

## LETTERS

# Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates

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Adapiform or 'adapoid' primates first appear in the fossil record in the earliest Eocene epoch (~55 million years (Myr) ago), and were common components of Palaeogene primate communities in Europe, Asia and North America<sup>1</sup>. Adapiforms are commonly referred to as the 'lemur-like' primates of the Eocene epoch, and recent phylogenetic analyses have placed adapiforms as stem members of Strepsirrhini<sup>2–4</sup>, a primate suborder whose crown clade includes lemurs, lorises and galagos. An alternative view is that adapiforms are stem anthropoids<sup>5</sup>. This debate has recently been rekindled by the description of a largely complete skeleton of the adapiform *Darwinius*<sup>6</sup>, from the middle Eocene of Europe, which has been widely publicised as an important 'link' in the early evolution of Anthropoidea<sup>7</sup>. Here we describe the complete dentition and jaw of a large-bodied adapiform (*Afradapis* gen. nov.) from the earliest late Eocene of Egypt (~37 Myr ago) that exhibits a striking series of derived dental and gnathic features that also occur in younger anthropoid primates—notably the earliest catarrhine ancestors of Old World monkeys and apes. Phylogenetic analysis of 360 morphological features scored across 117 living and extinct primates (including all candidate stem anthropoids) does not place adapiforms as haplorhines (that is, members of a *Tarsius*–Anthropoidea clade) or as stem anthropoids, but rather as sister taxa of crown Strepsirrhini; *Afradapis* and *Darwinius* are placed in a geographically widespread clade of caenopithecine adapiforms that left no known descendants. The specialized morphological features that these adapiforms share with anthropoids are therefore most parsimoniously interpreted as evolutionary convergences. As the largest non-anthropoid primate ever documented in Afro-Arabia, *Afradapis* nevertheless provides surprising new evidence for prosimian diversity in the Eocene of Africa, and raises the possibility that ecological competition between adapiforms and higher primates might have played an important role during the early evolution of stem and crown Anthropoidea in Afro-Arabia.

Birket Qarun Locality 2 (BQ-2) is a near-coastal fluvial freshwater deposit exposed in the Fayum Depression of northern Egypt that has produced a diverse mammalian fauna that includes primitive anthropoid<sup>4</sup> and crown strepsirrhine<sup>8</sup> primates. An age estimate of ~37 Myr ago (that is, earliest late Eocene or earliest Priabonian) for the locality is supported by palaeomagnetic reversal stratigraphy<sup>4,9</sup> as well as sequence stratigraphic and invertebrate biostratigraphic evidence from adjacent rocks<sup>10,11</sup>. The new genus and species of adapiform described here is one of the more common mammals at BQ-2, and is, by far, the largest primate from the locality.

Primates Linnaeus, 1758

Adapiformes Hoffstetter, 1977

Caenopithecinae Godinot, 1998

*Afradapis longicristatus* gen. et sp. nov.

**Etymology.** Generic name derived from *Afra*, Latin, Africa, and *adapis*, in reference to *Adapis* Cuvier, 1821. Specific epithet is from *longi*-, Latin, long, and *cristatus*, Latin, crested.

**Holotype.** CGM 83690, partial left mandible preserving P<sub>4</sub>–M<sub>3</sub> and masseteric fossa (Fig. 1r).

**Locality and horizon.** Early Priabonian (early late Eocene) Birket Qarun Locality 2 (BQ-2), Umm Rigl Member, Birket Qarun Formation, Fayum Depression, northern Egypt.

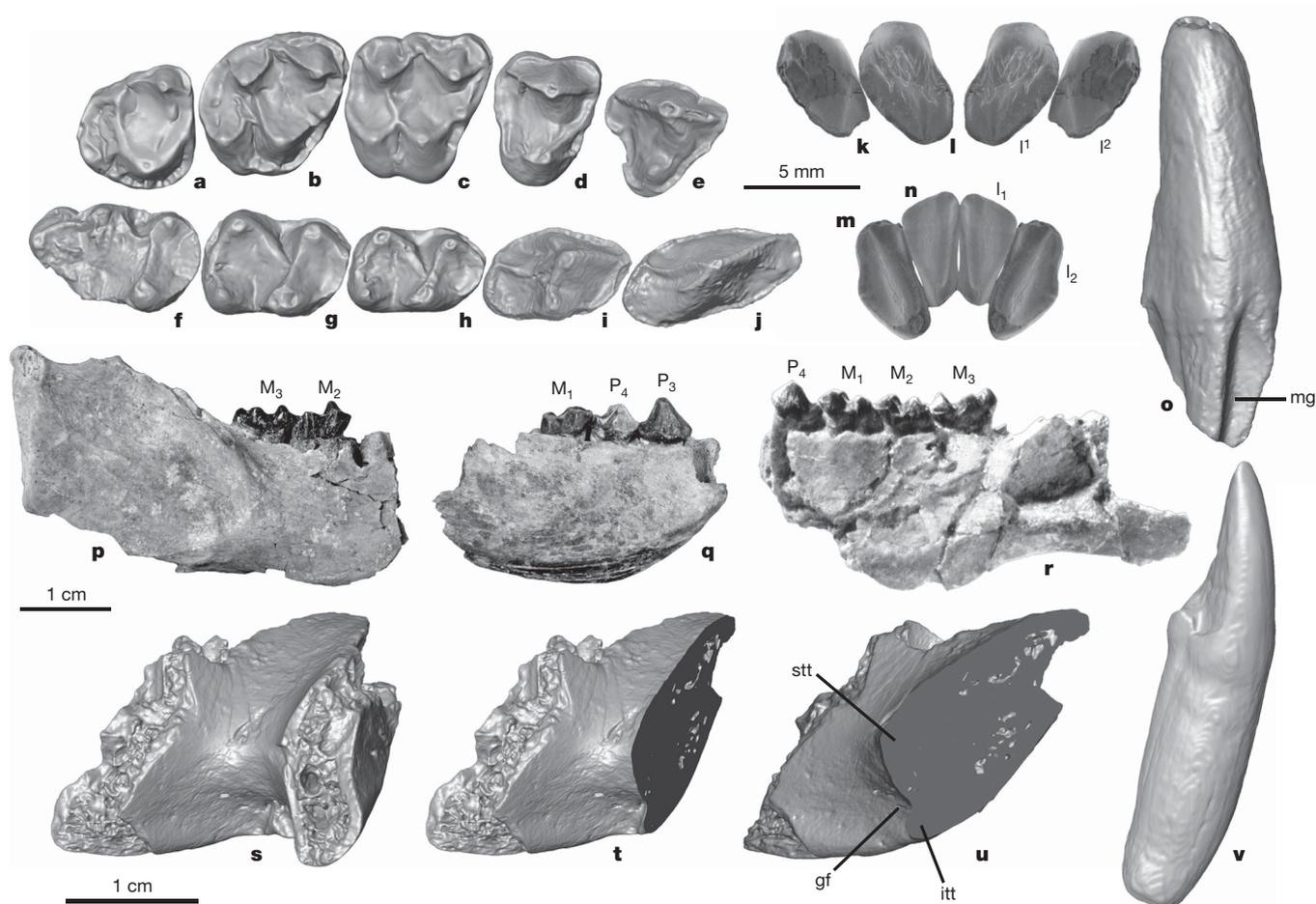
**Diagnosis.** Large adapiform (mean body mass estimates of 2,187 g ('prosimian' regression) and 3,262 g ('all primate' regression) based on M<sub>1</sub> area<sup>12</sup>; 3,283 g based on M<sub>2</sub> length<sup>13</sup>) that differs from other caenopithecine adapiforms in exhibiting the following combination of characters: absence of P<sub>2</sub>; tall and trenchant upper and lower third premolars; mesoconid variably present on lower molars, particularly on M<sub>1</sub>; no metastylids on M<sub>1–3</sub>; mesostyles, large hypocones and prehypocristae present on all upper molars; mandible with deep and short corpus, extensive masseteric fossa, ossified symphysis with transverse torus, short condylar neck and low condyle relative to the mandibular tooth row.

**Description.** Mandibular fragments collectively preserve the canine and postcanine tooth row and most of the corpus anterior to the M<sub>3</sub>, and definitively demonstrate that P<sub>2</sub> was absent (Figs 1q and 2). The corpus is very deep, the symphysis is fully ossified in DPC 21370J and DPC 24085A, and both specimens bear transverse tori superior and inferior to the genial tubercles (Fig. 1s–u). The lingual symphyseal shelf is long, extending back to the level of P<sub>4</sub>, and is oriented at roughly 45 degrees to the occlusal plane.

The lower incisor crowns of *Afradapis* are spatulate as in other known adapiforms, and bear lingual keels and weak lingual cingulids (Fig. 1m, n). The I<sub>1</sub> has a flat and sharp occlusal edge. The I<sub>2</sub> occlusal edge is in line with that of I<sub>1</sub> mesially, but then curves steeply distally. The alveoli for I<sub>1–2</sub> are only slightly procumbent. The upper incisors (Fig. 1k, l) are asymmetric and have occlusal surfaces that are rounded to either side of a lingual keel; their edges probably did not form a continuous blade. The upper central incisor crowns have well-developed mesial processes, but none of the isolated upper incisors has an interproximal wear facet, indicating that there was probably no midline contact and at least a small interincisal gap. The lower canine (Fig. 1v) is robust, protrudes high above the occlusal plane and bears a distal heel that is often worn from contact with the anterior edge of the upper canine. Many of the upper lateral incisors have a strong wear facet on their distal surfaces from contact with the lower canine. The upper canine has sharp mesial and distal edges, a weak lingual cingulum and a deep mesial groove (Fig. 1o). There is no clear evidence for sexual dimorphism in canine size.

The P<sub>3</sub> is particularly notable for being longer and taller than P<sub>4</sub> (Fig. 1j, q), and for having a long honing facet that develops from wear against the distal face of the upper canine. The P<sub>3</sub> roots are implanted

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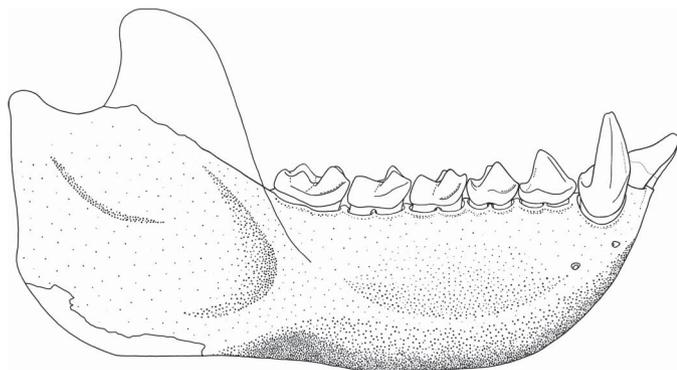
**Figure 1 | Dental and mandibular remains of *Afradapis longicristatus* gen. et sp. nov.** **a**,  $M^3$  (DPC 21458D); **b**,  $M^2$  (DPC 21370B); **c**,  $M^1$  (DPC 21366A); **d**,  $P^4$  (DPC 21370C); **e**,  $P^3$  (DPC 21500G); **f**,  $M_3$  (DPC 21366F, reversed); **g**,  $M_2$  (DPC 21366E); **h**,  $M_1$  (DPC 21456C); **i**,  $P_4$  (DPC 21548I); **j**,  $P_3$  (DPC 21500I, reversed); **k**,  $I^2$  (DPC 22440D; incisors are mirror-imaged to reconstruct incisor battery); **l**,  $I^1$  (DPC 22442K); **m**,  $I_2$  (DPC 21456G); **n**,  $I_1$  (DPC 21639E); **o**, upper canine (DPC 21578J) in oblique buccal view; **p**, mandible with  $M_{2-3}$  (DPC 23275); **q**, mandible with  $P_3$ – $M_1$  and lower canine alveolus (DPC

21458F); **r**, holotype lower mandible with  $P_4$ – $M_3$  (CGM 83690); **s**–**u**, micro-CT reconstruction of edentulous mandible preserving fused symphysis and transverse tori (DPC 21370J) in oblique posterior (**s**, **t**) and medial (**u**) views (specimen is digitally sliced along the midline of the symphysis in **t** and **u**); **v**, lower canine (DPC 21365E) in buccal view. Five millimetre scale bar is for **a**–**o** and **v**; upper 1 cm scale bar is for **p**–**r**; lower 1 cm scale bar is for **s**–**u**. **gf**, Genial fossa; **i**, incisor; **itt**, inferior transverse torus; **m**, molar; **mg**, mesial groove; **p**, premolar; **stt**, superior transverse torus.

obliquely with respect to those of  $P_4$ , and the long axes of the primary crests are strongly oblique with respect to the long axis of the tooth row. Among primates, this derived complex of features, along with the loss of  $P_2$ , is otherwise seen only in living and extinct catarrhine anthropoids, and is first documented among stem catarrhines three

million years later in the Fayum area<sup>14</sup>. Other caenopithecines retain a small, single-rooted  $P_2$  (refs 6, 15–18). The  $P_4$  (Fig. 1i, q, r) has a prominent, distolingually placed metaconid and a large talonid with a distinct cristid obliqua. Only  $P^3$  and  $P^4$  of *Afradapis* have been recovered as isolated teeth, consistent with  $P^2$  being absent. The  $P^3$  (Fig. 1e) has a tall, blade-like paracone and a very small protocone. The  $P^4$  (Fig. 1d) is slightly waisted and has a relatively well-developed protocone.

The upper and lower molars of *Afradapis* are superficially similar to those of some highly folivorous extant primates, such as those of platyrrhine howler monkeys (*Alouatta*) and lemuriform indriids such as the sifaka (*Propithecus*) and indri (*Indri*). *Afradapis*' elaborate shearing crests indicate that the species was likely to have been highly folivorous as well. The lower molars of *Afradapis* (Fig. 1f–h) lack paraconids, but otherwise have high cusps and long crests, and are often densely crenulated. Lower molar length increases, and the relative length of the trigonid basins decreases, distally along the toothrow. The hypoconulid is very small or absent on  $M_{1-2}$ , but the  $M_3$  has a large hypoconulid lobe. The upper molars (Fig. 1a–c) have moderately tall cusps and long, sharp crests.  $M^{1-2}$  have well-developed mesostyles, distinct buccal cingula, large hypocones (derived from the posterior cingulum), and trenchant postprotocristae and prehypocristae. A large paraconule is present along the preprotocrista, but there is no metaconule. Upper molars decrease in size, and have more rounded distal margins, moving



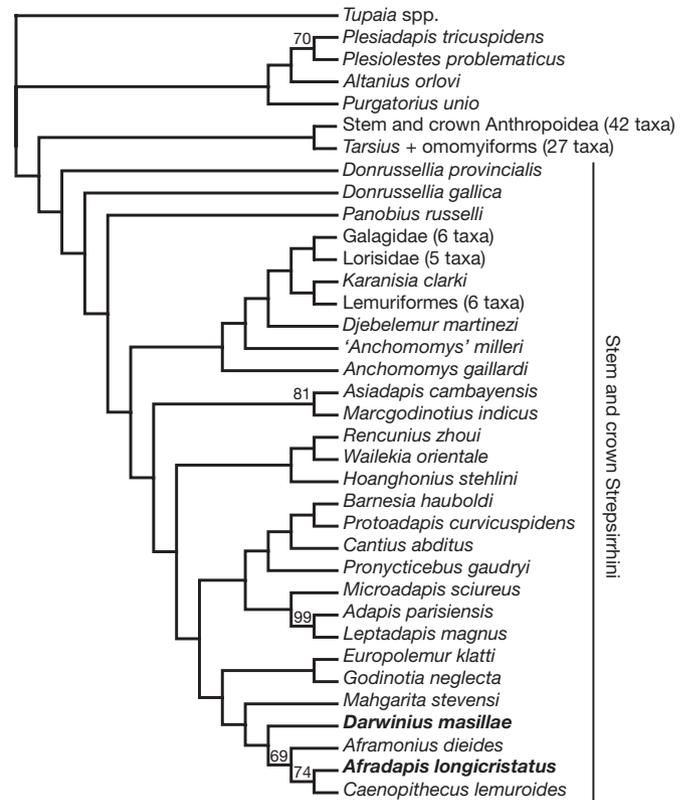
**Figure 2 | Reconstruction of the mandible and lower dentition of *Afradapis longicristatus*, gen. et sp. nov.** Reconstruction is based on combined information from specimens CGM 83690, DPC 23275, DPC 21458F and DPC 21370J.

distally along the toothrow. The  $M^3$  bears an expanded talon and a strongly convex distal margin, and has relatively small metacone, hypocone and paraconule cusps.

It has long been known that some adapiform lineages evolved derived morphological features that are also seen in living and extinct anthropoids (for example, fused mandibular symphyses, upper canines with mesial grooves, enlarged and spatulate upper and lower incisors, short and tall rostra)<sup>16</sup>. The phylogenetic significance of these features has been a source of ongoing debate for decades<sup>3,5,19,20</sup>. Of all known fossil prosimians (including *Darwinius*), *Afradapis* provides perhaps the most detailed examples of derived anthropoid-like adaptations in its dental and mandibular morphology. As is the case for many of the morphological features that some have argued link adapiforms to anthropoids, however, the anthropoid-like features of *Afradapis* (fused mandibular symphysis with transverse torus, deep mandibular corpus, deep masseteric fossa, large upper molar hypocones, absence of  $P^2/2$  and presence of an enlarged  $P_3$  with a honing facet for the upper canine) are not present in the most primitive undoubted fossil anthropoids, such as *Biretia*<sup>4</sup> and *Proteopithecus*<sup>21</sup>, indicating that the features are likely to have been acquired through convergent evolution.

Despite the key role that adapiforms have had in debates surrounding anthropoid and strepsirrhine origins, the group has been poorly sampled in recent analyses of primate interrelationships. We expanded on previous analyses<sup>4,22</sup> by scoring 117 living and extinct primates (including 24 adapiforms, eight of which were not sampled previously) for 360 morphological features and analysed the resulting data set using the heuristic search algorithm in PAUP\* 4.0b10 (ref. 23). Parsimony analysis places *Afradapis* and its caenopithecine relatives, including *Darwinius*, within a large clade of adapiform primates that includes European adapines and ‘cercamoniines’ and North American notharctines. This group, along with Asian sivaladapids and asiadapines<sup>24</sup>, is recovered as one of several sister clades of crown Strepsirrhini (Fig. 3; for methods see Methods; for character support, see Supplementary Information). Interestingly, *Afradapis* and the younger (~34 Myr ago) African caenopithecine *Aframoni* are placed as consecutive sister taxa of European middle Eocene *Caenopithecus*, indicating at least one dispersal across the Tethys Sea. Given that there is no other compelling evidence for mammalian faunal exchange between Europe and Afro-Arabia during the middle Eocene<sup>25,26</sup>, it is possible that the few derived dental features that *Afradapis* and *Caenopithecus* share to the exclusion of *Aframoni* evolved independently on the two landmasses from more generalized caenopithecine ancestors. More complete fossil evidence from the middle Eocene of Europe and Afro-Arabia will be required to provide a robust test of these alternative hypotheses.

The *Darwinius* holotype presents unique problems for phylogenetic analysis because the specimen is a juvenile, most of its bones are crushed or distorted, and many of the characters that have had a key role in primate phylogenetics (that is, features of the dentition, auditory region and ankle) cannot be evaluated. For instance, in our opinion the orientation of the fibular facet on the astragalus cannot be determined with confidence (*contra* ref. 6) because the astragalus is damaged, the orientation of the trochlear surface cannot be determined, and the fibular facet is almost entirely obscured by the fibular malleolus (see Fig. 11 in ref. 6). However, the topology presented in Fig. 3 does not change if *Darwinius* is scored as having a straight-sided fibular facet like haplorhines (and unlike all other adapiforms for which this region is known). Constraining caenopithecine adapiforms to be placed closer to crown Anthropoidea than two other groups (Eosimiidae and Amphipithecidae from the Paleogene of Asia<sup>27–29</sup>) that emerge as stem anthropoids in the unconstrained tree adds 12 steps to tree length (see Supplementary Information). Even in this much longer tree, *Darwinius* and other caenopithecines are most parsimoniously placed in a clade with more primitive adapiforms such as adapines, asiadapines and ‘cercamoniines’, and not as intermediate forms that might link these taxa to undoubted anthropoids.



**Figure 3 | Phylogenetic position of the adapiforms *Afradapis* and *Darwinius* within Primates.** Single tree recovered from parsimony analysis of a morphological character matrix containing 360 characters scored across 117 taxa. Tree length = 2,265.671; consistency index excluding uninformative characters = 0.1891; retention index = 0.5848; rescaled consistency index = 0.1120. Values above branches are bootstrap support, based on 1,000 pseudoreplicates. See Supplementary Information for full tree, matrix, methods and tests of alternative topologies.

The adapiform radiation produced an impressive range of morphologically diverse taxa whose evolutionary history is well documented in North America, Europe and, to a lesser extent, Asia. Adapiforms were not definitively known from Africa until the last decade, but it now seems that members of the group were not only present in Afro-Arabia, but were probably common and quite successful living alongside, and competing with, early anthropoid primates in the middle and late Eocene. Our analysis shows that adapiforms are unlikely to have given rise to Anthropoidea, but the former were evidently the first primates to invade and occupy anthropoid-like feeding niches in Africa. As early ecological competitors of stem and crown anthropoids, adapiforms may still have an important role for understanding the selection pressures that drove the origin and early evolution of Anthropoidea.

## METHODS SUMMARY

The morphological character matrix analysed in this study is a modified version of the matrix compiled and analysed in ref. 4. The results presented in Fig. 3 are based on parsimony analysis of the matrix with some multistate characters treated as ordered, and with ordered characters scaled, so that any single change within a character could only contribute a maximum of one step to tree length. For many characters, taxa exhibiting intraspecific variation were assigned an intermediate character state, rather than a traditional polymorphic (for example, '0/1') coding. Some characters documenting differences in premolar number were constrained by step matrices that did not allow premolar teeth to be re-acquired following an earlier loss. A molecular scaffold was implemented based on the results of molecular studies, particularly analysis of short interspersed elements (SINEs), that strongly support the monophyly of Malagasy lemuriforms, and, within Lorisiformes, a monophyletic Lorisidae and an *Arctocebus-Perodicticus* clade<sup>30</sup>. The matrix was analysed with random addition sequence and TBR branch swapping across 2,000 replicates. Tree lengths were recalculated

after networks were re-rooted with *Tupaia* spp. Bootstrap support derives from 1,000 pseudoreplicates.

**Full Methods** and any associated references are available in the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Author Contributions** E.R.S. and E.L.S. recovered the fossils of *Afradapis* along with other members of their field crews in Egypt; E.R.S. assembled the character matrix and all figures, created Figs 2 and 3, ran the phylogenetic analyses, and compiled the Supplementary Information document; E.R.S. and J.M.G.P. analysed the fossils and wrote the manuscript; D.M.B. and J.M.G.P. CT-scanned fossils and provided three-dimensional reconstructions for Fig. 1. D.M.B. scored plesiadapiforms in the character matrix and helped to write the manuscript. E.L.S. helped to write the manuscript.

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## METHODS

The character–taxon matrix used in this study is a modified version of the matrix compiled and analysed in ref. 4, expanded to include 360 characters and 117 taxa. Codings for crown primates are based on observations made on original material and casts by E.R.S., in some cases supplemented by codings provided by ref. 3. Characters derive from ref. 31 (abbreviation ‘D’ in matrix), ref. 32, ref. 33 (abbreviation ‘K’ in matrix), ref. 34, ref. 3 (abbreviation ‘R’ in matrix), ref. 35 (abbreviation ‘Y’ in matrix), and ref. 36 (abbreviation ‘YIP’ in matrix). Scorings for *Darwinius masillae* are based on observations made by E.R.S. on high-resolution casts of ‘Plate A’ made available for study by P. Gingerich, supplemented by photographs and micro-CT reconstructions published in ref. 6. Scorings for features preserved on ‘Plate B’ are based on ref. 37. Original adapiform fossil material was examined by E.R.S. at the Geiseltalmuseum (Halle, Germany), the Muséum National d’Histoire Naturelle (Paris, France), the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA), the University of Michigan Museum of Paleontology (Ann Arbor, Michigan, USA), and the Duke Lemur Center Division of Fossil Primates (Durham, North Carolina, USA). J.M.G.P. made observations on adapiform primates housed at the Naturhistorisches Museum Basel (Basel, Switzerland), the Institut des Sciences de l’Évolution, Université Montpellier II (Montpellier, France), the Muséum National d’Histoire Naturelle (Paris, France), and the Muséum d’Histoire Naturelle, Montauban (Montauban, France). Observations on plesiadapiforms by D.M.B. led to a number of corrections to character codings for *Plesiadapis tricuspidens* and *Plesiolestes problematicus* in the matrix published in ref. 4; several other cells previously coded as ‘missing’ for these taxa were also scored based on D.M.B.’s observations on original material and casts. Scorings for the asiadapines *Asiadapis* and *Marcgodinotius* are from ref. 24, supplemented by observations on casts.

The results presented in Fig. 3 of the main text are based on analysis of the matrix with some multistate characters treated as ordered (see character list), and with ordered characters scaled, so that any single change within a character could only contribute a maximum of one step to tree length. For many characters, taxa exhibiting intraspecific variation were assigned an intermediate character state, rather than a traditional polymorphic (for example, ‘0/1’) coding. Some characters documenting differences in premolar number (character 21, ‘P<sub>1</sub> presence’; character 22, ‘P<sub>2</sub> roots/presence’; character 120, ‘P<sub>1</sub> presence’; character 121, ‘P<sub>2</sub> root number/presence’) were constrained by step matrices that did not allow premolar teeth to be reacquired following an earlier loss (see character matrix). Although supernumerary teeth have been acquired in some highly specialized mammalian lineages, such as sirenians<sup>38</sup> and whales<sup>39,40</sup>, we consider reacquisition of previously lost premolars in these primate clades to be highly unlikely, and a reasonable assumption for phylogenetic analysis. A molecular scaffold (*sensu* ref. 41) was implemented based on the results of molecular studies, particularly analysis of SINEs, that strongly support the monophyly of Malagasy lemuriforms, and, within Lorisiformes, a monophyletic Lorisidae and an *Arctocebus*–*Perodicticus* clade<sup>30</sup>. The molecular scaffold used here is as follows: (*Tupaia* spp., (((*Arctocebus calabarensis*, *Perodicticus potto*), (*Loris tardigradus*, *Nycticebus coucang*)), (*Galagoides demidoffi*, *Otolemur crassicaudatus*, *Galago moholi*)), ((*Cheirogaleus major*, *Microcebus murinus*), (*Lemur catta*, *Varecia variegata*), *Propithecus* spp., *Lepilemur mustelinus*)), *Tarsius bancanus*, (*Aotus trivirgatus*, *Saimiri sciureus*)). The matrix was analysed using the heuristic search algorithm in PAUP\* 4.0b10 (ref. 23), with random addition sequence and TBR branch swapping across 2,000 replicates. In order to replicate the results presented here, the matrix (Part IV of the Supplementary Information) should be saved as a new document with extension ‘\*.nex’; the constraint tree (Part V of the Supplementary Information) should be saved as a new document with the same name as the matrix but with extension ‘\*.tre’. The matrix should then be loaded within PAUP\* (the backbone constraint will load automatically), and analysed using command line text ‘hsearch nreps=2000 addseq=random enforce=yes’. Tree lengths were recalculated after networks were re-rooted with *Tupaia* spp. Bootstrap support derives from 1,000 pseudo-replicates. Templeton and Kishino–Hasegawa tests of alternative hypotheses were calculated in PAUP\* 4.0b10. Character 216, ‘morphology of fibular facet’ was not scored for *Darwinius masillae* in the matrices used in searches for alternative topologies.

Scorings for two taxa deserve special mention. The trees in Fig. 3 of the main text and Part II of the Supplementary Information are based on analyses that

include characters from the NMMP 20 partial skeleton<sup>42</sup> in the *Pondaungia coteri* OTU. There is ongoing debate surrounding the allocation of these postcranial remains<sup>43</sup>, but they cannot be attributed to any other large-bodied primate taxon known from the Pondaung Formation. Until compelling evidence is provided for the presence of another taxon that could have left these remains, we consider attribution to *Pondaungia* to be the most parsimonious explanation. We did not score the alleged frontal bones that have been attributed to *Amphipithecus*<sup>44</sup>, following the concerns raised in ref. 45. Although the NMMP 20 postcranial bones have been interpreted as providing evidence for the adapiform affinities of amphipithecids<sup>46</sup>, the group is nevertheless still placed along the stem lineage of Anthropeida in our analysis. Parsimony analysis following exclusion of the character states observable on NMMP 20 places amphipithecids within crown Anthropeida as the sister group of living and extinct platyrrhine anthropoids, but the phylogenetic positions of *Darwinius* and *Afradapis* do not change (that is, adapiforms are placed as stem strepsirrhines, and *Darwinius* and *Afradapis* are placed within a clade of caenopithecines that forms the sister group of *Europolemur* and *Godinotia*). The ‘Shuanghuang petrosal’ described in ref. 47 is not scored as part of the *Eosimias sinensis* OTU in any of our analyses, following concerns of other authors<sup>48</sup> that this specimen might belong to one of several other small-bodied primate taxa known from the deposits that produced the fossil.

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