A new species of *Apidium* (Anthropoidea, Parapithecidae) from the Sirt Basin, central Libya: first record of Oligocene primates from Libya

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Abstract

A new species of *Apidium* is the most common primate currently known from a newly discovered site near Zallah Oasis in the Sirt Basin of central Libya. Based on current knowledge of the associated fauna, this new species of *Apidium* is early Oligocene in age, being roughly contemporaneous with faunas from Quarries G and V in the upper part of the Jebel Qatrani Formation in Egypt that also contain species of *Apidium*. A phylogenetic analysis based on dental characters indicates that the new species of *Apidium* from Libya is the sister group of *Apidium phiomense*. *Apidium bowni* and *Apidium moustafai* from the Jebel Qatrani Formation in the Fayum are similar in age to the new species of *Apidium* from Libya, but both of these Egyptian species are more distantly related to *Apidium phiomense* from younger stratigraphic levels in the Fayum. This phylogenetic pattern underscores the benefit of enhanced geographic sampling of the fossil record, even in cases where local records are thought to be reasonably comprehensive and well documented. Oligocene parapithecids can be partitioned into two clades corresponding to the subfamilies Parapithecinae (containing *Parapithecus* and *Simonsius*) and Qatraniinae (including *Qatrania* and *Apidium*). Climatic deterioration during the early Oligocene may have impacted the macroevolutionary dynamics of early Afro-Arabian anthropoids by fostering the fragmentation of forest habitats, thereby promoting allopatric speciation among widespread populations of *Apidium* and other arboreal taxa.

Keywords

Anthropoid, Fayum, Macroevolution, Paleontology, Phylogeny

Introduction

The early Oligocene parapithecoid primate *Apidium phiomense* enjoys the distinction of being the first Paleogene anthropoid ever described, even though it was not immediately recognized as such (Osborn, 1908; Simons, 1995a; Beard, 2002, 2004). Renewed efforts to collect fossil primates and other vertebrates from the Jebel Qatrani Formation in the Fayum Depression of northern Egypt during the second half of the twentieth century led to the discovery of two additional species of *Apidium*, *A. moustafai* and *A. bowni* (Simons, 1962, 1995b). *Apidium moustafai* and (especially) *A. bowni* are smaller than *A. phiomense*, and both occur lower in the Jebel Qatrani Formation than does *A. phiomense*. With the exception of a partial skull of *A. bowni* and a partial calcaneum of *A. moustafai*, both of the older species of *Apidium* known from the Fayum are represented solely by jaws and teeth. *Apidium phiomense*, on the other hand, is now one of the best documented Paleogene primate taxa known, being represented by a partial skull and other cranial fragments, numerous postcranial elements, and hundreds of teeth and jaw fragments (Fleagle and Simons, 1995; Simons, 1995a, 1995b).

Following the work of Fleagle and Kay (1987), a broad consensus has emerged regarding the phylogenetic position of *Apidium* and its close relatives within Parapithecidae with respect to other living and fossil anthropoids. Parapithecids are now generally accepted as a stem anthropoid clade, although their precise relationships with crown anthropoids and other stem anthropoid clades continue to be debated (Kay et al., 2004; Seiffert et al., 2005, 2009; Beard et al., 2009; Chaimanee et al., 2012; Ni et al., 2013). In contrast, the systematic relationships within Parapithecidae have received less attention

recently, and no one has ever attempted to reconstruct species-level relationships within the genus *Apidium*.

Prior to this report, *Apidium* was known only from the Jebel Qatrani Formation in the Fayum Depression of Egypt. In January 2013 we explored Paleogene rock strata exposed in the vicinity of Zallah Oasis in the Sirt Basin of central Libya (Fig. 1). Earlier work in this region has documented several occurrences of Paleogene mammals, all of which appear to be early Oligocene in age (Arambourg and Magnier, 1961; Arnould-Saget and Magnier, 1961; Arambourg, 1963; Fejfar, 1987; Coster et al., 2010, 2012). Our fieldwork in 2013 led to the discovery of a new site that has already yielded a surprisingly diverse assemblage of mammals and other vertebrates, including the first Oligocene primates to be recovered from Libya. We take this opportunity to describe a new species of *Apidium* from Libya, which appears to be the most common primate taxon from the Zallah Incision local fauna (Coster et al., 2015).

[Figure 1 near here]

Abbreviations are as follows: L, maximum mesiodistal length; W, maximum buccolingual width; CGM, Egyptian Geological Museum, Cairo, Egypt; DPC, Division of Fossil Primates, Duke Lemur Center (Durham, North Carolina, USA); YPM, Peabody Museum of Natural History, Yale University, (New Haven, Connecticut, USA); Z7I, Zallah 7 Incision locality fossils housed at the University of Tripoli, Libya.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Primates Linnaeus, 1758

Suborder Haplorhini Pocock, 1918

Infraorder Anthroidea Mivart, 1864

Family Parapithecidae Schlosser, 1911

Apidium Osborn, 1908

Type species—*Apidium phiomense* Osborn, 1908.

Included species—*Apidium phiomense* Osborn, 1908; *Apidium moustafai* Simons, 1962; *Apidium bowni* Simons, 1995b; *Apidium zuetina*, new species.

Emended diagnosis—Larger than *Biretia*. Lower molars differ from those of all other parapithecids in having centroconids and relatively longer M₃. Differs from *Simonsius* and *Parapithecus* in retaining two incisors in each jaw quadrant. P₃₋₄ differ from those of *Parapithecus* and *Simonsius* in retaining a vestigial cristid obliqua linking hypoconid and trigonid. P² differs from that of *Simonsius* in bearing a central cuspule or paraconule. M¹⁻² differ from those of *Simonsius* and *Biretia* in having pericones.

Discussion—Although *Apidium* is represented by multiple well preserved and relatively complete upper and lower dentitions, thorough descriptions of its dental anatomy have yet to be published (Osborn, 1908; Simons, 1962, 1995b; Szalay and Delson, 1979).

Systematically important specimens, such as the holotype of *Apidium bowni*, have never been figured (Simons, 1995b). As a result, overall size and the relative size of the lower molars have been the main features used to distinguish species of *Apidium* until now (Simons, 1995b). Correcting this problem is beyond the scope of this paper. However, in

order to justify erection of the new Libyan species proposed below, we provide some cursory observations on the dental anatomy of Fayum species of *Apidium* here.

[Figures 2-3 near here]

Apidium bowni from Quarry V in the Jebel Qatrani Formation is the smallest known species of *Apidium* (Fig. 2-3). In many ways its dental morphology is more primitive than that of either *A. moustafai* or *A. phiomense*, being strongly reminiscent of that of *Qatrania wingi* from Quarry E, which is located lower in Jebel Qatrani Formation. In particular, P₃₋₄ in *A. bowni* are notably more primitive than their counterparts in *A. moustafai* and *A. phiomense*. In *A. bowni* P₃₋₄ each bears a metaconid that is located relatively high on the trigonid, while remaining distal and inferior to the protoconid (Fig. 2A). The talonids of P₃₋₄ are simply constructed, consisting of an elevated hypoconid that gives rise to a short cristid obliqua, which connects the hypoconid mesially with the base of the metaconid. The lower premolars of *Apidium moustafai* and *A. phiomense* differ significantly from those of *A. bowni*, albeit in different ways. P₃₋₄ in *A. moustafai* are autapomorphous in that their metaconids have been displaced lingually, inferiorly, and distally (Fig. 2D). As a result, the metaconids on P₃₋₄ in *A. moustafai* have lost the close spatial connection with the protoconid that characterizes these teeth in *A. bowni*, *Biretia*, *Qatrania* and many other early anthropoids. Instead, the metaconids on P₃₋₄ in *A. moustafai* have become more closely affiliated (or “twinned”) with their respective hypoconids. P₃₋₄ in *A. phiomense* lack the metaconid displacement found in *A. moustafai*. However, in *A. phiomense* P₃₋₄ each possess a neomorphic crest located on the buccal side of the postvallid, which encloses a small talonid fovea that is bounded lingually by the hypoconid and cristid obliqua (Fig. 3).

P₃₋₄ in all species of *Apidium* are remarkably homodont, making it difficult to identify isolated examples of these teeth as to locus (Fig. 2-3). However, P₃ is typically oriented more obliquely in the tooth row than P₄, and this enhanced obliquity is reflected in the location of the mesial and distal interproximal wear facets on its crown as well as a more buccal location of the mesial root with respect to the distal root on P₃. Additionally, the trigonid of P₃ is relatively shorter mesiodistally than that of P₄ in *Apidium*. In buccal view, this difference is reflected in a sharper change in curvature from the buccal to the distal side of the trigonid on P₃, while on P₄ the distobuccal margin of the trigonid is more gently rounded.

Apidium zuetina, new species

Holotype—Z7I-1, right P₃ (Fig. 4A-C).

Hypodigm—The holotype; Z7I-2, right P² (Fig. 4E, H); Z7I-3, left P²; Z7I-4, left P⁴ (Fig. 4F, I); Z7I-5, left M² (Fig. 4G, J); Z7I-6, lingual fragment of left M²; Z7I-7, talonid fragment of right M₂ (Fig. 4D).

Type locality—Zallah 7 Incision Locality, Sirt Basin, Libya (Fig. 1B).

Known distribution—Early Oligocene of the Sirt Basin, central Libya.

Diagnosis—Medium-sized species of *Apidium*; smaller than *A. phiomense* and larger than *A. bowni*. P₃ differs from those of *A. bowni* and *A. moustafai* in having a vertically oriented crest on the postvallid that encloses a small talonid fovea. P₃ lacks the strong lingual deflection of the hypoconid that occurs in *A. moustafai*, yielding a shallower hypoflexid. M₂ differs from that of *A. bowni* in having a centroconid with a distolingual ridge that invades

the talonid, thereby approximating the entoconid. M² differs from that of *A. bowni* in having a weaker pericone and a neomorphic cuspule (or “dual conule”) between the paraconule and paracone. Major cusps of cheek teeth more inflated than in *A. moustafai* and *A. bowni*.

Etymology—Named for Zuetina Oil Company, in appreciation of the outstanding logistical support they provided during field work leading to the recovery of the hypodigm of this species.

[Figure 4 near here]

Description and comparisons

The holotype P₃ (L, 2.38 mm; W, 1.91 mm) shows an overall morphological pattern that is typical of *Apidium*, although distinctions from all three previously described species are apparent (Fig. 4A-C). Z7I-1 is identified as P₃ rather than P₄ on the basis of its mesiodistally abbreviated trigonid, the strong curvature of the distobuccal margin of its trigonid, and the location of its mesial and distal interproximal wear facets, which indicate a highly oblique alignment of the crown with respect to the long axis of the tooth row. The crown as a whole is relatively low and bunodont. Because the buccal side of the protoconid is noticeably inflated and the distal interstitial wear facet for P₄ forms an acute angle with the lingual side of the tooth, it is clear that the crown would have been oriented obliquely in the tooth row in life (with the long axis of the tooth being oriented in a mesiobuccal-distolingual direction). Such an oblique orientation of the lower premolars is typical for many basal anthropoid taxa, including species of *Apidium*. The trigonid of P₃ is dominated by the protoconid. There is no paraconid on P₃ in *A. zuetina*, while an incipient paraconid occurs in *A. bowni* and *A. moustafai*. A mesiolingual cingulid is present and relatively vertically

oriented on P₃ in *A. zuetina*; this structure is more nearly horizontal on P₃ in *A. bowni* and *A. moustafai*. The metaconid of P₃ is prominent and inflated in *A. zuetina*, occurring at a position inferior and distolingual to the protoconid, yet well above the level of the elevated hypoconid, which dominates the simple talonid. The P₃ metaconid is less inflated in *A. bowni*, and it appears to occur slightly higher on the trigonid than is the case in *A. zuetina*. In contrast, the P₃ metaconid in *A. moustafai* occurs lower and more distally on the trigonid, rendering it nearly the same height as the adjacent hypoconid, with which it is closely approximated. In terms of P₃ trigonid structure, *A. zuetina* generally resembles *A. phiomense*, which is larger and even more bunodont than the Libyan species. The P₃ talonid in *A. zuetina* is simply constructed, consisting of an elevated hypoconid and an extremely short cristid obliqua. There is neither a talonid basin nor an entoconid because the lingual side of the hypoconid slopes sharply toward the base of the crown. A short, weakly developed distolingual cingulid joins the base of the metaconid with the base of the hypoconid. Buccally, a hypoflexid is evident between the talonid and the postvallid. The hypoflexid is interrupted by a weak crest, which descends the postvallid to intersect with the buccal slope of the talonid near its buccal termination. A tiny fovea is enclosed between this weak postvallid crest and the hypoconid (Fig 4A, C). The talonid of P₃ in *A. bowni* generally resembles that of *A. zuetina*, although there is no development of the postvallid crest and tiny fovea found in *A. zuetina*. In contrast, the talonid of P₃ is remarkably derived in both *A. moustafai* and *A. phiomense*, albeit in different ways. In *A. moustafai* the hypoconid of P₃ (and P₄) has been deflected lingually, so that it lies immediately distal and adjacent to the metaconid. As a result, the hypoflexids of P₃₋₄ are much broader in *A. moustafai* than in other species of the genus. Like *A. bowni*, *A. moustafai* lacks the postvallid

crest and talonid fovea on P₃ that occurs in *A. zuetina*. In *A. phiomense* the P₃ talonid shows the same basic design found in *A. zuetina*, although the hypoflexid is less evident because the postvallid crest is more inflated, thereby occupying more of the space that would otherwise accommodate the hypoflexid. As in *A. zuetina*, the postvallid crest on P₃ (and P₄) in *A. phiomense* typically encloses a small fovea at the base of the postvallid immediately mesial to the hypoconid (Fig. 3B-C).

A right lower molar talonid fragment (Z7I-7; W, > 2.21 mm) is interpreted as pertaining to M₂ rather than M₁ on the basis of its well-developed centroconid, from which a spur of enamel extends distolingually toward the entoconid (Fig. 4D). In specimens of *A. moustafai* (e.g., YPM 18009) and *A. phiomense* (e.g., DPC 1102, DPC 20581) preserving serially associated lower molars, M₂ typically differs from M₁ in having a larger centroconid that produces a distolingual spur approaching the entoconid, as is the case in Z7I-7. Additional structures that can be observed on Z7I-7 include the entoconid, hypoconid and hypoconulid, all of which are strongly inflated such that their bases closely approximate one another. A distolingual fovea occurs behind the entoconid. In some individuals of *A. boweni* (e.g., DPC 6282), this distolingual fovea is absent because the entoconid and hypoconulid are weakly inflated, allowing a broad sulcus to separate them. In *A. moustafai* and variably in *A. boweni* (e.g., DPC 8707), the entoconid and hypoconulid are moderately inflated but a distinct distolingual fovea fails to develop because no shelf-like structure occurs behind the entoconid. In having a distolingual fovea and in showing highly inflated lower molar talonid cusps, *A. zuetina* closely resembles *A. phiomense*.

Currently, the upper dentition of *A. zuetina* is better documented than the lower dentition, with three tooth loci (P², P⁴ and M²) being represented by pristine specimens.

Two specimens in the current sample document P², but the crown of Z7I-2 (L, 1.87 mm; W, 2.53 mm) (Fig. 4E, H) is better preserved than that of Z7I-3. In occlusal outline P² approximates a rounded triangle, with the buccal margin being longer than the lingual margin. The paracone, which is tall and moderately inflated, dominates the buccal side of the crown. Pre- and postparacristae are present but weakly developed. A modest but continuous buccal cingulum arcs along the base of the paracone. The mesial and distal cingula are more pronounced, being lingually continuous with the small protocone. The distal cingulum is notably broad and shelf-like. Between the paracone and protocone, the intermediate cusp or paraconule is rounded and cusped, being taller and slightly more voluminous than the protocone. In occlusal outline and general morphology, P² in *A. zuetina* most closely resembles that of *A. boweni* (e.g., DPC 5264). In both *A. zuetina* and *A. boweni* the protocone of P² is smaller than the paraconule. The occlusal outline of P² in *A. moustafai* and *A. phiomense* is more transverse and more nearly rectangular. Additionally, both of the latter species differ from *A. zuetina* and *A. boweni* in having larger protocones and more mesiodistally extensive, ridge-like paraconules on P². As a result, P² in *A. boweni* and *A. zuetina* is readily distinguished from P³⁻⁴, while the three upper premolars are more nearly homodont in *A. moustafai* and (especially) *A. phiomense*. The root configuration of P² in *A. zuetina* is shown by Z7I-3, which bears two small buccal roots and one larger lingual root. Fleagle and Kay (1987) noted that species of *Apidium* are unusual among anthropoids in having triple-rooted P². The closely related parapiithecoid *Simonsius grangeri*, like most other anthropoids, has a double-rooted P².

P⁴ in *A. zuetina* is represented by Z7I-4 (L, 1.91 mm; W, 3.29 mm) (Fig. 4F, I), which displays the general morphology typical for species of *Apidium*. The tooth is quite

transverse in occlusal outline, being dominated by the paracone, paraconule and protocone, which are more or less aligned buccolingually. The crown as a whole is bunodont, and the three major cusps all show evidence of basal inflation. The paracone is low and surprisingly inflated, so that its buccal wall is less nearly vertical than is the case, for example, in P⁴ of *A. moustafai* (YPM 20913). In contrast to the condition in *A. bowni* and *A. moustafai*, in which the paracone of P⁴ is much taller than the protocone, there is little difference in the height of the paracone and protocone on P⁴ in *A. zuetina*. In the latter respect *A. zuetina* resembles *A. phiomense*. The paraconule is relatively isolated and cusped, and it lacks a distal extension of enamel as is typical for P⁴ in *A. phiomense*.

M² in *A. zuetina* is represented by Z7I-5 (L, 3.41 mm; W, 4.46 mm) (Fig. 4G, J), which is remarkably bunodont and nearly square in occlusal outline. Buccally, the crown is dominated by the paracone and metacone, the summits of which are located well internal to the buccal margin of the tooth due to their basal inflation. Paracone and metacone are connected by a short, weak, and mesiodistally straight centrocrista. The preparacrista and postmetacrista are even weaker, and both of the latter crests arc lingually to become continuous with the mesial and distal cingula, respectively. There is a faint and discontinuous buccal cingulum, better developed around the base of the paracone than distally. The bulbous protocone is neither as tall nor as voluminous as the paracone and metacone. The location of the protocone is relatively mesial and buccal, so that it lies nearer the paracone than the metacone. The protocone is connected to the adjacent paraconule by a short and weakly developed preprotocrista. The postprotocrista is absent, so that the protocone is separated from the adjacent metaconule by a furrow. A rounded preparaconule crista connects the paraconule to the mesial cingulum, but the metaconule is

isolated from the distal cingulum by a weak valley. Both conules are accompanied by smaller neomorphic cusps (or “dual conules”). The neomorphic cuspule associated with the paraconule is almost as large as the latter structure, being situated distobuccal to the paraconule at the base of the paracone. A smaller neomorphic cuspule is associated with the metaconule, lying immediately mesiobuccal to it. Because of the basal inflation of the three main trigon cusps and conules, the relatively buccal location of the protocone, and the presence of the neomorphic “dual conules,” the trigon basin itself is remarkably restricted. The lingual side of M² bears an extensive and complete lingual cingulum that supports both a pericone and a hypocone. The hypocone is particularly large and swollen, approximating the protocone in terms of its height and volume. Distobuccal to the hypocone, an additional neomorphic cuspule lies near the lingual terminus of the distal cingulum. The height of the lingual cingulum in the vicinity of the pericone is low relative to the protocone.

In several important ways, M² in *A. zuetina* resembles that of *A. phiomense* and differs from those of *A. bowni* and *A. moustafai*. For example, M² in *A. zuetina* and *A. phiomense* is significantly less transverse than M² in *A. bowni* and *A. moustafai*. The paracone and metacone are more swollen and bunodont in *A. zuetina* and *A. phiomense* than they are in *A. bowni* and *A. moustafai*. “Dual paraconules” are found on M² in *A. zuetina*, *A. moustafai*, and *A. phiomense*, but not in *A. bowni*. The neomorphic cuspule at the lingual terminus of the distal cingulum occurs in all species of *Apidium* except for *A. moustafai*. *A. moustafai* also differs from other species of *Apidium* in having little, if any, development of the pericone on the lingual cingulum of M². M² in *A. zuetina* differs from those of *A. bowni* and *A. phiomense* in having a relatively low lingual cingulum in the vicinity of the pericone, yielding a disparity in height between the protocone and pericone in *A. zuetina*.

Phylogenetic analysis

Methods

In order to evaluate the phylogenetic position of *Apidium zuetina* with respect to other species of *Apidium* and its potential impact on reconstructing phylogenetic relationships among other parapithecids, we constructed a data matrix consisting of 34 dental characters and eleven parapithecid species (Tables 1-2). Because our goal was limited to assessing phylogenetic relationships within the Parapithecidae and because most parapithecids are documented solely by dental remains, the data matrix was restricted to dental characters. Rather than coopting much larger data matrices that were assembled for larger-scale phylogenetic analyses (e.g., Ni et al., 2013), we chose to focus on dental characters that have been shown to be of systematic utility within Parapithecidae. Of the 34 dental characters selected for inclusion in our data matrix, seven are multistate characters. Four of these multistate characters were treated as “ordered” or “additive” because they appear to form natural morphoclines, while the three remaining multistate characters were treated as “unordered” or “non-additive” (see Table 1). All known parapithecid species aside from the poorly documented *Qatrania fleaglei* (Simons and Kay, 1988) and *Lokonepithecus manai* (Ducrocq et al., 2011) were included in the analysis. Following Beard (2013), we consider “*Abuqatrania*” *basiodontos* from L-41 in the Jebel Qatrani Formation (Simons et al., 2001) to be the oldest known species of *Qatrania* (i.e., *Qatrania basiodontos*).

[Tables 1-2 near here]

Parsimony analyses of the character-taxon matrix shown in Table 2 were undertaken using TNT or “Tree analysis using New Technology” (Goloboff et al., 2008). TNT requires a designated outgroup taxon to root the resulting trees. We chose *Biretia megalopsis* as our designated outgroup because species of *Biretia* are widely regarded as early, phylogenetically basal members of the parapithecoid clade and because *B. megalopsis* is better documented anatomically than *Biretia piveteaui* (Seiffert et al., 2005; Jaeger et al., 2010). The data were analyzed under the “New Technology search” option in TNT, using the sectorial search, ratchet, and tree fusing search methods (all with default parameters), followed by a round of tree bisection-reconnection branch swapping. Under these settings, iterations were run until the minimum length tree was found in 1000 separate replications. Relative stability of clades was assessed using bootstrap analyses (Felsenstein, 1985) and Bremer support indices (Bremer, 1988). Bootstrapping was based on 1000 replicates.

Results

Our analysis yielded a single most parsimonious tree with a branch length of 48 steps, a consistency index of 0.854, and a retention index of 0.885 (Fig. 5). *Apidium zuetina* from Zallah Oasis in central Libya is reconstructed as the sister taxon of *A. phiomense* from the upper part of the Jebel Qatrani Formation in the Fayum Depression of Egypt. The genus *Apidium* is shown to be monophyletic, with the two older species known from the Fayum (*A. moustafai* and *A. bowni*) being recovered as successive sister taxa to the *A. zuetina* + *A. phiomense* clade.

In contrast to earlier analyses of phylogenetic relationships among the Parapithecidae (Kay and Williams, 1994; Ross et al., 1998; Simons et al., 2001; Kay et al., 2004; Seiffert et al. 2005, 2009; Seiffert, 2012), *Qatrania* does not appear to be a phylogenetically basal member of the group. Instead, our analysis reconstructs *Qatrania* as the sister group of *Apidium*. *Parapithecus fraasi* and *Simonsius grangeri* are recovered as sister taxa, and this *Parapithecus* + *Simonsius* clade appears to be the sister group of the *Qatrania* + *Apidium* clade. Species of *Biretia* fall outside the clade containing all Oligocene members of the Parapithecidae, in agreement with earlier phylogenetic analyses (Seiffert et al., 2005, 2009; Seiffert, 2012).

[Figure 5 near here]

Discussion

Apidium zuetina from Zallah Oasis in Libya is phylogenetically close to *A. phiomense* from the Fayum, but *A. zuetina* is smaller and retains several primitive dental characters that have been modified in its nearest Egyptian relative. Based on the mammalian fauna associated with *A. zuetina* in the Zallah Incision local fauna, we interpret its age as close to that of Quarries V and G in the Fayum (30-31 Ma; see Coster et al., 2015). Such a correlation is consistent with the size and morphology of *A. zuetina*, which generally resembles *A. boweni* and *A. moustafai* from Quarries V and G in the Fayum in these respects. However, further work is needed to document the Zallah Incision local fauna more thoroughly.

The results of our phylogenetic analysis support a revised view of parapithecoid systematics. We recognize two clades of “advanced” parapithecids, which can be segregated into the subfamilies Parapithecinae and Qatraniinae. The Parapithecinae,

consisting of *Parapithecus fraasi* and *Simonsius grangeri*, includes taxa that are united by the loss of one or more lower incisor loci, complete suppression of lower molar paraconids, and various modifications of the lower premolars. *Parapithecus fraasi* and *Simonsius grangeri* are frequently referred to the same genus (Simons, 1974, 1986, 1995a, 2001; Simons and Rasmussen, 1991), but *Simonsius grangeri* is a highly autapomorphous parapithecoid that differs from *Parapithecus fraasi* in terms of lower dental formula, lower premolar morphology, and lower molar crown height (Kay and Williams, 1994). The morphological disparity distinguishing *Parapithecus fraasi* from *Simonsius grangeri* is significantly greater than that shown by other closely related anthropoids from the Fayum that are currently recognized at the generic level, such as *Proteopithecus sylviae* and *Serapia eocaena*. Accordingly, we follow multiple previous workers in recognizing *Simonsius* as warranting generic separation from *Parapithecus* (e.g., Kay and Williams, 1994; Ross et al., 1998; Kay et al., 2004). The subfamily Parapithecinae has been employed by earlier workers, but previous concepts of this taxon have always included *Apidium* as well as *Parapithecus* and *Simonsius* (e.g., Kay and Williams, 1994; Ross et al., 1998; Seiffert, 2007). Qatraniinae is an available name for the clade that includes *Qatrania* and *Apidium*. Previous workers have used this taxon as a wastebasket to accommodate *Qatrania* and other early anthropoids (e.g., *Proteopithecus*, *Serapia*, *Arsinoea*) thought to be specially related to undoubted parapithecoids (Kay and Williams, 1994; Ross et al., 1998). Based on the stratigraphic occurrence of the oldest known qatraniine *Qatrania basiodontos*, cladogenesis between Parapithecinae and Qatraniinae occurred sometime prior to deposition of Fayum locality L-41, which is currently thought to be latest Eocene or ~34 Ma in age (Seiffert, 2006). Such an early divergence date implies a ghost lineage spanning ~4

Ma for the Parapithecinae, which do not appear definitively in the fossil record until the upper part of the Jebel Qatrani Formation (although the precise age and type locality of *Parapithecus fraasi* remain unknown). Given the relatively small body size that characterized basal parapithecids belonging to the genus *Biretia* and early qatraniines such as *Qatrania wingi*, it is apparent that the larger body sizes that typify later parapithecines and advanced qatraniines such as *Apidium phiomense* were achieved through parallel evolution.

The discovery of *Apidium zuetina* in early Oligocene rocks of the Sirt Basin in central Libya raises the intriguing possibility that climatic deterioration following the Eocene-Oligocene boundary played a significant role in the macroevolutionary dynamics of early African anthropoids. Our work in Zallah Oasis indicates that the Zallah Incision local fauna containing *Apidium zuetina* derives from fluvial rocks occurring on a coastal plain that was located very near the ancient southern shoreline of the Tethys Sea. A very similar depositional environment has been reconstructed for early Oligocene *Apidium* species from the Jebel Qatrani Formation in Egypt (Bown et al., 1982; Bown and Kraus, 1988). It is hardly surprising that different species of *Apidium* inhabited different parts of the North African coastline during the early Oligocene. However, the fact that these closely related species occupied seemingly similar paleoenvironments implies the presence of some type of barrier to free dispersal and gene flow between *Apidium* populations occupying central Libya and northern Egypt at that time. One possibility requiring further investigation is that the cooler, drier climatic regime of the early Oligocene promoted the development of more heterogeneous environments across northern Afro-Arabia. If so, these relatively fragmented habitats would have stimulated speciation, especially among arboreal taxa

such as early anthropoids. Through time, as a function of oscillating climatic conditions, formerly segregated habitats might coalesce once again, allowing dispersal of certain *Apidium* populations into expanded ranges that were formerly occupied by allopatric species of the same genus. This model potentially explains the tree topology depicted in Figure 5, in which the Libyan species *A. zuetina* is more closely related to the Egyptian species *A. phiomense* than the latter is to older species of *Apidium* inhabiting the same area.

At first glance, this model emphasizing environmental patchiness and allopatric speciation seems subtle, especially when it is compared with older hypotheses that advocated a more direct role for Eocene-Oligocene climatic shifts during early anthropoid evolution (Cachel, 1979; Rasmussen et al., 1992). However, our understanding of early anthropoid phylogenetics and the geochronology of key Afro-Arabian sites has changed substantially since these hypotheses were proposed. As recently reviewed by Seiffert (2007), the well-documented Fayum record in northern Egypt suggests that Eocene-Oligocene climatic deterioration either had little impact on the origination and extinction of major anthropoid lineages or that any evolutionary response to climatic deterioration made by early anthropoids was delayed by millions of years with respect to the Eocene-Oligocene boundary. Based on the local biostratigraphic record in the Fayum, oligopithecids, qatraniine parapithecids, and possibly proteopithecids crossed the Eocene-Oligocene boundary (Seiffert, 2007). If we consider the Libyan record of Eocene anthropoids (Jaeger et al., 2010), it becomes clear that afrotarsiid anthropoids also crossed the Eocene-Oligocene boundary in North Africa. Finally, if the phylogeny depicted in Figure 5 is accurate, then parapithecine parapithecids also traversed the Eocene-Oligocene boundary, because the phylogenetic divergence between parapithecines and qatraniines

must antedate *Qatrania basiodontos*, which is documented from the latest Eocene L-41 locality in the Fayum. This leaves only propliopithecids as first appearing in the Fayum record during the early Oligocene. However, because the sister group of propliopithecids and later catarrhines likely consists of oligopithecids (e.g., Seiffert and Simons, 2001), even propliopithecids must have originated prior to the Eocene-Oligocene boundary, despite their relatively late appearance in the Fayum biostratigraphic record.

The ghost lineages of certain early anthropoid clades that are implied by current knowledge of early anthropoid phylogenetics bring this discussion full circle. Our model emphasizing environmental patchiness and allopatric speciation may be more broadly applicable than the case of *Apidium* focused upon here. That is, if this model is correct, we should expect most, if not all, local records of Afro-Arabian primate evolution during the late Eocene-early Oligocene interval to be incomplete reflections of phylogenetic reality. Clades that arise allopatrically should be confined to restricted ranges for extended periods of time, appearing only as ghost lineages in local records that lie outside their original ranges. Subsequent climatic oscillations will allow some of these clades to expand into new areas, and these taxa will appear suddenly in local records corresponding to these range expansions. According to this model, the impact of Eocene-Oligocene climatic deterioration on early African anthropoid evolution may well have been substantial, even if it was indirect. By increasing the fragmentation of habitats and promoting allopatric speciation, Eocene-Oligocene climatic deterioration favored higher alpha-level diversity among early Afro-Arabian anthropoids. As illustrated by the case of Libyan and Egyptian species of *Apidium*, this enhanced alpha-level diversity would then likely have resulted in greater interspecific competition and higher extinction rates. The overall effect of the cooler, drier

climatic conditions across the Eocene-Oligocene boundary was increased turnover among early Afro-Arabian anthropoids, higher levels of faunal provincialism within Afro-Arabia, and longer ghost lineages for certain taxa caused by extended periods of geographical sequestration. For these reasons, enhancing the geographic dimension of the fossil record of Afro-Arabian anthropoids during this key interval may well be as illuminating as augmenting its temporal component.

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Figure captions

Figure 1. (A) Map of Libya and adjacent areas showing the location of Zallah Oasis in the Sirt Basin. (B) Higher resolution map showing Zallah Oasis and the surrounding vicinity. Fossil sites depicted on the map are as follows: 1, Zallah 5 Rodent locality (see Coster et al., 2010, 2012); 2, Zallah 7 Incision locality; 3, fossil site located west of Zallah in Wadi Umm al Laban (see Fejfar, 1987); 4, fossil site located southeast of Zallah reported by Arambourg (1963).

Figure 2. Lower dentition of *Apidium bowni* and *Apidium moustafai* from the Jebel Qatrani Formation, Fayum Depression, Egypt. (A-C) *Apidium bowni*, DPC 6282, right dentary fragment preserving crowns of P₃-M₂ from Quarry V, in lingual (A), occlusal (B), and buccal (C) views. (D-F) *Apidium moustafai*, CGM 26919, holotype left dentary fragment preserving crowns of P₃-M₁ from Quarry G, in lingual (D), occlusal (E), and buccal (F) views.

Figure 3. Lower dentition of *Apidium phiomense* (DPC 1102) from Quarry I, Jebel Qatrani Formation, Fayum Depression, Egypt. Right dentary fragment preserving crowns of C₁-M₃ in lingual (A), occlusal (B), and buccal (C) views. Abbreviations for structures visible on the talonids of P₃₋₄ are: fvea, talonid fovea; and pvld, postvallid crest.

Figure 4. *Apidium zuetina*, new species, from the Zallah 7 Incision locality. Holotype right P₃ (Z7I-1) in occlusal (A), lingual (B), and buccal (C) views. Right M₂ talonid (Z7I-7) in occlusal view (D). Right P² (Z7I-2) in buccal (E) and occlusal (H) views. Left P⁴ (Z7I-4) in

buccal (F) and occlusal (I) views. Left M² (Z7I-5) in buccal (G) and occlusal (J) views.

Abbreviations are: ctrd, centroconid; entd, entoconid; fvea, talonid fovea; hyld, hypoconulid; hypd, hypoconid; and pvld, postvallid crest.

Figure 5. Single most parsimonious tree obtained from analysis of the character-taxon matrix shown in Table 2 using TNT (see text for further details). Bootstrap values are shown above branches. Bremer support is given below branches.

A

B

fig 1

fig 2

fig 3

fig 4

fig 5

Table 1

Dental characters selected for their phylogenetic utility among Parapithecidae.

1. I₁ present (0); or absent (1).
2. I₂ present (0); or absent (1).
3. P₂ lingual cingulid relatively linear mesiodistally (0); or deeply invaginated distally (1).
4. P₂ crown height lower than P₃ (0); equivalent in height (1), or taller than P₃ (2) **(ordered/additive)**.
5. P₂ hypoconid poorly developed or located well below level of P₃ trigonid (0); or elevated with respect to P₃ trigonid (1).
6. P₃ metaconid development: absent (0); weak (1); or strong (2) **(ordered/additive)**.
7. P₃ postvallid crest: absent (0); or present (1).
8. P₃ talonid fovea: absent (0); or present (1).
9. P₃ hypoconid: absent or indistinct (0); present (1); or present and elevated (2) **(ordered/additive)**.
10. P₃ cristid obliqua: present, runs toward postvallid (0); present, runs toward metaconid (1); or absent/indistinct (2) **(unordered/nonadditive)**.
11. P₄ entoconid: present (0); or absent (1).
12. P₄ cristid obliqua: present, runs toward postvallid (0); present, runs toward metaconid (1); or absent/indistinct (2) **(unordered/nonadditive)**.
13. P₄ lingual protocristid: present (0); or absent (1).
14. P₄ hypoconid: present but weak (0); or inflated and/or elevated (1).

15. P₄ preprotocristid: trenchant (0); or weak or absent (1).
16. P₄ metaconid position on trigonid: low (0); or high (1).
17. M₁ paraconid present (0); or absent (1).
18. M₁ lingual protocristid present (0); or absent (1).
19. M₁ centroconid absent (0); or present (1).
20. M₁ postentoconid sulcus absent (0); or present (1).
21. M₂ paraconid present (0); or absent (1).
22. M₂ centroconid absent (0); present, cuspidate (1); or present, with enamel ridge invading talonid (2) (**ordered/additive**).
23. M₂ hypoconulid present, connected to hypoconid by postcristid or fused with its base (0); or hypoconulid present, separated from hypoconid by sulcus (1).
24. M₃ paraconid present (0); or absent (1).
25. M₃ hypoconulid not significantly inflated (0); or significantly inflated, projects distally beyond hypoconid (1).
26. M₃ lingual protocristid present (0); or absent (1).
27. P² paraconule absent (0); or present (1).
28. P² double-rooted (0); or triple-rooted (1).
29. P⁴ paraconule absent or insignificant (0); or present and inflated (1).
30. M¹ pericone absent (0); or present (1).
31. M² pericone absent or indistinct (0); or present and significantly inflated (1).
32. M² paraconule present, located on preprotocrista (0); paraconule present, accompanied by dual conule located between preprotocrista and base of paracone

(1); or single conule present between preprotocrista and paracone (2)

(unordered/nonadditive).

33. M² hypocone present (0); or hypocone present, accompanied by neomorphic cusp on distal cingulum buccal to hypocone (1).

34. M² remnant of postprotocrista present (0); or absent (1).

Table 2

Character-taxon matrix employed for parsimony analysis using TNT. Abbreviation: P, polymorphic (i.e., 0&1).

<i>Simonsius grangeri</i>	11010 11002 12101 11101 10010 10010 0201
<i>Parapithecus fraasi</i>	10010 10012 12111 11101 10010 1???? ???? ?
<i>Apidium bowni</i>	00??? 10021 11111 10011 01101 11111 1011
<i>Apidium moustafai</i>	??121 20021 11111 1P111 11111 1111P 1101
<i>Apidium zuetina</i>	????? 21121 ????? ????? ?21?? ?111? 1111
<i>Apidium phiomense</i>	00121 21121 11111 1P111 12111 11111 1111
<i>Qatrania wingi</i>	????? ????? 11111 10001 P0101 1???? ???? ?
<i>Qatrania basiodontos</i>	????? ????? 11111 10001 00101 1???? ???? ?
<i>Biretia fayumensis</i>	????? 01010 00000 00000 P00P0 0??00 0000
<i>Biretia megalopsis</i>	??100 01010 00000 00000 00000 0??00 0000
<i>Biretia piveteaui</i>	????? ????? ????? ????? 00000 0??00 0000