

Late middle Eocene epoch of Libya yields earliest known radiation of African anthropoids

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Reconstructing the early evolutionary history of anthropoid primates is hindered by a lack of consensus on both the timing and biogeography of anthropoid origins^{1–3}. Some prefer an ancient (Cretaceous) origin for anthropoids in Africa or some other Gondwanan landmass⁴, whereas others advocate a more recent (early Cenozoic) origin for anthropoids in Asia^{1,2,5}, with subsequent dispersal of one or more early anthropoid taxa to Africa. The oldest undoubted African anthropoid primates described so far are three species of the parapithecoid *Biretia* from the late middle Eocene Bir El Ater locality of Algeria⁶ and the late Eocene BQ-2 site in the Fayum region of northern Egypt⁷. Here we report the discovery of the oldest known diverse assemblage of African anthropoids from the late middle Eocene Dur At-Talah escarpment in central Libya. The primate assemblage from Dur At-Talah includes diminutive species pertaining to three higher-level anthropoid clades (Afrotarsiidae, Parapithecidae and Oligopithecidae) as well as a small species of the early strepsirhine primate *Karanisia*. The high taxonomic diversity of anthropoids at Dur At-Talah indicates either a much longer interval of anthropoid evolution in Africa than is currently documented in the fossil record or the nearly synchronous colonization of Africa by multiple anthropoid clades at some time during the middle Eocene epoch.

The chronology and biogeography of anthropoid origins have long been debated^{1–7}. Molecular estimates of anthropoid origins typically advocate an early origin for the group, often extending back to the late Cretaceous⁸. In contrast, palaeontological data generally support a Cenozoic origin for anthropoids, although a wide range of potential origination dates have been suggested on the basis of fossils, of ages ranging from Palaeocene to later Eocene¹. Similarly, there is no current consensus on where anthropoids originated. Since the discovery of a series of diverse anthropoid faunas in the Fayum region of Egypt, it has often been assumed that Africa was the birthplace of the anthropoid clade^{9–11}. This interpretation has been challenged by the discovery of multiple taxa of basal anthropoids in Asia^{5,12–15} and the recent finding that the putative early or middle Eocene African anthropoid *Algeripithecus* is actually a strepsirhine¹⁶. With the possible exception of the enigmatic *Altiatlasius koulchii* from the late Palaeocene epoch of Morocco¹⁷, the oldest African anthropoids acknowledged so far come from the late middle Eocene (about 40 Myr ago) Bir El Ater locality in Algeria⁶. Here we augment the record of African anthropoids from the late middle Eocene on the basis of a new micromammal assemblage from Dur At-Talah in central Libya (Fig. 1). This fauna includes a small-bodied strepsirhine and a diversity of basal anthropoids, including primitive representatives of Afrotarsiidae, Parapithecidae and Oligopithecidae. The age and diversity of the Dur At-Talah primate fauna indicates substantial gaps in either the African or the Asian fossil record of anthropoid evolution (and possibly both).

The Dur At-Talah escarpment was first explored palaeontologically during the second half of the twentieth century¹⁸. This early phase of exploration yielded a vertebrate fauna mainly composed of taxa having medium to large body size, such as the early proboscideans *Barytherium grave*, *Arcanothierium savagei* and *Moeritherium chehbeurameuri*. Our recent fieldwork at Dur At-Talah has focused on enhancing the vertebrate record from this region by concentrating on the previously neglected microfauna. In addition to the primates reported here, five taxa of phiomysid rodents have been identified so far¹⁹. Biostratigraphic correlation based mainly on rodents and proboscideans suggests that the Dur At-Talah fauna approximates that from Bir El Ater in Algeria¹⁹, which is regarded as late middle Eocene^{20,21}. This correlation is supported by the new data from fossil primates described here. Available biostratigraphic evidence is also consistent with palaeomagnetic data from the Dur At-Talah section, which suggest correlation with Chron 18n.1n (38–39 Myr ago; late Bartonian)¹⁹. Specimens described here are housed in the palaeontological collections of Al Fateh University (Tripoli, Libya).

Primates Linnaeus, 1758
Strepsirhini Geoffroy, 1812
Lorisiformes Gregory, 1915
Karanisia Seiffert *et al.*, 2003
Karanisia arenula, sp. nov.

Holotype. DT1-42, left M₂ (Fig. 2e).

Horizon and locality. DT-Loc.1, Bioturbated Unit, Bartonian Dur At-Talah escarpment, central Libya¹⁹.

Diagnosis. Differs from *Karanisia clarki*²² in being smaller (adult body mass is estimated at 120–132 g). For hypodigm, description and metrics, see Supplementary Information.

Etymology. arena (Latin): sand, refers to the sandy matrix that yielded the hypodigm; -ula (Latin): diminutive suffix, in allusion to the small size of this species.

Anthropoidea Mivart, 1864
Afrotarsiidae Ginsburg and Mein, 1987
Afrotarsius Simons and Bown, 1985
Afrotarsius libycus, sp. nov.

Holotype. DT1-35, left M₁ or M₂ (Fig. 2k, l).

Horizon and locality. DT-Loc.1, Bioturbated Unit, Bartonian Dur At-Talah escarpment, central Libya¹⁹.

Diagnosis. Differs from *Afrotarsius chatrathi*²³ in having narrower lower molars bearing hypoconid and entoconid cusps that are less isolated and less spire-like. Hypoconulid of M₁ or M₂ projects farther distally than in *A. chatrathi*. Adult body mass estimated at 130–232 g. For hypodigm, description and metrics, see Supplementary Information.

Etymology. Refers to the provenance of this species.

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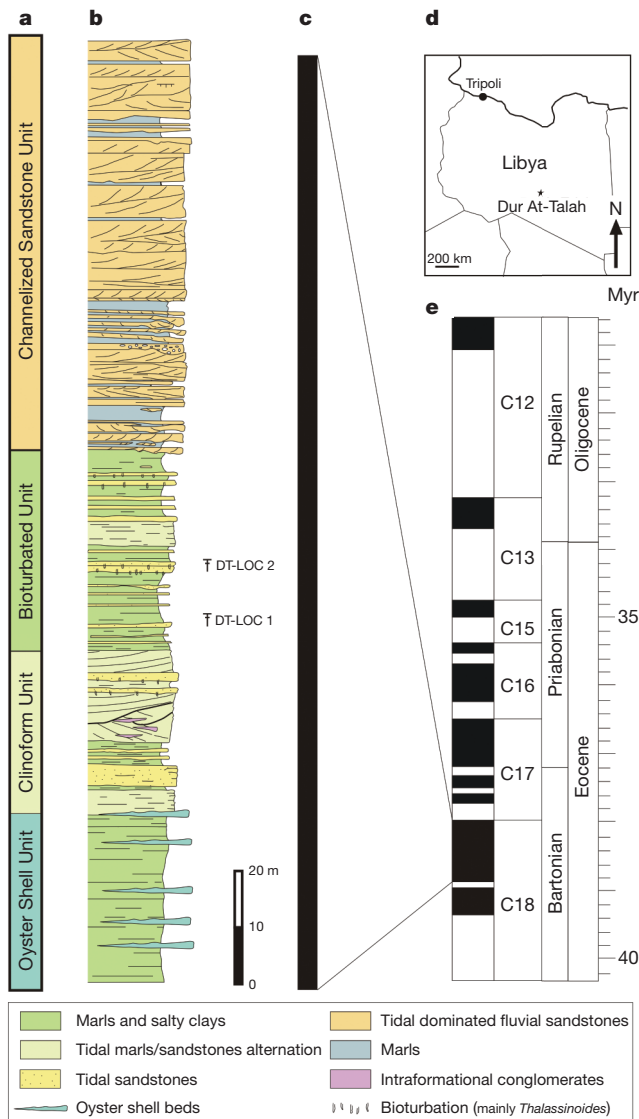


Figure 1 | Stratigraphy and correlation of the Dur At-Talah section. **a**, Stratigraphic units¹⁹. **b**, Lithology and sedimentology of the section. **c**, Local magnetic polarity stratigraphy (black bar indicates zone of normal polarity). **d**, Map of Libya showing the geographic position of the Dur At-Talah escarpment. **e**, Preferred correlation to the Geomagnetic Polarity Time Scale^{19,29}.

Parapithecidae Schlosser, 1911
Biretia piveteaui de Bonis et al., 1988

Referred material. DT1-26, left M¹; DT1-27, right M²; DT1-28, right M³; DT1-29, left M₃; DT2-23, right M³; DT2-24, right M₂ (Fig. 2q–w).

Horizon and locality. DT-Loc.1 and DT-Loc.2, Bioturbated Unit, Bartonian Dur At-Talah escarpment, central Libya¹⁹.

Emended diagnosis. *Biretia piveteaui*⁶ (adult body mass estimated at 292–470 g) is larger than *B. fayumensis*. M^{1–2} differ from those of *B. fayumensis*⁷ and *B. megalopsis*⁷ in having more isolated metaconules lacking any connection with either the protocone or the metacone. M³ mesiodistally shorter than that of *B. megalopsis*. M³ with smaller metacone and less extensive trigon lacking metaconule, in contrast to that of *B. megalopsis*. For description and metrics, see Supplementary Information.

Oligopithecidae Simons, 1989
Talahpithecus parvus, gen. et sp. nov.

Holotype. DT1-31, left M¹ or M² (Fig. 2n).

Horizon and locality. DT-Loc.1, Bioturbated Unit, Bartonian Dur At-Talah escarpment, central Libya¹⁹.

Diagnosis. Smaller (adult body mass estimated at 226–376 g) than *Catopithecus* and *Oligopithecus*. Upper molars without mesostyle and with smaller hypocone than in *Catopithecus*. Crests surrounding upper molar trigon more trenchant than in *Oligopithecus* and *Catopithecus*. Lower molars with relatively narrower talonid and higher trigonid with more nearly vertical postvallid than in *Oligopithecus* and *Catopithecus*. For hypodigm, description and metrics, see Supplementary Information.

Etymology. talah (Arabic): tree, refers to the provenance of this genus; parvus (Latin): small, refers to the size of this species.

All four primate taxa currently known from Dur At-Talah are remarkably small, ranging from 120 to 470 g in estimated adult body mass. Such a small size distribution for the earliest known African radiation of anthropoids reinforces the conclusion drawn from analysis of the middle Eocene primate assemblage of Shanghuang, China, that the origin of anthropoids occurred at very small body size²⁴. Indeed, if recent phylogenetic analyses recognizing oligopithecids as early members of the catarrhine clade are correct⁷, the small size of *Talahpithecus parvus* would suggest that even the origin of crown anthropoids and the platyrrhine/catarrhine divergence occurred at small body mass. However, by the time of the late Eocene L-41 primate fauna from the Fayum region of Egypt¹⁰, larger anthropoid taxa had begun to supplant these diminutive taxa, and this trend towards increasing body mass among early African anthropoids continued into the Oligocene epoch. The common occurrence of *Biretia piveteaui* at both Bir El Ater and Dur At-Talah supports a similar age for these faunas. The small size of *Karanisia arenula* from Dur At-Talah in comparison with *K. clarki* from BQ-2 in the Fayum, as well as the small size and primitive anatomy of *Talahpithecus parvus* in comparison with Fayum oligopithecids such as *Catopithecus browni*, reinforce biostratigraphic data from rodents and proboscideans suggesting that Dur At-Talah is roughly equivalent to Bir El Ater in age. Both of the latter faunas seem to be older than BQ-2 in the Fayum¹⁹.

The phylogenetic affinities of three of the four primate taxa documented at Dur At-Talah are uncontroversial, but there is no current consensus regarding the broader affinities of *Afrotarsius*, represented at Dur At-Talah by *A. libycus*. Originally described as a possible African tarsiid (hence the generic name)²³, multiple subsequent authors have suggested that *Afrotarsius* is a basal member of the anthropoid clade^{9,25,26}. The previously unknown upper-molar morphology of *Afrotarsius*, documented here, supports an attribution of this genus to Anthropoidea rather than Tarsiidae (or Tarsiiformes). Like those of Asian eosimiid anthropoids (*Eosimias*, *Phenacopithecus* and *Bahinia*)^{5,14}, the upper molars of *Afrotarsius* bear an elongated postmetacrista and an enlarged shelf-like structure buccal to the metacone. The upper molars of *Afrotarsius* and eosimiids also share transversely oriented crests that variably connect the paracone and metacone with their associated conules (or remnants thereof). The upper molars of *Afrotarsius* differ from those of eosimiids in retaining continuity between the postmetaconule crista and the postcingulum, which is lost in eosimiids. As noted by previous authors²⁵, M₃ of *Afrotarsius* is distinctively anthropoid-like (and differs from that of tarsiids) in having a remarkably abbreviated hypoconulid lobe (Fig. 2m). In view of these anatomical characters, we regard *Afrotarsius* as a relatively basal member of the anthropoid clade. However, substantial additional evidence will be required to ascertain how *Afrotarsius* relates to other early anthropoid taxa, particularly eosimiids. Dental similarities between *Afrotarsius* and tarsiids probably reflect the convergent acquisition of trenchant molar crests as an adaptation for insectivory.

The presence of three distinct clades of anthropoids (*Afrotarsiidae*, *Parapithecidae* and *Oligopithecidae*) in the late middle Eocene Dur At-Talah fauna is surprising, especially in view of the lower diversity of early anthropoids that has been described so far from the BQ-2 locality of late Eocene age in northern Egypt⁷. Recent comprehensive analyses of early anthropoid relationships disagree on many aspects of tree

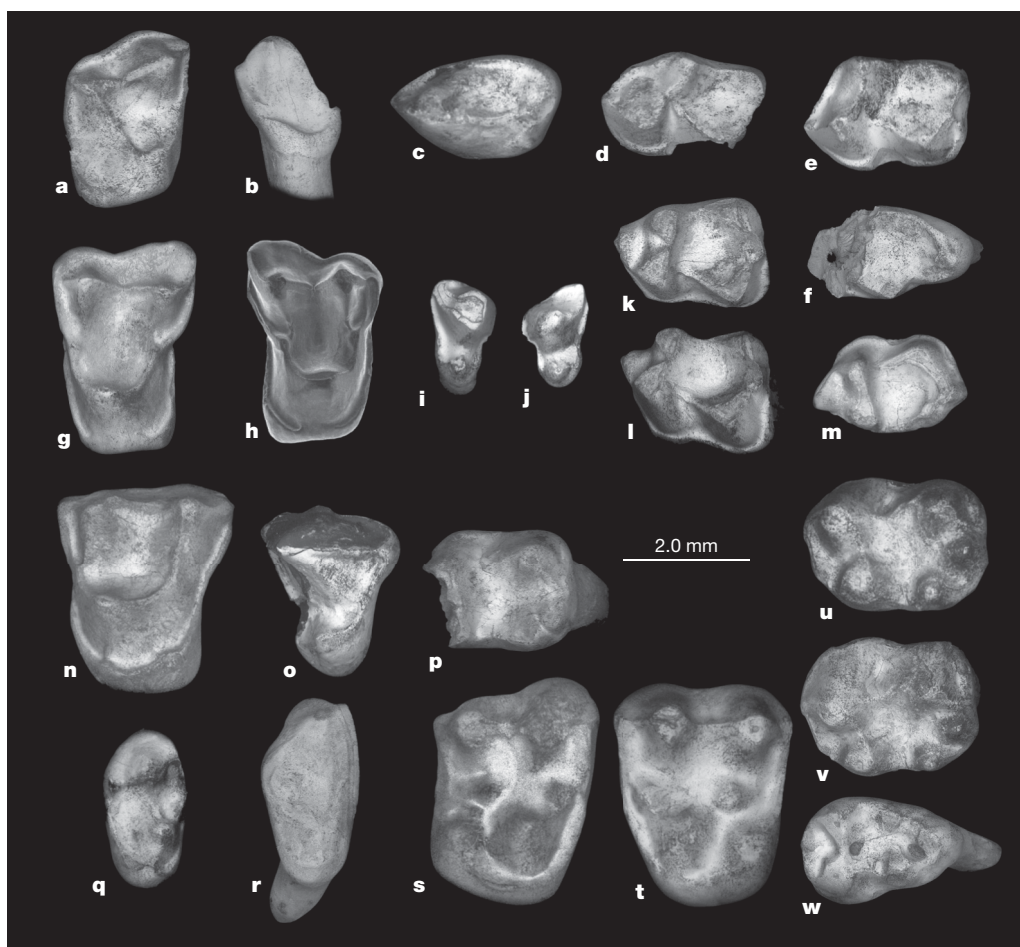


Figure 2 | Scanning electron microscope images of fossil primate teeth from Dur At-Talah. **a–f**, *Karanisia arenula* sp. nov. **a**, Right M^3 (DT1-37), occlusal view. **b**, Right P_3 (DT1-38), lingual view. **c**, Left P_4 (DT1-39), occlusal view. **d**, Left M_1 (DT1-41), occlusal view. **e**, Holotype left M_2 (DT1-42), occlusal view. **f**, Fragmentary left M_3 (DT1-43), occlusal view. **g–m**, *Afrotarsius libycus* sp. nov. **g**, Left M^2 (DT1-33), occlusal view. **h**, Right M^2 (DT1-34), occlusal view. **i**, Right P^3 (DT1-31), occlusal view. **j**, Left P^3 (DT1-32), occlusal view. **k**, Holotype left M_1 or M_2 (DT1-35), occlusal view. **l**, Holotype left M_1 or M_2

(DT1-35), oblique buccal view. **m**, Right M_3 (DT1-36), occlusal view. **n–p**, *Talahpithecus parvus* gen. et sp. nov. **n**, Holotype left M^1 or M^2 (DT1-31), occlusal view. **o**, Right P^4 (DT1-30), mesial oblique view. **p**, Fragmentary right M_1 or M_2 (DT1-32), occlusal view. **q–w**, *Biretia piveteaui*. **q**, Right M^3 (DT2-23), occlusal view. **r**, Right M^3 (DT1-28), occlusal view. **s**, Right M^2 (DT1-27), occlusal view. **t**, Left M^1 (DT1-26), occlusal view. **u**, Right M_2 (DT2-24), occlusal view. **v**, Right M_2 (DT2-24), oblique buccal view. **w**, Left M_3 (DT1-29), occlusal view.

topology^{7,27}, but all current reconstructions of early anthropoid phylogeny insist that the three anthropoid clades represented at Dur At-Talah occupy disparate positions on the evolutionary tree. The high degree of morphological, taxonomic and presumably ecological diversity apparent in the Dur At-Talah anthropoid fauna can be explained only by a substantial interval of earlier evolutionary history for this group. Given the apparent absence of anthropoids in significantly older, but reasonably well sampled, Eocene African localities such as Glib Zegdou in western Algeria¹⁶, it seems doubtful that the ‘missing’ evolutionary history of the Dur At-Talah anthropoids can be explained simply by reference to the poorly sampled early Cenozoic fossil record of Africa. An alternative hypothesis that now demands serious consideration is that multiple Asian anthropoid clades may have colonized Africa more or less synchronously during the middle Eocene, alongside anomaluroid and hystricognathous rodents. In either case, further palaeontological exploration of middle Eocene localities in Africa and Asia will be necessary to illuminate this poorly documented interval of primate evolutionary history.

METHODS SUMMARY

Taxonomic allocation. Fossil specimens from Dur At-Talah were segregated into taxa on the basis of both metric and morphological compatibility. Specimens from Dur At-Talah were extensively compared with original specimens and casts of African and Asian fossil primates to establish the systematic affinities of the Dur At-Talah taxa.

Estimation of body mass. Mean estimates of adult body mass for each primate taxon from Dur At-Talah were obtained by using the regression equations provided by Conroy²⁸. Conroy’s regressions estimate body mass on the basis of M_1 area. This tooth locus is not definitively known for any of the Dur At-Talah anthropoid taxa, because M_1 and M_2 are not readily distinguished in *Afrotarsius* and because the sole lower molar currently known for *Talahpithecus parvus* is fragmentary (see Supplementary Information). In these cases, M_2 dimensions may have been substituted for M_1 (as was certainly the case for *Biretia piveteaui*). Two regression equations were used to estimate adult body mass for each primate taxon known from Dur At-Talah. Conroy’s ‘all primates’ regression was used in every case, although more taxonomically restricted regressions were also employed (Conroy’s ‘prosimians’ regression was used for *Karanisia*, and Conroy’s ‘monkeys’ regression was used for the anthropoids).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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1. Beard, K. C. *The Hunt for the Dawn Monkey: Unearthing the Origins of Monkeys, Apes, and Humans* (Univ. California Press, Berkeley, 2004).
2. Beard, K. C. in *Primate Biogeography* (eds Lehman, S. G. & Fleagle, J. G.) 439–467 (Springer, 2006).
3. Williams, B. A., Kay, R. F. & Kirk, E. C. New perspectives on anthropoid origins. *Proc. Natl Acad. Sci. USA* **107**, 4797–4804 (2010).
4. Miller, E. R., Gunnell, G. F. & Martin, R. D. Deep time and the search for anthropoid origins. *Yearb. Phys. Anthropol.* **48**, 60–95 (2005).
5. Jaeger, J.-J. et al. A new primate from the middle Eocene of Myanmar and the Asian early origin of anthropoids. *Science* **286**, 528–530 (1999).

6. de Bonis, L., Jaeger, J.-J., Coiffait, B. & Coiffait, P.-E. Découverte du plus ancien primate catarrhinien connu dans l'Éocène supérieur d'Afrique du Nord. *C. R. Acad. Sci.* **306**, 929–934 (1988).
7. Seiffert, E. R. *et al.* Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. *Science* **310**, 300–304 (2005).
8. Bininda-Emonds, O. R. P. *et al.* The delayed rise of present-day mammals. *Nature* **446**, 507–512 (2007).
9. Fleagle, J. G. & Kay, R. F. The phyletic position of the Parapithecidae. *J. Hum. Evol.* **16**, 483–532 (1987).
10. Simons, E. L. Diversity in the early Tertiary anthropoid radiation in Africa. *Proc. Natl Acad. Sci. USA* **89**, 10743–10747 (1992).
11. Ciochon, R. L. & Gunnell, G. F. Chronology of primate discoveries in Myanmar: influences on the anthropoid origins debate. *Yearb. Phys. Anthropol.* **45**, 2–35 (2002).
12. Beard, K. C., Qi, T., Dawson, M. R., Wang, B.-Y. & Li, C.-K. A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature* **368**, 604–609 (1994).
13. Beard, K. C., Tong, Y.-S., Dawson, M. R., Wang, J.-W. & Huang, X.-S. Earliest complete dentition of an anthropoid primate from the late middle Eocene of Shanxi Province, China. *Science* **272**, 82–85 (1996).
14. Beard, K. C. & Wang, J.-W. The eosimiid primates (Anthropoidea) of the Heti Formation, Yuanqu Basin, Shanxi and Henan Provinces, People's Republic of China. *J. Hum. Evol.* **46**, 401–432 (2004).
15. Beard, K. C. *et al.* A new primate from the Eocene Pondaung Formation of Myanmar and the monophyly of Burmese amphipithecids. *Proc. R. Soc. Lond. B* **276**, 3285–3294 (2009).
16. Tabuce, R. *et al.* Anthropoid versus strepsirhine status of the African Eocene primates *Algeripithecus* and *Azibius*: craniodental evidence. *Proc. R. Soc. Lond. B* **276**, 4087–4094 (2009).
17. Sigé, B., Jaeger, J.-J., Sudre, J. & Vianey-Liaud, M. *Altiatlasius koulchii* n. gen. et sp., primate omomyidé du Paléocène supérieur du Maroc, et les origines des euprimates. *Palaeontographica A* **214**, 31–56 (1990).
18. Wight, A. W. R. in *The Geology of Libya* Vol. 1 (eds Salem, M. J. & Busrewil, M. T.) 309–325 (Academic, 1980).
19. Jaeger, J.-J. *et al.* New rodent assemblages from the Eocene Dur At-Talah escarpment (Sahara of central Libya): systematic, biochronological, and palaeobiogeographical implications. *Zool. J. Linn. Soc.* **160**, 195–213 (2010).
20. Tabuce, R., Coiffait, B., Coiffait, P.-E., Mahboubi, M. & Jaeger, J.-J. A new species of *Bunohyrax* (Hyracoidea, Mammalia) from the Eocene of Bir el Ater (Algeria). *C. R. Acad. Sci.* **331**, 61–66 (2000).
21. Tabuce, R., Coiffait, B., Coiffait, P.-E., Mahboubi, M. & Jaeger, J.-J. A new genus of Macroscelidea (Mammalia) from the Eocene of Algeria: a possible origin for elephant-shrews. *J. Vertebr. Paleontol.* **21**, 535–546 (2001).
22. Seiffert, E. R., Simons, E. L. & Attia, Y. Fossil evidence for an ancient divergence of lorises and galagos. *Nature* **422**, 421–424 (2003).
23. Simons, E. L. & Bown, T. M. *Afrotarsius chatrathi*, first tarsiiform primate (?Tarsiidae) from Africa. *Nature* **313**, 475–477 (1985).
24. Gebo, D. L., Dagosto, M., Beard, K. C. & Qi, T. The smallest primates. *J. Hum. Evol.* **38**, 585–594 (2000).
25. Ginsburg, L. & Mein, P. *Tarsius thailandica* nov. sp., premier Tarsiidae (Primates, Mammalia) fossile d'Asie. *C. R. Acad. Sci.* **304**, 1213–1215 (1987).
26. Beard, K. C. A new genus of Tarsiidae (Mammalia: Primates) from the middle Eocene of Shanxi Province, China, with notes on the historical biogeography of tarsiers. *Bull. Carnegie Mus. Nat. Hist.* **34**, 260–277 (1998).
27. Kay, R. F., Williams, B. A., Ross, C. F., Takai, M. & Shigehara, N. in *Anthropoid Origins: New Visions* (eds Ross, C. F. & Kay, R. F.) 91–135 (Kluwer/Plenum, 2004).
28. Conroy, G. C. Problems of body-weight estimation in fossil primates. *Int. J. Primatol.* **8**, 115–137 (1987).
29. Gradstein, F. M., Ogg, J. G. & Smith, A. G. *A Geological Time Scale 2004* (Cambridge Univ. Press, 2004).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions M.Br., M.Sa., O.H. and J.-J.J. designed and organized the project. J.-J.J., Y.C., X.V., M.Be., M.S., A.A.B., B.M. and L.M. collected palaeontological data. M.Be., P.C., M.Sch., O.HI, P.D. and E.M. collected geological and palaeomagnetic data. J.-J.J., Y.C. and K.C.B. analysed the data. J.-J.J. and K.C.B. wrote the manuscript.

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METHODS

Taxonomic allocation. Fossil specimens from Dur At-Talah were segregated into taxa on the basis of both metric and morphological compatibility. The following taxa of Eocene–Oligocene primates from Africa and Asia formed the comparative sample used to make taxonomic decisions regarding the Dur At-Talah primates: *Karanisia clarki*, *Saharagalago misrensis*, *Tarsius eocaenus*, *Xanthorhysis tabrumi*, *Afrotarsius chatrathi*, *Eosimias sinensis*, *E. centennicus*, *E. dawsonae*, *Phenacopithecus krishtalkai*, *P. xueshii*, *Bahinia pondaungensis*, *Biretia piveteaui*, *B. fayumensis*, *B. megalopsis*, *Qatrania wingi*, *Arsinoea kallimos*, *Serapia eocaena*, *Proteopithecus sylviae*, *Catopithecus browni*, *Oligopithecus rogeri*.

Measurements. Standard measurements (mesiodistal length, buccolingual width; separate width measurements for lower molar trigonids and talonids) were obtained for each tooth in the current sample (Supplementary Table 1). Measurements were taken to the nearest 0.01 mm with digital calipers. Equivalent dimensions were estimated in the case of two fragmentary specimens (DT1-32 and DT1-43).

Body mass estimation. Estimates of adult body mass for each primate taxon from Dur At-Talah were obtained by using the regression equations provided by Conroy²⁸. Conroy's regressions estimate body mass on the basis of M_1 area. For *Karanisia arenula* body mass was estimated from the mean M_1 area of the two available specimens (DT1-40 and DT1-41). Two estimates of the adult body mass of *Karanisia arenula* were obtained, using Conroy's 'all primates' and 'prosimians' regressions, respectively. The body mass of *Afrotarsius libycus* was estimated from the dimensions of the holotype lower molar (DT1-35), which is either an M_1 or an M_2 . The body mass of *Biretia piveteaui* was estimated on the basis of DT2-24, regarded here as an M_2 . These teeth do not differ appreciably in size in *Afrotarsius chatrathi*²³ and Fayum species of *Biretia*⁷, suggesting that any error introduced by substituting the dimensions of M_2 for those of M_1 here is negligible. Body mass of *Talahpithecus parvus* was assessed on the basis of DT1-32, a fragmentary M_1 or M_2 whose length can only be estimated because of breakage. Two estimates of the adult body mass of each of the three anthropoid taxa represented at Dur At-Talah were obtained, using Conroy's 'all primates' and 'monkeys' regressions, respectively.