

Additional remains of *Wadilemur elegans*, a primitive stem galagid from the late Eocene of Egypt

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The late Eocene prosimian *Wadilemur elegans* from the Jebel Qatrani Formation, northern Egypt, was originally interpreted as an anchomomyin adapiform primate based on limited information from the lower molars and distal premolars. Recently recovered fossils attributable to this species, including a proximal femur, the fourth upper premolar and first and second upper molars, and a mandible preserving the lower second premolar and lower canine and incisor alveoli, reveal a number of derived morphological similarities shared with crown strepsirrhines and, in particular, Miocene-to-Recent stem and crown galagids, to the exclusion of known adapiforms. Phylogenetic analysis of 359 morphological features scored across 95 living and extinct crown primate taxa supports a stem galagid placement for *Wadilemur* and older *Saharagalago*, and a close relationship between crown strepsirrhines and the Eocene African taxa "*Anchomomys*" *milleri*, *Djebelemur*, and *Plesiopithecus* (none of which appear to be closely related to European anchomomyins). This scheme of relationships supports the hypothesis that crown Strepsirrhini is of Afro-Arabian origin and that lemuriforms likely colonized Madagascar by crossing the Mozambique Channel. *Wadilemur*'s known dental and postcranial morphology provides additional support for the hypothesis that galagids and lorises had diverged by the close of the middle Eocene, and, by bolstering the ≈ 37 million-year-old calibration point for crown lorisiform origins provided by *Saharagalago*, indirect support for the hypothesis of an ancient origin of crown Strepsirrhini and crown Primates.

Fayum | Galagidae | Lorisiformes | Strepsirrhini | primates

The time and place of origin of the crown strepsirrhine or "toothcombed" prosimian clade, the group containing the Malagasy lemurs, African galagos, and Afro-Asian lorises, has long been a matter of great interest to primatologists (1–4). For many decades, the oldest undoubted fossil members of crown Strepsirrhini were early Miocene [≈ 20 Megannum (Ma, Megannum = million years old)] lorisiforms from Kenya and Uganda (5–10), but the recent discovery of a ≈ 37 Ma stem galagid (*Saharagalago*) in northern Egypt (11) has almost doubled this minimum paleontological estimate for the time of origin of both crown lorisiforms and crown strepsirrhines. Independent estimates for the timing of the loris-galago divergence derived from DNA sequence data (12–14) have since come to show remarkable congruence with this fossil evidence in supporting a middle Eocene origin for crown lorisiforms, but this critical new calibration point within crown Strepsirrhini also lends indirect support to the controversial hypothesis of a ≈ 80 Ma origin for crown primates (13, 15, 16) that is inconsistent with current interpretations of the fossil record documenting early primate evolution (e.g., ref. 17). Given the pivotal role that *Saharagalago* has come to play in debates surrounding the timing of crown lorisiform, lemuriform, strepsirrhine, and primate origins (13, 14, 18), it is important that an Eocene divergence of lorises and galagos continues to be tested with additional fossil evidence. Here, we describe new fossils that indicate that *Wadilemur elegans*, a ≈ 35 –35.4 Ma strepsirrhine primate from late Eocene

deposits of the Jebel Qatrani Formation exposed in the Fayum Depression, northern Egypt, is not an anchomomyin adapiform as originally thought (19) but is rather a primitive stem galagid lorisiform. These data strengthen support for the hypothesis of Seiffert *et al.* (11), Yoder and Yang (13), and Roos *et al.* (14) that lorises and galagos had already diverged by the close of the middle Eocene.

Systematic Paleontology

Primates, Linnaeus, 1758; Strepsirrhini, Geoffroy, 1812; Lorisiformes, Gregory, 1915; Galagidae, Gray, 1825; *Wadilemur*, Simons, 1997.

Type Species. *W. elegans*, Simons, 1997.

Holotype. CGM 42211, a right mandible preserving p3-m3 and partial ascending ramus.

Hypodigm. The type specimen; DPC 13093, right M2 (Fig. 1A and B); DPC 13439, a left mandible preserving p4-m3, damaged p3, and partial ascending ramus; DPC 13608, right maxilla preserving M1, damaged P4, and broken roots of P3 (Fig. 1A and B); DPC 13999, a left femur preserving proximal end and most of the diaphysis (Fig. 2); and DPC 16872, a left mandible preserving p2-m2 and alveoli for anterior dentition (Fig. 1E and F).

Type Locality. Late Eocene Quarry L-41, Lower Sequence of Jebel Qatrani Formation, Fayum Depression, northern Egypt. Suggested correlation with Geomagnetic Polarity Timescale is Chron 15r (20), between 35.043 and 35.404 Ma (21).

Emended Diagnosis. *W. elegans* differs from all other living and extinct primates in exhibiting the following combination of features: deep notch between the metacone and hypocone along the distal border of M1-2, demarcating a distinctive distolingually protruding lobe supporting hypocone; buccally oriented postmetacristae on upper molars; P4 with long and buccally oriented postparacrista and small hypocone, but no metacone; buccally situated hypoconid on p4, long and trenchant p4 cristid obliqua oriented lingually to meet the distal face of protoconid; no metaconid or entoconid present on p4; protoconids of p2-4 mesially oriented, overlapping hypoconids of adjacent teeth; p2 slightly larger than p3, moderately caniniform; no buccal cingulids on p2-m3; m1 cristid obliqua variably ascends posterior trigonid wall to connect with metaconid; lower molar cusps less acrodont than those of early Miocene *Komba* and most crown galagids; gluteal tuberosity present and distinct from greater trochanter; cylindrical femoral head with well developed fovea capitis and flattened posterior and medial surfaces.

Abbreviations: C.I., confidence interval; Ma, Megannum.

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DPC 13608 preserves the three roots of an upper third premolar, the damaged crown of an upper fourth premolar, and a complete upper first molar (Fig. 1*A* and *B*). The P4 is 2.15 mm wide and has a long postparacrista but no development of a metacone as in crown galagids. The distal border is deeply notched, and there is a well developed postprotocrista coursing distally from the protocone to meet a small hypocone. The first upper molar is 2.85 mm wide and 2.2 mm long and is similar to that of *Saharagalago*, *Komba*, and crown galagids in having a deep notch on the distal border between the metacone and hypocone, a well developed hypocone, no lingual or anterior cingulum, a small paracone, no metaconule, a trenchant postprotocrista, a buccally oriented postmetacrista, and a buccally placed paracone. DPC 13093 is a probable M2 (3.05 mm wide, 2.15 mm long), and its morphology is very similar to M1 aside from being relatively broad.

DPC 13999 is a partial left femur from Quarry L-41 (Fig. 2). The specimen is ≈ 35.5 mm long and preserves the entire proximal portion and a significant section of the shaft. It is generally well preserved with the entire head, neck, greater trochanter, and gluteal tuberosity present, but the lesser trochanter and the posterior and distal aspect of the shaft are damaged. It is clear from the preserved morphology that the shaft is long, straight, and mediolaterally compressed. Measurements of various anatomical features are provided in Tables 1–5, which are published as supporting information on the PNAS web site. Femoral head dimensions of DPC 13999 provide mean body mass estimates (22) of 84.5 g [femoral head height; 95% confidence interval (C.I.) = 45–159 g] and 86.9 g (anteroposterior femoral head breadth; 95% C.I. = 36–209 g). These results suggest that DPC 13999 belonged to an animal slightly larger than the smallest living galagid, *Galagoides demidoff* (60–63 g), and about the size of the cheirogaleid lemur *Microcebus rufus* (82–92 g) (23). Body mass estimates for *W. elegans* are based on the area of the first lower molar range from 91 to 118 g (average of 112 g), with 95% C.I. ranging from 33 to 365 g given Conroy's (24) "prosimian" regression of the first lower molar area on body mass. These values overlap widely with estimates calculated from the single known m1 of the stem strepsirrhine *Anchomomys milleri* (mean of 77 g, 95% C.I. = 38–157 g), also from Quarry L-41, and so it is possible, based purely on consideration of body size, that DPC 13999 belongs to that species and not *W. elegans*. *W. elegans* is, however, much more abundant at Quarry L-41 and shares derived dental features with galagids that are not present in *A. milleri*. Given these considerations, and the fact that DPC 13999 is very similar to Miocene-Recent galagids in its overall morphology (see below), the most parsimonious allocation is clearly to *W. elegans* and not *A. milleri*. It is highly unlikely that DPC 13999 belongs to a tarsiid primate because there is no record of this family at Quarry L-41, and indeed there is no record of Tarsiidae in Afro-Arabia before the appearance of *Afrotarsius* in the early Oligocene (25).

Proximally, the femoral head extends up to the level of the greater trochanter. The fovea capitis is as large as in living galagids, and the femoral head is cylindrical in shape, with the flattened posterior and medial surfaces characteristic of extant galagids and tarsiids (Fig. 2*D*). Where the neck is not damaged posteriorly, it appears that the articular surface of the femoral head extends onto the posterior and dorsal portions of the neck as in modern galagids and lorises, but this character may not be as well developed as in extant taxa. In this feature, *Wadilemur* more closely resembles the Miocene galagids from east Africa (10, 26). Possibly as a result of the more restricted articular surface, the neck is anteroposteriorly thin in comparison to extant galagids, in which the expansion of the articular surface onto the neck creates a generally thicker and more cylindrical appearance (Fig. 2*F*). The head sits on a short neck that measures ≈ 2.8 mm from the center of the head to the long axis

of the shaft. The index of neck length to shaft breadth taken just distal to the lesser trochanter is 111 and is lower than the same index in extant galagids, which ranges from ≈ 120 to 154 (27). This difference is likely the result of a relatively thicker shaft breadth than of an unusually short neck. The neck angle is $\approx 112^\circ$, which is on the lower end of the range of living galagids and is lower than that of other nonleaping strepsirrhines (Table 4) (27, 28).

The greater trochanter is broad and overhangs the anterior aspect of the femoral shaft, creating a raised pillar and triangular depression on the anterior surface of the femur (Fig. 2*B*). Similar anterior development of the greater trochanter is present in all extant leaping prosimians, some anthropoids, and various omomyids, but is most clearly expressed in modern galagids and tarsiids (27, 29, 30). This anterior expansion is thought to increase the leverage of the leg extensor muscle vastus lateralis that is best developed in leapers and active quadrupeds (27, 29–31). In DPC 13999, the greater trochanter is not as laterally expanded as in extant galagids, in which it forms a continuous lateral ridge extending distal to, and including, the third trochanter. In contrast to living small-bodied galagids, DPC 13999 has a small but distinct third trochanter. The third trochanter is also distinct from the greater trochanter in the Miocene galagid *Komba* (10), so this arrangement likely represents the primitive condition within Galagidae. In superior view, the anterior portion of the greater trochanter is angled medially (Fig. 2*D*). This configuration is similar to that in extant galagids (Fig. 2*E*) in which the greater trochanter is set at an angle with the posterior projection facing laterally and the anterior portion facing medially (32). The damaged lesser trochanter projects posteromedially at an angle of $\approx 20^\circ$ relative to a reference axis through the femoral head and greater trochanter. This angle is higher than in extant galagids, which range from $\approx 7^\circ$ to 16° , and is most similar to lemuriforms such as *Microcebus murinus* (27).

Cross-sectional scans from high-resolution x-ray computed tomography reveal that the femoral shaft, where undistorted, has the same anteroposteriorly elliptical, mediolaterally compressed form observable in extant galagids. From the well preserved cross-sectional scans in Fig. 2*G*, various geometric properties can be calculated, including the cortical bone area and the second moments of area and section moduli about the anteroposterior and mediolateral axes (see Table 6, which is published as supporting information on the PNAS web site). Although the midshaft is typically the point along the shaft at which these parameters are measured and compared across taxa (33–35), the absence of a distal end makes determination of the midshaft impossible. These data can nevertheless be useful to illustrate the cross-sectional geometry of the specimen and to infer possible loading conditions at various levels along the shaft. The section moduli, Z_{a-p} and Z_{m-l} , reflect the bending strength in the anteroposterior and mediolateral planes, respectively, and extant leaping strepsirrhines have been shown to have greater femoral rigidity, in general, and greater anteroposterior bending strength, in particular, than primates with more generalized locomotor behavior (33–35). The index of Z_{a-p} to Z_{m-l} in DPC 13999 indicates that the cortical bone is distributed in such a way as to best resist bending loads in the parasagittal plane rather than in the coronal plane.

In its proximal femoral anatomy, *Wadilemur* exhibits many of the femoral morphological features traditionally linked with an increased emphasis on vertical clinging and leaping. Some of the characters shared with modern galagids include a cylindrical femoral head, a large fovea capitis, a short neck oriented generally perpendicular to the shaft, a large, anteriorly developed greater trochanter that overhangs the anterior aspect of the shaft, and a straight, and presumably long, shaft with an anteroposteriorly elliptical cross-section (31–33, 35–40). The primary observation driving the alleged correlation of these femoral

characters with vertical clinging and leaping locomotion is their shared presence in both Galagidae and Tarsiidae. Despite the presence of these femoral characters in specialized leapers such as *Galago senegalensis*, *Galagoides alleni*, and all species of *Tarsius*, their presence in nonspecialized leapers, such as the mainly quadrupedal galagids *Otolemur crassicaudatus* and *G. demidoff*, suggests that many of these features may not be directly related to the specialized vertical clinging and leaping practiced by *G. senegalensis*. In isolation from other anatomical characters such as relative limb lengths, elongated tarsals, and other aspects of the hindlimb, pelvis, and spine, these features of the proximal femur cannot be considered definitive indicators of vertical clinging and leaping in fossil lorisiforms. A conservative interpretation would therefore be that *Wadilemur* engaged in a mix of active arboreal quadrupedalism and leaping, perhaps most similar to the pattern observable in extant galagids such as *G. demidoff* and *O. crassicaudatus*. The fact that the Miocene stem galagid *Komba* does not show the extreme pedal adaptations observable in crown galagids and also retains some primitive femoral characters, such as a restricted femoral head articular surface and a distinct third trochanter (10), lends further support to our hypothesis that the locomotor behavior of *Wadilemur* may have been relatively generalized.

Phylogenetic Analysis. To test a galagid versus adapiform placement for *Wadilemur*, 359 morphological characters, most of which derive from previous estimates of Paleogene primate (41–43) and extant strepsirrhine (44, 45) phylogeny, were scored for 100 living and extinct taxa (see Data Set 1, which is published as supporting information on the PNAS web site). Polymorphisms were scored as an intermediate character state (46, 47). Two analyses were undertaken: an “ordered/unordered” analysis in which some multistate characters were ordered and scaled so that all characters were of equal weight, and an “unordered” analysis in which all multistate characters were unordered. In both analyses, characters defining incisor and premolar number were scored as irreversible so that species or higher-level clades could not regain teeth that had been lost earlier in their evolutionary history. In both analyses, a version of the “molecular scaffold” technique of Springer *et al.* (48) was used, in this case constraining heuristic searches in PAUP 4.0B10 (49) to recover those primate clades that are supported by Alu short interspersed nuclear elements (14) as these markers are likely to provide virtually homoplasy-free evidence for phylogenetic relationships (50) (see Data Set 2, which is published as supporting information on the PNAS web site). In both analyses, 10,000 random addition replicates (tree bisection and reconnection algorithm, 20-second time limit on each replicate in the unordered analysis) recovered topologies in which *Saharagalago* and *Wadilemur* are nested deep within crown Strepsirrhini as consecutive sister taxa of a clade containing the Miocene stem galagid *Komba* and crown Galagidae (Fig. 3). Importantly, with increased character and taxon sampling, the loris-like strepsirrhine *Karanisia*, which was found to be a crown lorisid in a previous phylogenetic analysis (11), was placed as a stem lorisiform in the ordered/unordered analysis and as a stem strepsirrhine in the unordered analysis. As such, the Adams consensus tree summarizing information from all of the trees recovered in both analyses places *Karanisia* in an unresolved position at the base of crown Strepsirrhini.

Discussion

Simons’ (19) diagnosis of *W. elegans* was based on information from two mandibles that together preserve information from p3–m3 but no alveoli for more anterior teeth. Similarities in lower molar morphology shared by *Wadilemur*, the contemporaneous form *Anchomomys milleri* (also from L-41), older *Djebelemur* from Chambi, Tunisia (51), slightly younger *Omanodon* and

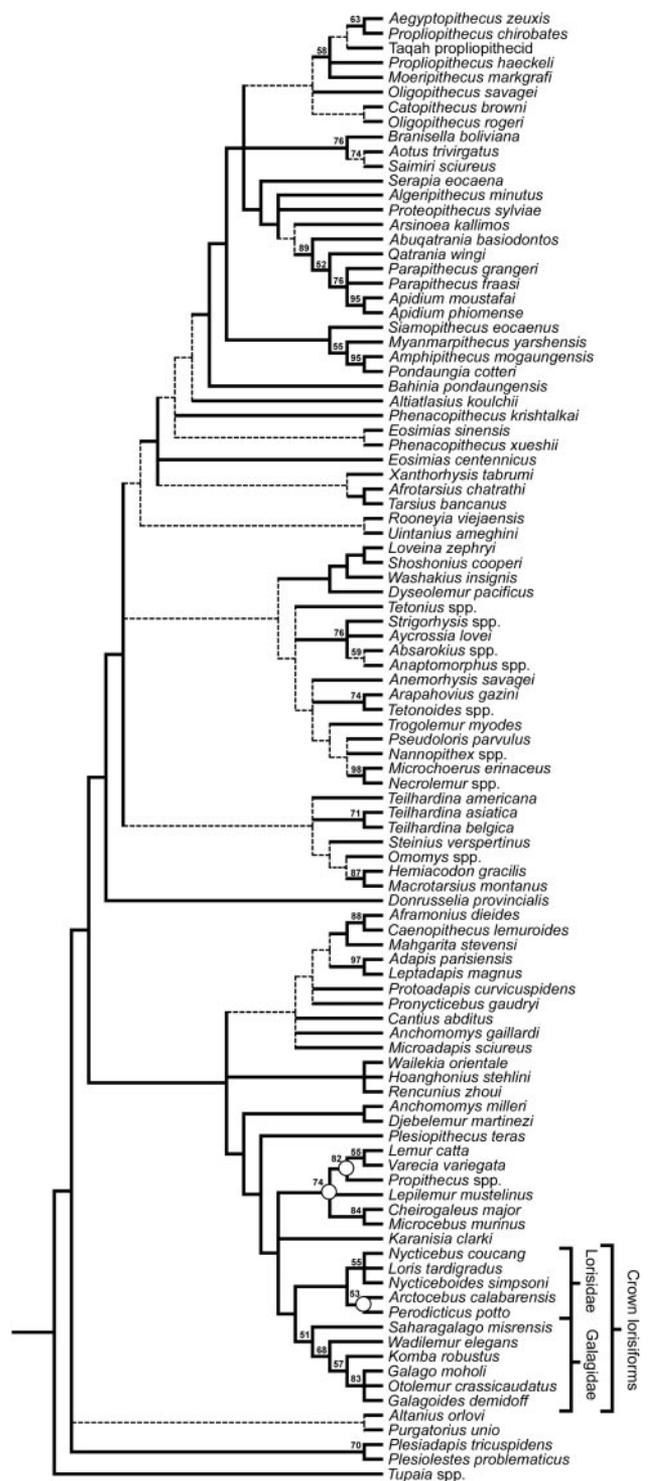


Fig. 3. Strict/Adams consensus tree summarizing all 142 trees recovered in the ordered/unordered analysis [40 equally parsimonious trees (EPTs), tree length (TL) = 2,052.341, consistency index = 0.2118, and rescaled consistency index (RCI) = 0.1249] and unordered (102 EPTs, TL = 3,701, consistency index = 0.2570, and RCI = 0.1387) parsimony analyses of 359 morphological characters. Solid lines in the cladogram indicate which clades are present in the strict consensus, whereas dotted lines indicate which clades are present in the Adams consensus tree, which relocates those taxa that are placed in conflicting positions in the tree, either within or across analyses, to the node held in common by all such conflicting positions. Open circles indicate clades supported by Alu short interspersed nuclear elements that were not recovered in unconstrained analyses of morphological data. Bootstrap support values >50 (derived from analysis of the ordered/unordered data set only) are shown above branches.

Shizarodon from Taqah, Oman (52), and *Anchomomys* species from Europe (53), led Simons to assign *Wadilemur* to the alleged cercamoniine notharctid adapiform clade Anchomomyini after the earlier tentative conclusions of Gheerbrant *et al.* (52) regarding the affinities of *Omanodon* and *Shizarodon*. The alleged anchomomyins from the Eocene of Afro-Arabia have had a convoluted taxonomic history since their initial descriptions: for instance, Godinot (54) considered *Djebelemur*, *Omanodon*, and *Shizarodon* to be either anthropoids or, less likely, crown strepsirrhines (“lemuriforms” in his usage); Shoshani *et al.* (55) placed *Omanodon* and *Shizarodon* within Anthropoidea; the phylogenetic analysis of Marivaux *et al.* (56) found *Wadilemur* to be an adapiform sister group of a clade containing European adapids and an *Omanodon*-*Anchomomys*-*Europolemur* clade; and, finally, the phylogenetic analysis of Seiffert *et al.* (11) recovered an *A. milleri*-*Djebelemur* clade that was found to be more closely related to *Plesiopithecus* and crown Strepsirrhini than either Adapidae or Notharctidae. The phylogenetic analysis presented herein, which constitutes the most comprehensive available assessment of relationships among early Afro-Arabian strepsirrhines, clearly supports a stem galagid placement for *Wadilemur* and continues to support a close relationship between an *A. milleri*-*Djebelemur* clade and crown Strepsirrhini.

The fact that the lower dental features of the stem galagid *Wadilemur* are similar enough to Afro-Arabian stem strepsirrhines such as *A. milleri* that these taxa were initially placed together in the tribe Anchomomyini suggests that the Afro-Arabian “anchomomyins” are probably of key importance for our understanding of crown strepsirrhine origins. In this regard, it is important that our phylogenetic analysis does not support the hypothesis that *A. milleri* is a close relative of European *Anchomomys* (represented in our analysis by *A. gaillardi*), and thus does not necessarily provide evidence for a trans-Tethyan migration independent of other Eocene Afro-Arabian non-adapid strepsirrhines (52, 57). Given our identification of the Eocene African taxa “*A. milleri*,” *Djebelemur*, and *Plesiopithecus* as successive sister taxa of crown Strepsirrhini to the exclusion of Holarctic adapiforms, it instead appears increasingly likely that these taxa are all derived from an ancient single colonization of Afro-Arabia that ultimately gave rise to crown Strepsirrhini. The extent to which dental resemblances between European anchomomyins, “*A. milleri*,” *Djebelemur*, *Omanodon*, and various crown strepsirrhines are due to convergence, plesiomorphy, or both is unclear because all of these taxa remain so poorly known, but if *Djebelemur* is in fact early Eocene (Ypresian) in age (58), then its precocious development of the anchomomyin-like molar features that only appear much later (mid-Lutetian) in the better sampled European record (54, 59) seems, to us, to argue in favor of convergence.

As the dental and femoral morphology of *Wadilemur* provides substantial paleontological support for the hypothesis of a middle Eocene divergence of lorises and galagos (11, 13, 14) these data therefore also lend indirect support to the hypothesis of a late Cretaceous (≈ 80 Ma) origin of crown primates that derives from this and/or other well supported paleontological calibration points within Primates and Placentalia (12, 13, 15, 16). At present, there is no satisfying paleontological explanation for this phenomenon, given that the oldest probable crown primate, *Altiatlasius*, is only late Paleocene in age (60), and the dental morphology of putative stem strepsirrhines (adapiforms) and stem or crown haplorhines (omomyiforms) are very difficult to distinguish at the time of their first appearances in the earliest Eocene of Asia (61), Europe, and North America (17). Although the ≈ 25 Ma discrepancy between the fossil and molecular data for crown primate origins may appear to be irreconcilable at present given the paleontological evidence currently available, the case of the late Eocene Afro-Arabian stem and crown strepsirrhine radiation provides an interesting cautionary tale for

those who might dismiss such a hypothesis based solely on lack of fossil evidence. Note, for instance, that as with the omomyiforms and adapiforms that first appear in the earliest Eocene of Europe and North America (17), the lower molar and premolar dentitions of later Eocene Afro-Arabian strepsirrhine taxa differ only very slightly, despite the fact that some of these taxa (*Saharagalago* and *Wadilemur*) are evidently nested deeply within crown Strepsirrhini, whereas at least one species (“*A. milleri*”) clearly lacks a toothcomb and is therefore likely to be a stem strepsirrhine. In the absence of molecular evidence bearing on divergence dates within crown Strepsirrhini (13, 14), taxa such as “*A. milleri*” and *Wadilemur* would presumably be (and indeed were previously) interpreted as close relatives that shared a recent common ancestry, but in this case it is known that various forms of data, including a long sequence of morphological and molecular apomorphies supporting crown lorisiform monophyly, indicate that the origin of crown Strepsirrhini (and thus the last common ancestor of “*A. milleri*” and *Wadilemur*) must considerably predate the origin of crown lorisiforms. Indeed, a ≈ 25 Ma ghost lineage for stem lorisiforms, a gap similar in length to that implied for crown primates given an ≈ 80 Ma estimate for their origin, now seems entirely reasonable, if not an underestimate (13, 15). The fact that there are, as yet, few, if any, taxa that could be called stem lorisiforms in the Afro-Arabian fossil record is almost certainly due to inadequate paleontological sampling, and the same problem could be obscuring earlier evidence for crown primate origins; given the absence of known late Cretaceous mammal-bearing localities in equatorial Afro-Arabia and precollision southern Asia, both of which have been proposed as possible centers of origin for crown primates (62, 63), an appropriate test of the ≈ 80 Ma estimate for crown primate origins simply may not yet be available.

Finally, although a number of Afro-Arabian stem strepsirrhines, in particular “*A. milleri*,” *Djebelemur*, *Omanodon*, and *Plesiopithecus*, appear to us to provide strong evidence for an Afro-Arabian origin of crown strepsirrhines (late Eocene African *Aframonius* is almost certainly nested within a separate Eurasian adapiform radiation, see Fig. 3), such a scenario may be viewed with skepticism until bona fide stem lemuriforms are recovered from the Paleogene of Afro-Arabia. However the molecular evidence bearing on the timing of the lemuriform colonization of Madagascar suggests to us that any discovery of Afro-Arabian stem lemuriforms is, in fact, rather unlikely. For instance, Yoder and Yang’s (13) Bayesian posterior mean estimates for the origins of crown Strepsirrhini and crown Lemuriformes differ by only 6.5 Ma, whereas the estimates of Roos *et al.* (14) for the same nodes are separated by only 3 Ma. The combined likelihood that (i) this relatively brief phase of stem lemuriform evolutionary history would be captured in the late Cretaceous or early Paleocene Afro-Arabian mammalian fossil record (even if such a record existed) and (ii) that numerous demonstrable lemuriform apomorphies would have appeared over the course of this interval seems to us to be quite low. More important, however, is the fact that there is no reason to believe that the origin of crown lemuriforms should have been coincident with their colonization of Madagascar. It is, in fact, more likely that the dispersal to Madagascar occurred earlier than the origin of crown lemuriforms, implying a duration of extra-Madagasy stem lemuriform evolution that would be even shorter than the aforementioned 3 Ma and 6.5 Ma molecular estimates separating the origins of crown Strepsirrhini and crown Lemuriformes. Indeed, given the absence of any other satisfying explanation for the lorisiform-lemuriform divergence, there is little reason to suspect that the origin of crown Strepsirrhini would not have been essentially coincident with (and, thus, due to) the strepsirrhine dispersal to Madagascar. Such a scenario would imply that stem and crown lemuriforms never existed outside of Madagascar, whereas stem strepsirrhines and stem

and crown lorisiforms did. Thus far, this is the pattern observable in the Paleogene fossil record documenting Afro-Arabian strepsirrhine evolution.

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