may thus be far more significant for large-scale environmental changes than previously thought. ☐

Methods

Dried and ground sediment samples were ultrasonically extracted with organic solvents. Total lipid fractions (containing the alkenones) were obtained by methylation of the extract, elution over a small silica column using ethyl acetate and silylation. Apolar fractions (containing the *n*-alkanes) were obtained by column chromatography over $AgNO_3$-impregnated, activated Al_2O_3 eluted with hexane:dichloromethane (9:1). Internal standards were added for quantification. Compounds were analysed on a Hewlett Packard 5890 series II gas chromatograph using flame ionization detection (FID) and identified by gas-chromatography mass-spectrometry analyses of selected samples. Quantification of compounds was performed by peak area integration in FID chromatograms. For SST estimation, the simplified unsaturation index ($U^{K'}_{37}$) was calculated from the peak areas of the di- and triunsaturated C_{37} alkenones in total lipid fractions. The conversion to SST estimates was done using: SST (°C) $= (U^{K'}_{37} - 0.044)/0.033$ (ref. 27). The standard deviation (± 1 s.d.) based on duplicate and triplicate analyses of our samples is 0.3 °C. The compound-specific stable carbon isotopic composition of *n*-alkanes was measured through gas chromatography isotope ratio monitoring mass spectrometry using a Finnigan Delta C mass spectrometer. CO_2 gas with known isotopic composition was used as reference. Analyses were done at least in duplicate. Standard deviations of $\delta^{13}C$ values (± 1 s.d.) were better than 0.5‰ against PDB.

Received 28 August 2002; accepted 18 February 2003; doi:10.1038/nature01500.

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Acknowledgements We thank the Ocean Drilling Program for providing samples. The investigations were supported by the Research Council for Earth and Life Sciences with financial aid from the Netherlands Organisation for Scientific Research.

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

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Fossil evidence for an ancient divergence of lorises and galagos

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Morphological, molecular, and biogeographic data bearing on early primate evolution suggest that the clade containing extant (or 'crown') strepsirrhine primates (lemurs, lorises and galagos) arose in Afro-Arabia during the early Palaeogene[1], but over a century of palaeontological exploration on that landmass has failed to uncover any conclusive support for that hypothesis[2]. Here we describe the first demonstrable crown strepsirrhines from the Afro-Arabian Palaeogene—a galagid and a possible lorisid from the late middle Eocene of Egypt, the latter of which provides the earliest fossil evidence for the distinctive strepsirrhine toothcomb. These discoveries approximately double the previous temporal range of undoubted lorisiforms and lend the first strong palaeontological support to the hypothesis of an ancient Afro-Arabian origin for crown Strepsirrhini and an Eocene divergence of extant lorisiform families[1,3].

The primate clade Strepsirrhini—now represented by the distinctive 'toothcombed' prosimians of the Old World tropics and Madagascar—is one of the three major extant primate groups alongside Anthropoidea (monkeys, apes and humans) and Tarsiiformes (tarsiers). Within Strepsirrhini, it is clear that a major dichotomy exists between a monophyletic Lorisiformes (containing African galagos or 'bushbabies' and African and Asian lorises) and a monophyletic (and wholly Malagasy) Lemuriformes[1,4–6], but a poor strepsirrhine fossil record has left the age and place of origin of their common ancestor open to debate[7,8]. Given the probable paraphyly of African lorisiforms with respect to Asian lorises[1,3,6], the proximity of Madagascar to the African mainland[9], and the distribution of more generalized primates in the Palaeogene fossil record of northern continents and Africa[10], it is now generally believed that extant strepsirrhines shared a common Afro-Arabian ancestor[1,3], but the earliest undoubted record of crown Strepsirrhini has long been that of early Miocene (about 20 Myr old) lorisids (lorises) and galagids (galagos) from east Africa[11,12]. These Miocene lorisiforms considerably postdate estimates of basal strepsirrhine divergence times that have been reconstructed using local molecular clocks, which suggest a divergence of lorisiforms and lemuriforms 50–62 Myr ago, and a much wider window of 23–55 Myr for the divergence of lorisids and galagids[1,3,6].

Palaeontological work in 2001 led to the recovery of two Palaeogene lorisiforms from a single fossil locality, Birket Qarun Locality 2 (BQ-2), that is situated 183 m below the contact of the Qasr el Sagha and Jebel Qatrani formations north of Birket Qarun in the Fayum Depression, Egypt. This horizon was recently placed in the lowermost (Umm Rigl) Member of the Qasr el Sagha Formation[13], but renewed work indicates that these fossiliferous alluvial sediments are lithologically distinctive and best retained in the Birket Qarun Formation (T.M. Bown, personal communication), as suggested by earlier research[14,15]. Broadly contemporaneous deposits in the Fayum Depression have been assigned either a basal Priabonian[13] (earliest late Eocene, <36.9 Myr ago) or Bartonian (late middle Eocene, 41.2–36.9 Myr ago)[16] age; we favour the latter interpretation as it is more consistent with palaeomagnetic[17] and faunal[18] evidence from overlying sediments. Specimens described here were recovered either by dry-sieving of loose sediment or by quarrying of bioclastic ironstone conglomerate.

Primates Linnaeus, 1758
Strepsirrhini Geoffroy, 1812
Lorisiformes Gregory, 1915
?Lorisidae Gray, 1821
Karanisia gen. nov.

Etymology. In reference to the nearby Ptolemaic/Roman ruins of Karanis.
Diagnosis. Differs from all other lorisiforms in exhibiting the following combination of characters: unicuspid lower fourth premolar P_4 with continuous buccal and lingual cingulids, continuous buccal cingulids on lower molars, M_3 longer than M_2 with a large hypoconulid lobe, no P^4 metacone or hypocone, complete buccal and lingual cingula on P^4 through M^3, upper molars with hypocone lobe, weakly concave distal margins (Fig. 1a) and small crestiform hypocones.

Karanisia clarki sp. nov.

Etymology. Specific name is in honour of the late anatomist Wilfred Le Gros Clark, who predicted that expeditions to the Fayum region would shed light on early strepsirrhine evolution.
Holotype. CGM 40265, left mandible preserving M_1 to M_3 (Fig. 1c).
Horizon and locality. Bartonian Birket Qarun Formation, northern Egypt, locality BQ-2.
Diagnosis. As for genus; mean body mass estimate of 273 g (95% confidence interval = 241–304 g) based on M_1 area[19]. For hypodigm, description, and metrics, see Supplementary Information.

Primates Linnaeus, 1758
Strepsirrhini Geoffroy, 1812
Lorisiformes Gregory, 1915
Galagidae Mivart, 1864
Saharagalago gen. nov.

Etymology. Generic name is a combination of *sahara*, Arabic word for desert, and the common name for members of the family Galagidae.
Diagnosis. Differs from other living and extinct galagids in having having upper molars that are relatively less broad buccolingually, a trenchant prehypocrista coursing from the hypocone to the postprotocrista, and continuous buccal cingulids on lower molars.

Saharagalago misrensis sp. nov.

Etymology. From *Misr*, Arabic word for Egypt.
Holotype. CGM 40266, a left M_1 (Fig. 1f).
Horizon and locality. Bartonian Birket Qarun Formation, northern Egypt, locality BQ-2.
Diagnosis. As for genus; body mass estimate of 122 g based on M_1 area. For hypodigm, description, and metrics, see Supplementary Information.

An isolated lower canine attributable to *K. clarki* exhibits extreme mesiodistal compression, a grossly elongate and procumbent crown, a mesially inflected root, a lingually restricted distal cingu-

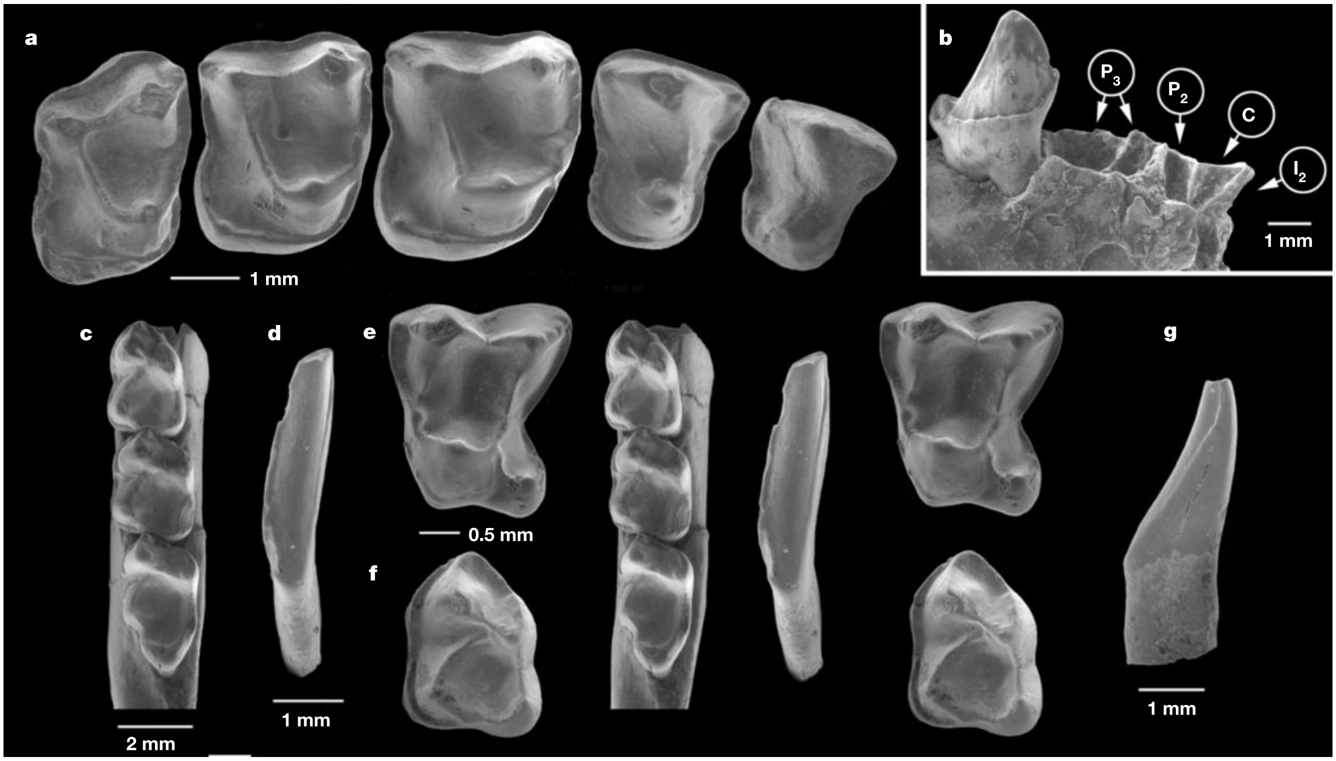

Figure 1 Middle Eocene lorisiforms from northern Egypt. **a**, isolated upper teeth of *Karanisia clarki* gen et sp. nov.: P^3 (DPC 21371B), P^4 (DPC 21214E, reversed), M^1 (DPC 21639C), M^2 (DPC 21636E), M^3 (DPC 21365C)]. **b**, right mandible of *K. clarki* (DPC 21249) illustrating size and orientation of damaged alveoli for lower anterior dentition. P, premolar; C, canine; I, incisor. **c**–**g**, Stereomicrographs of **c**, *K. clarki* holotype (CGM 40265), left mandible preserving M_1 to M_3; **d**, isolated left lower canine (DPC 21487B) of *K. clarki*; **e**, *Saharagalago misrensis* gen et sp. nov. probable M^1 (DPC 21214B); **f**, *S. misrensis* holotype M_1 (CGM 40266); **g**, *K. clarki* left lower canine (DPC 21487B), mesial face.

lum, and no distal interstitial wear facet, as is typical of crown strepsirrhine canines (Fig. 1d, g). The size and morphology of the anterior alveoli preserved in a partial mandible of this taxon (Fig. 1b) help to confirm that this tooth was incorporated into a toothcomb like that observable in all extant strepsirrhines aside from the autapomorphic aye-aye (*Daubentonia*). The mesial face of the canine preserves a number of irregularly spaced microscopic grooves coursing perpendicular to the long axis of the crown that are consistent with those created by the passage of hair during grooming[20]. In the upper dentition, *Karanisia* and *Saharagalago* share a constellation of characters (concave distal crown margin delimiting a large hypocone lobe, small paraconule confluent with preprotocrista, no metaconule, trenchant postprotocrista) that is otherwise restricted to Miocene–Recent lorisiforms in the entirety of primate evolutionary history. The upper molar features that *Saharagalago* shares with Miocene–Recent galagids (even greater emargination of the distal crown margin, lingual distension of the hypocone lobe with respect to the lingual face of the protocone, absence of lingual and buccal cingula, long and buccally directed postmetacrista, flaring of the molar margin buccal to the metacone, presence of a prehypocrista) are even more distinctive and of more restricted distribution (Fig. 2).

An equally weighted parsimony analysis (Fig. 3) of 2,079 nucleotide characters (previously published[21] mitochondrial cytochrome *b* and nuclear interphotoreceptor retinoid binding protein (IRBP) genes), 279 morphological characters, and one biogeographic character provides reasonably strong support for *Saharagalago*'s galagid status, while *Karanisia* is precariously placed within a poorly supported Lorisidae as the sister taxon of extant *Arctocebus*. The possibility of a *Karanisia*–*Arctocebus* clade might be easily dismissed were it not for the fact that molecular sequence data have uniformly rendered Lorisidae paraphyletic with respect to Galagidae[6,21], thus implying that divergences among extant lorises (whether paraphyletic or monophyletic[21,22]) are likely to have occurred very shortly after the appearance of crown Lorisiformes. With *Saharagalago* now documenting the divergence of Galagidae from other lorisiforms by the late middle Eocene, we see no compelling basis for rejecting *Karanisia*'s crown lorisid placement on either temporal or available morphological grounds, although missing data and weak bootstrap support certainly leave open the possibility that *Karanisia* is a more basal stem lorisid or stem lorisiform. Unfortunately, this genus sheds little light on the affinities of an isolated primate M^3 from the early Oligocene of Egypt originally identified as lorisiform[23], but more recently reinterpreted as being anthropoid[24,25] or possibly plesiopithecid[22]; more material of this taxon is needed before any of these competing hypotheses can be decisively rejected.

The great antiquity of Galagidae implied by these discoveries is consistent with the inferred[1] early Eocene divergence of galagids and lorisids based on the mitochondrial cytochrome *b* gene, but contrasts strongly with the suggested[6] early Miocene divergence of these families based on the nuclear ε-globin locus. Some interpretations of the scanty lorisiform fossil record have similarly suggested a possible early Miocene divergence of lorisids and galagids[22], but new fossils from the early Miocene of east Africa appear to attest to a much more ancient split[26], as do our discoveries. As a means for investigating the possible implications of these ancient fossil lorisiforms for the timing of crown strepsirrhine origins, we employed heuristic quartet dating (using QDate v. 1.11[27]) of the concatenated cytochrome *b* and IRBP data set of ref. 21 using what is presumably a highly conservative[1,3,6] (but palaeontologically unverified) minimum estimate of crown lemuriform origins equal to our similarly conservative inferred minimum split of galagids and Asian lorisids at 38 Myr ago. The resulting window of minimum estimates for the

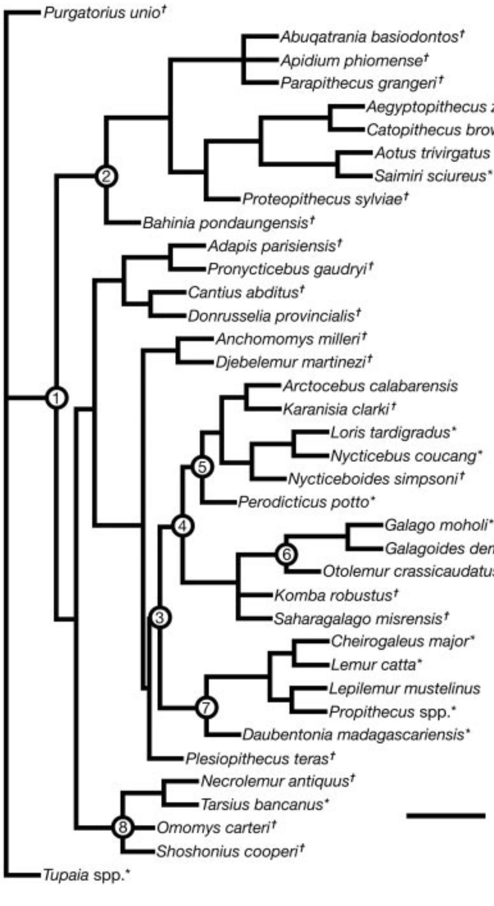

Figure 3 Strict consensus of 16 equally parsimonious trees recovered in PAUP 4.0 b10 (ref. 30). Data derived from an equally weighted parsimony analysis of a matrix containing 38 taxa and 2,359 molecular, morphological, and biogeographic characters. Branches are scaled relative to bootstrap support (1,000 replicates). Asterisks denote taxa for which cytochrome *b* and IRBP sequences are available; daggers denote fossil taxa. In cases where the majority-rule bootstrap topology resolved polytomies present in the strict consensus topology, those clades are here shown as resolved. Numbered nodes are: (1) crown Primates, (2) Anthropoidea, (3) crown Strepsirrhini, (4) crown Lorisiformes, (5) crown Lorisidae, (6) crown Galagidae, (7) crown Lemuriformes, and (8) Tarsiiformes. Tree length = 3,807, consistency index excluding uninformative characters = 0.40, retention index = 0.48. Assigning morphological characters weights eight times those of molecular characters produced no change in topology; constraining the tree to recover Haplorhini (a *Tarsius*–Anthropoidea clade excluding Strepsirrhini) did not alter relationships within crown Strepsirrhini. Scale bar represents 100 bootstrap support units.

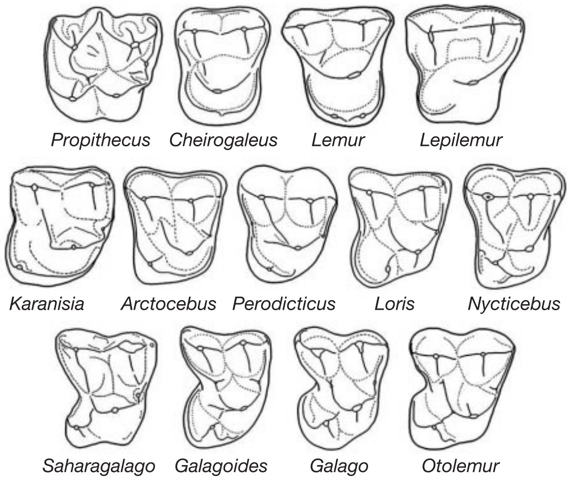

Figure 2 First upper molars of extant strepsirrhines represented in cladistic analysis (modified from Maier[29]) compared with those of *K. clarki* and *S. misrensis* (reversed).

age of the last common ancestor of lorisiforms and lemuriforms ranged from 49.7 to 53.3 Myr ago (95% confidence interval = 46.9–57.3 Myr ago).

Given that molecular dating has consistently supported an earlier origin for crown lemuriforms than for crown lorisiforms[1,3,6], and that palaeontological sampling of the early crown strepsirrhine radiation remains woefully inadequate[8,28], it is remarkable that such early dates are likely to considerably underestimate the true antiquity of the lemuriform–lorisiform split. Nevertheless, by doubling the previous minimum paleontological estimate for the age of crown Lorisiformes, *Karanisia* and *Saharagalago* provide the first convincing fossil evidence attesting to such an ancient origin for crown Strepsirrhini, and further bolster the hypothesis that that clade originated on the Afro-Arabian landmass[1,3]. These taxa also help to inform at least one other major outstanding issue within the clade—the timing of the lemuriform colonization of Madagascar[9]. Although Marivaux *et al.*[7] have recently suggested that early Oligocene *Bugtilemur* from Pakistan is a cheirogaleid lemur specifically aligned with extant *Cheirogaleus* (a conclusion that we must view with skepticism given *Bugtilemur*'s location and age), the current restriction of lemurs to Madagascar would, nevertheless, still be most parsimoniously explicable as the result of a single invasion[1,3]. As molecular data suggest that *Daubentonia* diverged from other crown lemuriforms very shortly after the appearance of crown strepsirrhines[1,3,6], and before the divergence of galagids from other lorisiforms, it is now reasonable to infer that, at the very latest, lemurs reached Madagascar by the late middle Eocene. ☐

Received 9 October 2002; accepted 3 February 2003; doi:10.1038/nature01489.

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Supplementary Information accompanies the paper on *Nature*'s website (◗ **http://www.nature.com/nature**).

Acknowledgements We thank K. Soliman, A. Swedan, A. Hassen, F. Imbabi, and the numerous other scientists from the Egyptian Geological Survey and Mining Authority and the Egyptian Geological Museum who have supported and facilitated our collaborative palaeontological work in northern Egypt. P. Chatrath managed field operations in Egypt. T. M. Bown discovered BQ-2, and together with M. Mathison measured the geological section reported herein. T. M. Bown, P. Chatrath and M. Mathison also helped with collecting during the 2001 season along with A. Abd el-Ghafar, M. Abd el-Ghany, Y. Abd el-Razik, H. Ali, J. Fleagle, G. Kamel, A. Hassen, M. Hassen Taha, C. Heesy, L. Jolly, P. Lewis, G. Mohamed, S. Mohamed, R. Patnaik and M. Zakaria. We thank F. Ankel-Simons, R. Martin, J. Rossie, T. Ryan, C. Simons and A. Yoder for discussion and/or comments on the manuscript. Recent work in Egypt has been generously supported by a National Science Foundation grant to E.L.S. and Leakey Foundation grants to E.R.S.

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

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Earliest known crown-group salamanders

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Salamanders are a model system for studying the rates and patterns of the evolution of new anatomical structures[1–4]. Recent discoveries of abundant Late Jurassic and Early Cretaceous salamanders are helping to address these issues[5–8]. Here we report the discovery of well-preserved Middle Jurassic salamanders from China, which constitutes the earliest known record of crown-group urodeles (living salamanders and their closest relatives). The new specimens are from the volcanic deposits of the Jiulongshan Formation (Bathonian)[9–13], Inner Mongolia, China, and represent basal members of the Cryptobranchidae, a family that includes the endangered Asian giant salamander (*Andrias*) and the North American hellbender (*Cryptobranchus*). These fossils document a Mesozoic record of the Cryptobranchidae, predating the previous record of the group by some 100 million years[14–17]. This discovery provides evidence to support the hypothesis that the divergence of the Cryptobranchidae from the Hynobiidae had taken place in Asia before the Middle Jurassic period.

Amphibia Linnaeus, 1758
Lissamphibia Haeckel, 1866
Caudata Scopoli, 1777
Urodela Dumeril, 1806
Cryptobranchoidea Dunn, 1922
Cryptobranchidae Fitzinger, 1826
Chunerpeton tianyiensis gen. et sp. nov.

Holotype. Chinese Academy of Geological Sciences (CAGS)-IG-02051, natural mould of dorsal and ventral aspects of an articulated