Relative to skull length, the interorbital breadth fits to the best-fit line for early Tertiary euprimates[14]. The convergence degree (51°) falls in the range of basal euprimates[15] and that of extant prosimians[16]. Because the frontal bone is crushed, precise measurement for the frontation of the orbits is not available.

However, because the well-preserved inferior-medial margin of the orbit is inclined caudally, the eyes must have had a low degree of frontation.

The lower jaws are nearly complete. The symphysis is unfused, and nearly horizontal, similar to that of *T. belgica*. Both the coronoid process and condyle are much higher than the tooth row. The angular process is straight and long, with its end posterior to the condyle. *Donrussellia magna*, another known earliest-Eocene euprimate with well-preserved mandible[17], differs from *T. asiatica* in possessing a much lower condyle and less prominent angular process.

The dental morphology of *T. asiatica* falls well in the diagnosis of the genus *Teilhardina*. In particular, the new species greatly resembles *T. belgica*.

The upper canine is sharp, slender and bodkin-like. Teeth P^{1-2} are reduced in size and simple in morphology. The P^3–M^3 teeth are closely similar to those of *T. belgica*. The minor differences between the two species mainly lie in molars: the M^1 in *T. asiatica* is more smoothly curved in its anterolingual margin and more protuberant at its posterolingual corner. The upper teeth of *T. americana* are saliently different from those of *T. asiatica* and *T. belgica* in having the *Nannopithex*-fold, a stronger lateral cingulum, and a more rectangular outline in the M^1 and M^2.

The lower canine is also bodkin-like with slightly procumbent root. The large canine alveolus in the mandible of *T. belgica* indicates the presence of a tall and sharp canine, as in *T. asiatica*. The lower canine of *T. americana* is also tall, but clearly premolariform. Its crown is buccolingually expanded, and has a definite border above
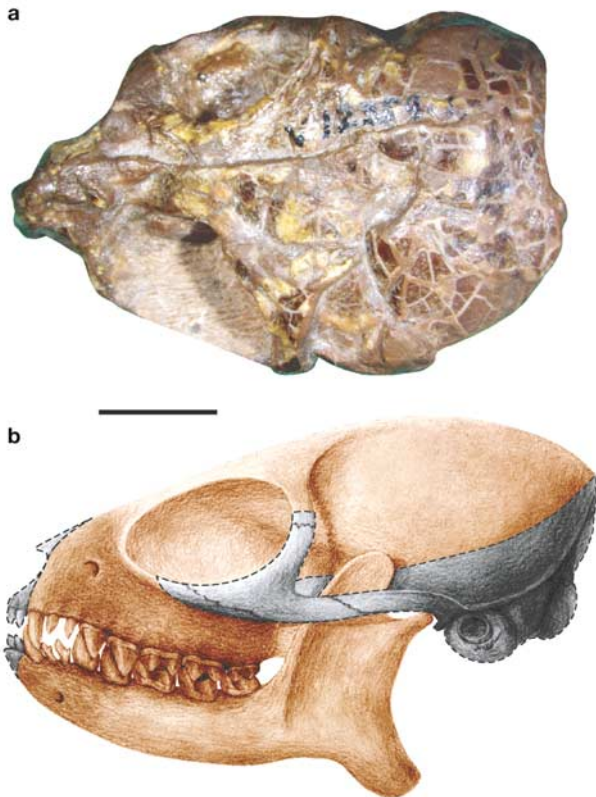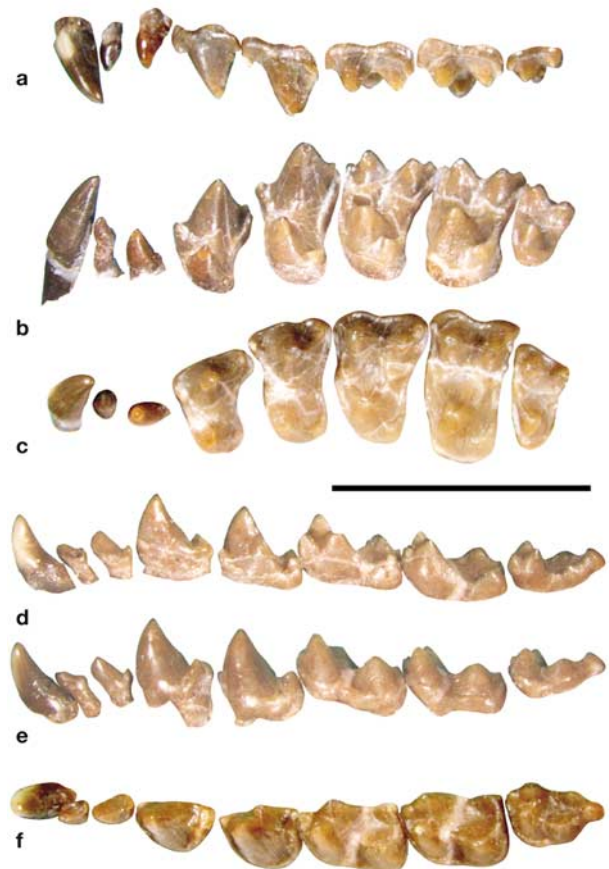

Figure 1 The skull of *Teilhardina asiatica* sp. nov. (IVPP V12357). **a**, Dorsal view of the skull. **b**, Reconstruction of the skull based on IVPP V12357, with grey shadow indicating the missing parts. Scale bar, 5 mm.

Figure 2 The dentition of *Teilhardina asiatica* sp. nov. (IVPP V12357). **a–c**, Lateral, occlusolingual and occlusal view of the left upper teeth row. **d-f**, Reversed lingual, lateral and occlusal view of the left lower teeth row. Scale bar, 5 mm.

the root. The premolarization of the lower canine is probably associated with the incisor I_1 enlargement. Later North American species of *Teilhardina* have an enlarged I_1, and their lower canines are premolariform and greatly reduced in size.

The P_{1-2} teeth are small and simple in morphology. Both are loosely spaced and implanted in line with other cheek teeth. Reduction of the P_1 is an evolutionary trend among species of *Teilhardina*[18]. *T. belgica* and *T. americana* possess a laterally displaced and very small P_1, whereas other derived North American species may completely lack the tooth. The P_1 of *T. asiatica* is less reduced and not laterally displaced in comparison with those of *T. belgica* and *T. americana*, representing a more primitive condition within the genus.

The differences in the P_3–M_3 teeth among *T. belgica*, *T. americana* and *T. asiatica* are minor. *T. americana* is more derived than the other two species in having a relatively higher metaconid on the P_4 and a higher entoconid on lower molars. *T. asiatica* possesses a slightly more distinctive cuspule on the posterolingual end of the heel of P_3 and P_4.

An isolated incisor derived from the type specimen is identified as I_2, judging from its wear facet. The tooth is tiny compared with the canine and has a relatively robust root. The neck and root of the tooth are mesiodistally compressed, whereas the crown is labiolingually compressed. The previously known lower incisor of the

North American *Teilhardina* is enlarged and lanceolate. The incisor alveolus of *T. belgica* indicates that the primitive state of the lower incisor of *Teilhardina* may be small. *T. asiatica* shows that the un-enlarged lower incisor of *Teilhardina* is not lanceolate but more nearly spatulate.

Previously, six species of *Teilhardina* have been reported based primarily on dental material: *T. belgica*, *T. americana*, *T. brandti*, *T. crassidens*, *T. tenuicula*, and *T. demissa*. Among those, *T. belgica* is considered to be the most primitive species, whereas *T. americana* is more derived than *T. belgica*. The earliest Eocene *T. brandti* is represented by only one M_2, and its taxonomic validity is questionable owing to the limited material[19]. Other North American species of *Teilhardina* are all considered to be more derived than *T. americana*. *T. asiatica* is morphologically very close to *T. belgica*, and some dental characters, such as less reduced P_1 and loosely spaced anterior premolars, are more primitive than the latter.

Steinius vespertinus was previously considered to be dentally as primitive as *Teilhardina* or more so[3,20]. However, the anteroposteriorly compacted P_1 and P_2, enlarged I_1, wider lateral cingulids on premolars and molars in *S. vespertinus* indicate that it is more derived than *T. asiatica* and *T. belgica*. The relative size of P_3 to M_1 and the length/width ratios of P_3 and P_4 among *S. vespertinus*, *T. asiatica* and *T. belgica* are similar, making it improper to evaluate evolutionary degree among these species using those features. Relatively larger M_3 in *S. vespertinus* is probably a derived character of omomines rather than a primitive trait relative to that of *Teilhardina*.

Our morphology analysis suggests that *T. asiatica* is a basal omomyid and cannot be far from the euprimate stem. This view is consistent with the results of a cladistic analysis (Fig. 3). Our phylogenetic analysis supports the previous hypothesis that euprimates are basally dichotomous[4,14,21,22]. *T. asiatica* and *T. belgica* form a sister-group that is situated at the base of the omomyid–tarsier–
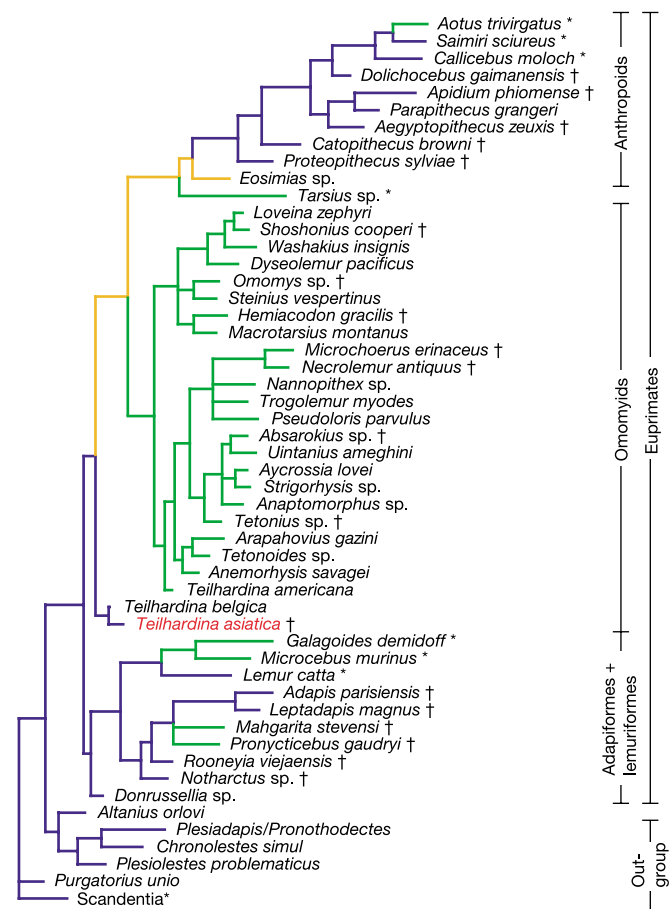

Figure 3 Strict consensus of 33 equally parsimonious trees with the optimization of activity patterns. Tree length = 2,076, Consistency index (CI) = 0.3685, Retention index (RI) = 0.5519. Asterisks denote extant taxa. Daggers denote the terminal taxa presenting reconstructions of activity patterns (data are from refs 7, 23, 30). Blue, diurnal; green, nocturnal; orange, equivocal. Scale bar, 30 characters.
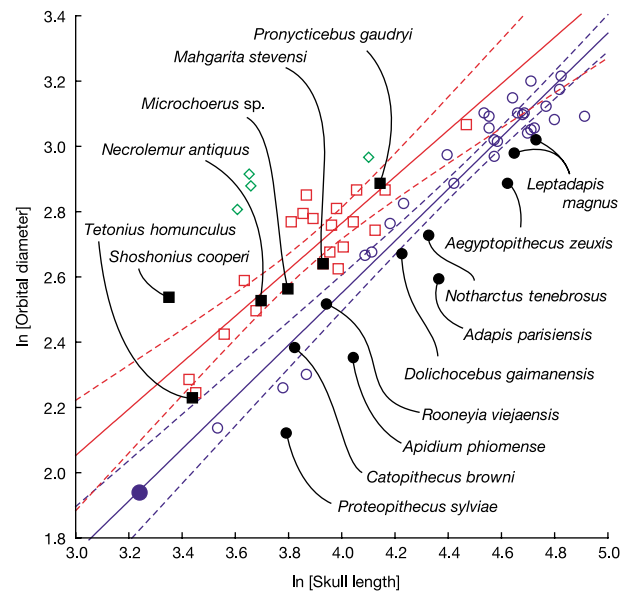

Figure 4 Bivariate plot of ln[orbital diameter] and ln[skull length] for extant and fossil primates. The red and blue lines are linear fits for extant nocturnal strepsirrhines and extant diurnal primates respectively. Dashed lines show 95% confidence intervals. Open blue circle, extant diurnal primates; red square, extant nocturnal strepsirrhines; green rhombus, extant nocturnal haplorhines; solid blue circle, *Teilhardina asiatica*; filled black circle, reconstructed diurnal fossil primates; filled black square, reconstructed nocturnal fossil primates. We note that *T. asiatica* falls in the extrapolated range of diurnal primates.

anthropoid clade. Interestingly, however, the more derived *T. americana* is not grouped with *T. asiatica* and *T. belgica*, suggesting that the conventional *Teilhardina* is probably a polyphyletic taxon (see Supplementary Information).

Based on the functional/adaptive interpretation of the relative size of orbits, omomyids, except phylogenetically enigmatic *Rooneyia*, were reconstructed as nocturnal animals[7,13,23]. *T. asiatica* as the most primitive omomyid, however, shows relatively smaller orbital size compared to other omomyids, and falls in the extrapolated range of diurnal forms rather than nocturnal ones (Fig. 4, see also Supplementary Information). This argues that the nocturnality of omomyids must be a derived activity pattern. Because *T. asiatica* is phylogenetically near the root of the euprimate radiation, the reconstruction of diurnal activity pattern for the species counts as evidence against the proposal that the ancestral euprimates were nocturnal. On the basis of the current phylogenetic relationship (Fig. 3), it is the most parsimonious interpretation that the last common ancestor of euprimates was diurnal.

The body weight of *T. asiatica* estimated from the M_1 size is about 28 g, well under the Kay's threshold[4,24,25]. The M_2 shear ratio[26] of 2.09 falls into the range of primates feeding on insects[26]. In addition, with its large canines, and sharp-pointed premolars with well-developed shearing crests, *T. asiatica* is undoubtedly insectivorous. Relatively large and convergent orbits indicate that *T. asiatica* must rely more on vision for predation than plesiadapiforms (although it may also have well-developed vibrissae). From this aspect, the new skull undermines a recent hypothesis that the euprimate was evolved from a *Carpolestes*-like terminal fruit-feeder in the latest Palaeocene[11]. The last common ancestor of stem euprimates, if it mirrored *T. asiatica* in morphology, would be portrayed as a small, diurnal, visually oriented predator. This would have positioned earliest euprimates in a very different ecological niche from that occupied by apparently more frugivorous, less visually oriented carpolestids, and would therefore argue against the hypothesis that euprimates replaced carpolestids ecologically in the Eocene[11] (see also ref. 12). ☐

Methods

Measurements

Measurements were taken with an optical reticle on a Motic microscope. Infraorbital foramen and tooth measurements were taken at magnifications of ×30, others at ×6. Teeth are denoted as I for incisor, C for canine, P for premolar, and M for molar. Super- and subscript numbers indicate upper and lower teeth.

Cladistic analysis

The data used in the analyses were derived from a published matrix[21]. We modified the original data set to incorporate recent findings, expanding it to include 12 additional characters and three additional taxa. In total, 303 characters (194 dental, 49 cranial, 56 postcranial and four soft tissue characters) and 52 taxa (five as outgroup) were included. All characters were equally weighted; partial characters were determined as ordered. A heuristic search was undertaken in PAUP 4.0b10 (ref. 27) with 5,000 replications. A strict consensus tree of all equally most parsimonious alternatives was computed.

Dietary habits and activity pattern reconstruction

Primate dietary habits are closely linked with body size. Leaf-eating primates have body weights of greater than 500 g (Kay's threshold), whereas insectivorous primates tend to weigh less than this limit[4,24,25]. We estimated the body weight of *T. asiatica* from the M_1 area by using Gingerich's empirical equation for tarsioids[25]. An insectivorous primate can also be distinguished from a fruit-eating one by its more-developed molar shearing crests[24,26,28]. We measured the length of shearing crests 1–6 on M_2 as defined in ref. 28, and calculated the mean shear ratio following ref. 26.

Osteological evidence from living primates reveals that the orbit size relative to skull length is strongly correlated with activity pattern[7,13,14,23]. When ln[orbit length] is plotted against ln[skull length], the nocturnal and diurnal primates have different best-fit lines. The nocturnal primate has relatively larger orbit length than the diurnal form for a given skull length. Natural logarithmic species means of orbital diameter and skull length for 52 extant primate species (28 diurnal primates; 20 nocturnal strepsirrhines; four nocturnal haplorhines) from publications[23] were analysed using a bivariate plot. Large-bodied diurnal primates (for example, baboon, gelada, mandrill, chimpanzee and human) are not included in the analysis because they are much more derived than other primates in skull shape. Regression lines for diurnal primates and nocturnal strepsirrhines were calculated separately: for diurnal primate, ln[orbital diameter] $= -0.64 + 0.80 \times$ ln[skull length],

$R^2 = 0.92$; for nocturnal strepsirrhines, ln[orbital diameter] $= -0.08 + 0.71 \times$ ln[skull length], $R^2 = 0.79$. Measurements (in millimetres) for *T. asiatica* and the other 15 fossil euprimates were plotted together with the extant species to determine the most likely activity patterns.

To detect the evolution of euprimates' activity patterns from a phylogenetic perspective, we optimized the reconstructed activity patterns for fossil euprimates together with the extant ones on the phylogeny tree, using the maximum parsimony rule. Character mapping was conducted in MacClade 3.0 (ref. 29).

1. Simons, E. L. *Primate Evolution: an Introduction to Man's Place in Nature* (Macmillan, New York, 1972).
2. Szalay, F. S. & Delson, E. *Evolutionary History of the Primates* (Academic, London, 1979).
3. Rose, K. D., Godinot, M. & Bown, T. M. in *Anthropoid Origins* (eds Fleagle, J. G. & Kay, R. F.) 1–28 (Plenum, New York, 1994).
4. Fleagle, J. G. *Primate Adaptation and Evolution* 2nd edn (Academic, London, 1999).
5. Bowen, G. J. *et al.* Mammalian dispersal at the Paleocene/Eocene boundary. *Science* 295, 2062–2065 (2002).
6. Cartmill, M. in *The Functional and Evolutionary Biology of Primates* (ed. Tuttle, R.) 97–122 (Aldine Atherton, Chicago, 1972).
7. Heesy, C. P. & Ross, C. F. Evolution of activity patterns and chromatic vision in primates: morphometrics, genetics and cladistics. *J. Hum. Evol.* 40, 111–149 (2001).
8. Li, W.-H. Genetic systems of color vision in primates. *Am. J. Phys. Anthropol.* 30 (suppl.), 318 (2000).
9. Tan, Y. & Li, W.-H. Trichromatic vision in prosimians. *Nature* 402, 36 (1999).
10. Surridge, A. K., Osorio, D. & Mundy, N. I. Evolution and selection of trichromatic vision in primates. *Trends Ecol. Evol.* 18, 198–205 (2003).
11. Bloch, J. I. & Boyer, D. M. Grasping primate origins. *Science* 298, 1606–1610 (2002).
12. Kirk, E. C., Cartmill, M., Kay, R. F. & Lemelin, P. Comment on "Grasping primate origins". *Science* 300, 741 (2003).
13. Kay, R. F. & Cartmill, M. Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea? Primates), with a description of a new genus and species. *J. Hum. Evol.* 6, 19–53 (1977).
14. Martin, R. D. *Primate Origins and Evolution: a Phylogenetic Reconstruction* (Chapman and Hall, London, 1990).
15. Ravosa, M. J., Noble, V. E., Hylander, W. L., Johnson, K. R. & Kowalski, E. M. Masticatory stress, orbital orientation and the evolution of the primate postorbital bar. *J. Hum. Evol.* 38, 667–693 (2000).
16. Ross, C. F. Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. *J. Hum. Evol.* 29, 201–227 (1995).
17. Godinot, M. *et al.* Nouvelles données sur les mammifères de Palette (Eocène inférieur, Provence). *Münchner Geowiss. Abh.* 10, 237–288 (1987).
18. Bown, T. M. & Rose, K. D. Patterns of dental evolution in Early Eocene Anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. *J. Paleontol.* 61(s; supplement), 1–162 (1987).
19. Gunnell, G. F. & Rose, K. D. in *The Primate Fossil Record* (ed. Hartwig, W. C.) 45–82 (Cambridge Univ. Press, Cambridge, 2002).
20. Rose, K. D. & Bown, T. M. Additional fossil evidence on the differentiation of the earliest euprimates. *Proc. Natl Acad. Sci. USA* 88, 98–101 (1991).
21. Ross, C., Williams, B. A. & Kay, R. F. Phylogenetic analysis of anthropoid relationships. *J. Hum. Evol.* 35, 221–306 (1998).
22. Kay, R. F., Ross, C. & Williams, B. A. Anthropoid origins. *Science* 275, 797–804 (1997).
23. Kay, R. F. & Kirk, E. C. Osteological evidence for the evolution of activity pattern and visual acuity in primates. *Am. J. Phys. Anthropol.* 113, 235–262 (2000).
24. Kay, R. F. The functional adaptation of primate molar teeth. *Am. J. Phys. Anthropol.* 43, 195–216 (1975).
25. Gingerich, P. D. Early Cenozoic Omomyidae and the evolutionary history of Tarsiiform primates. *J. Hum. Evol.* 10, 345–374 (1981).
26. Williams, B. A. & Covert, H. H. New early Eocene anaptomorphine primate (Omomyidae) from the Washakie Basin, Wyoming, with comments on the phylogeny and paleobiology of anaptomorphines. *Am. J. Phys. Anthropol.* 93, 323–340 (1994).
27. Swofford, D. L. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4* (Sinauer, Sunderland, 2000).
28. Kay, R. F. & Hiiemae, K. M. Jaw movement and tooth use in recent and fossil primates. *Am. J. Phys. Anthropol.* 40, 227–256 (1974).
29. Maddison, W. P. & Maddison, D. R. *MacClade: Analysis of Phylogeny and Character Evolution, Version 3.0* (Sinauer, Sunderland, 1992).
30. Covert, H. H. in *Creatures of the Dark: The Nocturnal Prosimians* (eds Alterman, L., Doyle, G. A. & Izard, M. K.) 495–509 (Plenum, New York, 1995).