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## Diets of fossil primates from the Fayum Depression of Egypt: a quantitative analysis of molar shearing

Over the last 90 years, Eocene and Oligocene aged sediments in the Fayum Depression of Egypt have yielded at least 17 genera of fossil primates. However, of this diverse sample the diets of only four early Oligocene anthropoid genera have been previously studied using quantitative methods. Here we present dietary assessments for 11 additional Fayum primate genera based on the analysis of body mass and molar shearing crest development. These studies reveal that all late Eocene Fayum anthropoids were probably frugivorous despite marked subfamilial differences in dental morphology. By contrast, late Eocene Fayum prosimians demonstrated remarkable dietary diversity, including specialized insectivory (*Anchomomys*), generalized frugivory (*Plesiopithecus*), frugivory+insectivory (*Wadilemur*), and strict folivory (*Aframomius*). This evidence that sympatric prosimians and early anthropoids jointly occupied frugivorous niches during the late Eocene reinforces the hypothesis that changes in diet did not form the primary ecological impetus for the origin of the Anthropoidea. Early Oligocene Fayum localities differ from late Eocene Fayum localities in lacking large-bodied frugivorous and folivorous prosimians, and may document the first appearance of primate communities with trophic structures like those of extant primate communities in continental Africa. A similar change in primate community structure during the Eocene–Oligocene transition is not evident in the Asian fossil record. Putative large anthropoids from the Eocene of Asia, such as *Amphipithecus mogaungensis*, *Pondaungia cotteri*, and *Siamopithecus eocaenus*, share with early Oligocene Fayum anthropoids derived features of molar anatomy related to an emphasis on crushing and grinding during mastication. However, these dental specializations are not seen in late Eocene Fayum anthropoids that are broadly ancestral to the later-occurring anthropoids of the Fayum's upper sequence. This lack of resemblance to undisputed Eocene African anthropoids suggests that the “progressive” anthropoid-like dental features of some large-bodied Eocene Asian primates may be the result of dietary convergence rather than close phyletic affinity with the Anthropoidea.

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### Introduction

Fossil primates from the Fayum badlands of Egypt comprise the most diverse and comprehensively studied group of Paleogene primates known from a single geographic locale (Simone & Rasmussen, 1994a; Simons, 1998). At least 17 genera of Fayum

primates are currently recognized (Table 1), including ten anthropoid genera (*Aegyptopithecus*, *Propliopithecus*, *Apidium*, *Parapithecus*, *Oligopithecus*, *Qatrania*,<sup>1</sup>

<sup>1</sup>Species of *Qatraria* studied here include *Q. wingi* from quarry E, *Q. fleaglei* from quarry M, and an undescribed new species of *Qatraria* from quarry L-41, herein referred to as “L-41 *Qatraria* sp.”

**Table 1** Ages of Fayum primates

Locality	Species	Age (Ma)
Quarries I, M	<i>Aegyptopithecus zeuxis</i> (A-PR) <i>Afrotarsius chatrathi</i> (P) <i>Apidium phiomense</i> (A-PA) <i>Parapithecus fraasi</i> (A-PA) <i>Parapithecus grangeri</i> (A-PA) <i>Propliopithecus chirobates</i> (A-PR) <i>Qatrania fleaglei</i> (A-PA) Possible Lorisidae sp. indet. (P?)	33.1–33.4
Quarries V, G	<i>Apidium bowni</i> (A-PA) <i>Apidium moustafai</i> (A-PA) <i>Propliopithecus ankeli</i> (A-PR)	33.8–34.0
Quarry E	<i>Oligopithecus savagei</i> (A-OL) Omomyidae sp. indet. (P) <i>Qatraria wingi</i> (A-PA)	34.0–35.1
Quarry L-41	<i>Aframonius diedes</i> (P) <i>Anchomomys milleri</i> (P) <i>Arsinoea kallimos</i> (A-IS) <i>Catopithecus browni</i> (A-OL) <i>Plesiopithecus teras</i> (P) <i>Proteopithecus sylviae</i> (A-PD) <i>Qatraria</i> sp. (A-PA) <i>Serapia eocaena</i> (A-PA) <i>Wadilemur elegans</i> (P)	35.6–35.9
Provenance Unknown	<i>Parapithecus fraasi</i> (A-PA) <i>Propliopithecus haekeli</i> (A-PR) <i>Propliopithecus markgrafi</i> (A-PR)	Early Oligocene?

Abbreviations: A=anthropoid, IS=*incertae sedis*, OL=oligopithecine, P=prosimian, PA=parapithecid, PD=proteopithecid, PR=propliopithecine.

Ages of quarries follow [Kappelman \(1992\)](#). The Fayum upper sequence includes early Oligocene quarries V, G, I, and M; the lower sequence includes late Eocene quarries E and L-41.

*Catopithecus*, *Proteopithecus*, *Serapia*, and *Arsinoea*) and 7 prosimian<sup>2</sup> genera (*Afrotarsius*, *Wadeilemur*, *Anchomomys*, *Aframonius*, *Plesiopithecus*, an unnamed lorisid,<sup>3</sup> and an

<sup>2</sup>We have chosen to use the gradistic term “prosimian” to refer to all nonanthropoid primates because questions regarding the higher-level phylogenetic affinities of Fayum taxa are beyond the scope of this paper. As used here, “prosimian” thus refers to any primate that lacks the distinguishing anatomical hallmarks of the Anthropoidea, such as a postorbital septum composed primarily of a flange from the zygomatic and the complete obliteration of the stapedial artery ([Ross, 1994](#)).

<sup>3</sup>We follow [Schwartz et al. \(1998\)](#) in preferring the commonly-used family name “Lorisidae” to the infrequently-used name “Loridæ” that has technical priority ([Jenkins, 1987](#)).

unnamed omomyiform) ([Kay et al., 1981](#); [Simons & Kay, 1983](#); [Simons & Bown, 1985](#); [Fleagle & Kay, 1987](#); [Simons, 1989, 1992, 1997a](#); [Simons et al., 1995](#); [Fleagle, 1999](#)). These taxa are primarily collected from six major quarries that are distributed across two stratigraphic horizons ([Table 1](#)). The older horizon (the “lower sequence”) includes quarries E and L-41 and has been dated using paleomagnetic correlation to the late Eocene (~36–34 Ma; [Kappelman, 1992](#)). The younger horizon (the “upper sequence”) includes quarries V, G, I, and M, and has been dated to the early Oligocene (~34–33 Ma; see [Table 1](#)). Most Fayum quarries are taxonomically diverse,

and exhibit between three and five sympatric primate species (Simons & Rasmussen, 1994a). However, late Eocene quarry L-41 has produced an unparalleled nine genera of fossil primates (Simons, 1989, 1992, 1997a; Simons *et al.*, 1995).

Diets of some upper sequence anthropoids (i.e., those from early Oligocene Fayum localities) have been studied quantitatively through analyses of molar shearing crest development (Kay & Simons, 1980) and dental microwear and microstructure (Teaford *et al.*, 1996). These studies agree that most species of *Apidium*, *Parapithecus*, *Aegyptopithecus*, and *Propliopithecus* were primarily frugivorous. The only exception is *Parapithecus grangeri*, which demonstrates better developed molar shearing crests than extant frugivorous hominoids and thus may have included a relatively large proportion of leaves in its diet (Kay & Simons, 1980). However, studies of dental microwear clearly demonstrate that *P. grangeri* was not a strict folivore (Teaford *et al.*, 1996). These data suggest that although *P. grangeri* is the most folivorous primate known from the Fayum's upper sequence, this species probably consumed significant quantities of both leaves and fruit (Teaford *et al.*, 1996).

In contrast to the studies of Kay & Simons (1980) and Teaford *et al.* (1996), all dietary assessments for primates from late Eocene Fayum localities have been made on a qualitative basis. Due to relatively small estimates of body mass (i.e., ~300 g) and the apparent weak development of molar shearing crests, Simons & Kay (1983) suggested that *Qatrania wingi* from quarry E primarily fed on fruit or gum. Similarly, small body size estimates and general features of molar anatomy led Rasmussen & Simons (1992) to conclude that *Oligopithecus savagei* from quarry E, and *Catopithecus browni* and *Proteopithecus sylviae* from quarry L-41 were “frugivores/insectivores” (p. 491), comparable in dietary habits to extant *Saimiri* and

*Callimico*. The assessment of a frugivorous/insectivorous diet for *Oligopithecus* and *Catopithecus* was reaffirmed by Simons *et al.* (1994), who noted that these genera could not have been folivorous due to small body size and the “absence of specific buccal shearing crests and styles that occur among folivores” (p. 185). These authors further suggested that the “extreme upper molar bunodonty” of *Proteopithecus* and *Qatrania* is indicative of a more frugivorous diet than *Oligopithecus* and *Catopithecus*, and that the flat molar surfaces of *Arsinoea kallimos* (also from L-41) may be an adaptation for hard object feeding (Simons *et al.*, 1994:189).

The only Fayum prosimians for which dietary hypotheses have been advanced are *Plesiopithecus teras* and *Aframomius diedes* from L-41. Simons *et al.* (1994) suggested that the large and procumbent anteriormost mandibular teeth of *Plesiopithecus* are an adaptation for “gnawing on resistant food items” (p. 193) in the context of mixed herbivory comparable to that exhibited by modern sciurids. Simons (1998) has also argued that the well developed molar shearing crests and comparatively large body size of *A. diedes* indicate that this species was at least partly folivorous.

The goal of this paper is to provide a more thorough and quantitative assessment of the diets of Fayum primates through an analysis of body mass and molar shearing crest development. In so doing we have attempted to document dietary changes in various evolving lineages through time, as well as to contrast the manner in which dietary niches have been partitioned between anthropoids and prosimians in the lower (late Eocene) and upper (early Oligocene) sequences. With respect to each of these secondary goals, the unusually high primate taxonomic diversity and dense sampling of the Fayum geological section have provided an opportunity for detailed analysis not possible at many other Paleogene sites.

## Methods

### *Reconstructing fossil primate diets*

**Body size.** Body size is one of the most important factors to be considered in assessing the diets of fossil primates. All extant primates that are primarily insectivorous are relatively small (i.e., below 300 g), while extant primates that are primarily folivorous have much larger body masses (i.e., above 600 g; Kay & Covert, 1984; Smith & Jungers, 1997). Because these size ranges do not overlap it is possible to distinguish insectivores from folivores on the basis of body size alone. Accordingly, a body size rubicon of 500 g ("Kay's Threshold") has often been used as a *prima facie* criterion to distinguish insectivorous and folivorous fossil taxa (Gingerich, 1980, 1981; Kay & Covert, 1984). By contrast, frugivorous primates are distributed across a wide range of large and small body sizes (Kay & Simons, 1980). This large size range for frugivores makes it impossible to use estimates of body mass to differentiate frugivores from insectivores or folivores. However, because fruits tend to contain little protein, frugivorous primates must rely on either insects or leaves (both protein-rich) as a secondary food source (Kay & Covert, 1984; Lambert, 1998). The body mass distributions of frugivorous primates that secondarily exploit either insects or leaves closely match the respective body mass distributions of insectivorous and folivorous primates (Kay & Simons, 1980). Though additional overlap occurs, most frugivore-insectivores have body masses less than 1600 g, while frugivore-folivores tend to have body masses greater than 1000 g (Kay & Simons, 1980; Kay & Covert, 1984). The body size range between 1000 g and 1600 g thus represents an interval within which assessments of the likely protein source of extinct frugivorous primates cannot be made based on body size alone (Kay & Simons, 1980).

**Molar shearing crests.** One means of distinguishing frugivorous primates from similarly sized insectivores or folivores is to calculate shearing quotients (henceforth called "SQs") as a relative measure of molar shearing crest development (Kay & Simons, 1980; Anthony & Kay, 1993; Kay & Ungar, 1997; Meldrum & Kay, 1997). In all SQ analyses, a regression line (the "SQ reference line") is fit to a log-transformed bivariate plot of molar length and the summed lengths of molar shearing crests. The SQ reference line may be calculated in any numbers of ways, provided that residuals from the line may be used to distinguish between extant taxa with high and low molar shearing across a range of molar sizes. For instance, the SQ reference line may be empirically derived from all (e.g., Covert, 1985) or a subset (Kay & Simons, 1980; Anthony & Kay, 1993) of the data, or it may be calculated with a slope that is assigned *a priori* (Meldrum & Kay, 1997). However, as long as the SQ reference line describes a range of similarity in shearing crest development (i.e., the line is not surrounded by extant taxa with relatively high shearing at one end, but relatively low shearing at the other), these differences in the manner with which the line is calculated will have little effect on the outcome of the analysis.

The utility of the SQ as a predictor of diet depends on the fact that insectivores and folivores rely on food sources that are structurally similar to each other, but structurally very different from those consumed by frugivores (Kay & Covert, 1984). Primates that include significant quantities of leaves and insects in their diets require better development of molar shearing crests in order to more finely comminute the structural carbohydrates they ingest, whether they be in the form of chitin (from insects) or cellulose and hemicellulose (from leaves). Thorough mastication of insects and leaves is necessary because the digestibility of chitin and cellulose is inversely proportional to particle size

(Sheine & Kay, 1977; Kay & Sheine, 1979). Frugivorous primates do not require comparable development of molar shearing crests because fruits need not be finely comminuted in order to be fully digested (Sheine & Kay, 1977). Accordingly, analyses of molar shearing crest development permit discrimination between insectivores/folivores with long, trenchant shearing crests and frugivores with shorter shearing crests (Kay & Simons, 1980; Kay & Covert, 1984).

Unlike fruits, leaves and insects, the dietary significance of plant exudates is often overlooked in quantitative dietary analyses. Though gummivory is uncommon in most mammalian orders, several callitrichid, galagid, and cheirogaleid primate species rely on gums as their primary food source (Lambert, 1998). Like insectivores, gummivores tend to be relatively small. This relationship is probably due to the fact that a large-bodied primate would experience considerable difficulty meeting its absolute energy requirements by feeding primarily on exudates. As with insects, exudates are typically available only in relatively limited quantities per feeding bout, and there is likely a limit to the quantity of exudates that can be harvested each day from any given area of forest. The largest extant gummivorous primate (*Phaner furcifer*) has a mean body mass of only 460 g (Smith & Jungers, 1997), suggesting that fossil taxa with body masses above Kay's Threshold are unlikely to have been primarily gummivorous. Gummivores also exhibit poorly developed molar shearing crests comparable to those seen in frugivores (Anthony & Kay, 1993; Meldrum & Kay, 1997). Accordingly, fossil taxa that demonstrate little molar shearing capacity and have estimated body masses less than 500 g could either have been frugivorous or gummivorous. Though the gross morphology of the anterior dentition may provide evidence of gummivorous habits (e.g., as in *Cebuella*, *Phaner*, and *Euoticus*),

attempts to distinguish between gummivores and small frugivores can only be made on an *ad hoc* qualitative basis for extinct species.

Like exudates, seeds comprise a significant proportion of the diet of some primate species, but are often not considered in quantitative dietary analyses. Meldrum & Kay (1997) have shown that platyrhine seed predators that specialize in eating hard seeds and fruits with tough peri- and endocarps (e.g., *Cebus*, *Pithecia*, *Cacajao*, and *Chiropotes*; Kinzey, 1992; Kinzey & Norconk, 1993) exhibit very poorly developed molar shearing crests. This poor shearing crest development is presumably related to the ability to generate high occlusal loads in the context of feeding on hard, relatively brittle food items (Lucas & Teaford, 1994). Accordingly, extinct species which show evidence of exceptionally poor molar shearing crest development must be recognized as having exhibited the potential for hard seed predation (Meldrum & Kay, 1997).

#### *Measurements and calculations*

Measurements of fossil taxa were made at the Duke University Primate Center using original dental material or high-resolution epoxy casts. Included specimens are listed in Table 2. The lengths of shearing crests 1–6 (Kay, 1977; Figure 1), the mesiodistal crown length, and the buccolingual crown width of the  $M_1$  and  $M_2$  were measured using a Nikon dissecting microscope fitted with a calibrated reticle. Only specimens exhibiting minimal wear were included in the analyses of molar shearing.

Body mass was estimated using the all-primate, prosimian, and anthropoid least-squares regression equations presented in Conroy (1987). The equations are:

$$\text{All Primate } \ln(B) = 1.784 \ln(A) + 2.54$$

$$\text{Prosimian } \ln(B) = 1.614 \ln(A) + 2.67$$

$$\text{Anthropoid } \ln(B) = 1.570 \ln(A) + 3.38$$

**Table 2** Included fossil specimens

Species	Catalog no.	Locality
<i>Aframomius diedes</i>	DPC 17828, DPC 11595, CGM 42202, DPC 16708, DPC 17951	L-41
<i>Afrotarsius chatrathi</i>	CGM 42830	M
<i>Anchomomys milleri</i>	CGM 42847	L-41
<i>Arsinoea kallimos</i>	CGM 42310	L-41
<i>Catopithecus browni</i>	DPC 11541, DPC 11566, DPC 11627, DPC 11943, DPC 12147, DPC 15339	L-41
<i>Oligopithecus savagei</i>	DPC 2957	E
<i>Plesiopithecus teras</i>	CGM 42291, DPC 11636, DPC 13607	L-41
<i>Proteopithecus sylviae</i>	CGM 41917, DPC 10370, DPC 13615, DPC 15305, DPC 15416	L-41
<i>Qatrania</i> sp. (L-41)	98-1061, DPC 14236, DPC 18305	L-41
<i>Qatrania wingi</i>	DPC 6125	E
<i>Qatrania fleaglei</i>	CGM 41850	M
<i>Serapia eocaena</i>	CGM 42286, DPC 12708, DPC 15685, DPC 15686, DPC 7340	L-41
<i>Wadilemur elegans</i>	CGM 42211, DPC 13439	L-41

Abbreviations: CGM—Cairo Geological Museum; DPC—Duke Primate Center.

where  $B$  is body mass in grams and  $A$  is the area of  $M_1$  in millimeters.  $M_1$  area is calculated as the product of the crown length and width. Mean  $M_1$  crown areas and body mass estimates for all fossil taxa studied are presented in Table 3. In making our final dietary assessments (see Tables 6 and 7) we have chosen to assume that the prosimian equation produces the most accurate body mass estimates for the fossil prosimians included in this analysis, and that the anthropoid equation produces the most accurate body mass estimates for the fossil anthropoids.<sup>4</sup>

As noted by Kay & Covert (1984), the choice of an appropriate comparative sample for calculating SQs is critical due to the influence of phylogeny on dental anatomy. In many aspects of their molar morphology, lower sequence Fayum primates<sup>5</sup> are far more primitive than any post-

Eocene catarrhines (e.g., *Sivapithecus* and *Aegyptopithecus*; Figure 1). For instance, all lower sequence primates demonstrate some difference in height between the trigonid and talonid and conspicuously lack wear facet X (see Kay, 1977, for a description of terminology). Furthermore, lower sequence anthropoids retain  $M_1$  paraconids and show no trace of the distal fovea that characterizes dentally advanced catarrhines (Figure 1). In light of these plesiomorphies shared by many lower sequence primates, the use of extant hominoids as an SQ reference population (as in Kay & Simons, 1980) would clearly be inappropriate for this analysis. Fortunately, three other data sets on molar shearing in extant primates are available for comparison. Covert (1985) presented dietary information and molar shearing crest data for 29 prosimian species ( $n=153$ ). Similarly, Anthony & Kay (1993) and Meldrum & Kay (1997) published lengths of  $M_1$  shearing crests for 18 platyrhine species ( $n=114$ ). Prosimians and platyrhines are more comparable in molar morphology to lower sequence primates than catarrhines because prosimians and platyrhines retain some separation of the trigonid and talonid basins and lack wear facet X (Figure 1; Kay, 1977).

<sup>4</sup>One potential problem with the use of molar area to estimate body mass in a dietary analysis is the fact that species with similar body sizes but different diets also demonstrate systematic differences in molar size (Kay, 1975; Lucas & Teaford, 1994). However, because we are limited by the scarcity of additional fossil evidence upon which estimates of body mass can be made (e.g., postcrania), some degree of circularity in the present study is unavoidable.

<sup>5</sup>These dental generalizations also apply to *Afrotarsius chatrathi* and *Q. fleaglei* from upper sequence quarry M.

In calculating SQs, the methodologies set forth in both [Covert \(1985\)](#) and [Anthony & Kay \(1993\)](#) were followed without modification. The lengths of shearing crests 1–6 were summed and averaged within species to calculate the mean total shearing (MTS). MTS and mean molar length for prosimians ( $M_2$ ) and platyrhines ( $M_1$ ) were natural log-transformed and expressed as bivariate plots using the statistical program JMP version 3.1.5. Least-squares regression lines were then fit to these scattergrams using molar length as the independent variable ([Figure 2](#)).<sup>6</sup>

All sampled extant prosimians were included in the calculation of the prosimian regression line ([Covert, 1985](#)), but following [Anthony & Kay \(1993\)](#), *Brachyteles* and *Alouatta* were excluded from the platyrhine regression line in order to prevent it from being “pulled upward” ([Anthony & Kay, 1993:362](#)). The platyrhine SQ reference line is thus fit only to primarily frugivorous and gummivorous species (see footnote 6). The exclusion of *Brachyteles* and *Alouatta* is justified by the fact that the  $M_1$  lengths of the most insectivorous (*Saimiri* and *Callimico*) and folivorous (*Alouatta* and *Brachyteles*) platyrhines (range of  $\ln M_1$  lengths = 0.96–1.98) are substantially larger as a group than the combined  $M_1$  lengths of

more frugivorous and gummivorous platyrhines (range of  $\ln M_1$  lengths = 0.58–1.70) ([Figure 2](#)). As a result, fitting a line to the total sample of extant platyrhines would produce a slope that is exceptionally high, and thus cause large folivores to fall too close to the regression line. If *Brachyteles* and *Alouatta* were not excluded, the reference line could not be used to reliably discriminate between taxa with high and low molar shearing because the line would cross from a domain indicative of low shearing (at low  $M_1$  lengths) to a domain indicative of high shearing (at high  $M_1$  lengths). By contrast, in the prosimian sample, the range of insectivore and folivore  $M_1$  lengths broadly overlaps the range of frugivore and gummivore  $M_1$  lengths ([Figure 2](#)). Accordingly, these data may be analyzed using [Covert’s \(1985\)](#) method of calculating an SQ reference line (i.e., an empirical fit to the entire sample) without losing the ability to distinguish between taxa with high and low molar shearing.

Expected MTS values for fossil taxa were calculated based on known  $M_2$  length using the prosimian regression equation and known  $M_1$  length using the platyrhine regression equation ([Figure 2](#)). Real MTS deviations from the regression line were expressed as percent differences from the expected MTS using the formula:

$$\frac{[(\text{observed MTS} - \text{expected MTS}) / \text{expected MTS}] \times 100}{}$$

<sup>6</sup>Following [Meldrum & Kay \(1997\)](#), *Saimiri* and *Callimico* are represented in [Figure 2](#) as “insectivores” because these genera are the most insectivorous platyrhines. However, it should be noted that fruit rather than insects is probably the major dietary component of these two genera. Although *Saimiri* spends between 70 and 80% of its foraging time searching for and consuming insects ([Mittermeier & van Roosmalen, 1981; Terborgh, 1983](#)), stomach contents of wild-shot individuals are typically composed primarily of fruit and other plant matter ([Fooden, 1964; Baldwin & Baldwin, 1981](#)). Despite a dearth of quantitative dietary data for *Callimico goeldii*, most accounts of this species’ diet emphasize the importance of fruit as well as insects ([Heltne \*et al.\*, 1981; Pook & Pook, 1981, 1982](#)). Accordingly, *Saimiri* and *Callimico* probably do not represent exceptions to [Kay & Covert’s \(1984\)](#) observation that primarily insectivorous primates always fall near or below 300 g in body mass.

The size-adjusted measurement of relative molar shearing thus obtained is the SQ ([Kay & Simons, 1980; Anthony & Kay, 1993; Kay & Ungar, 1997](#)). Taxa with more molar shearing than expected based on the comparative sample demonstrate positive SQs, while those with less molar shearing than expected have negative SQs. SQs calculated using  $M_2$  shearing crest measurements (henceforth “ $M_2$  SQs”) are presented in [Table 4](#); SQs calculated using  $M_1$  shearing

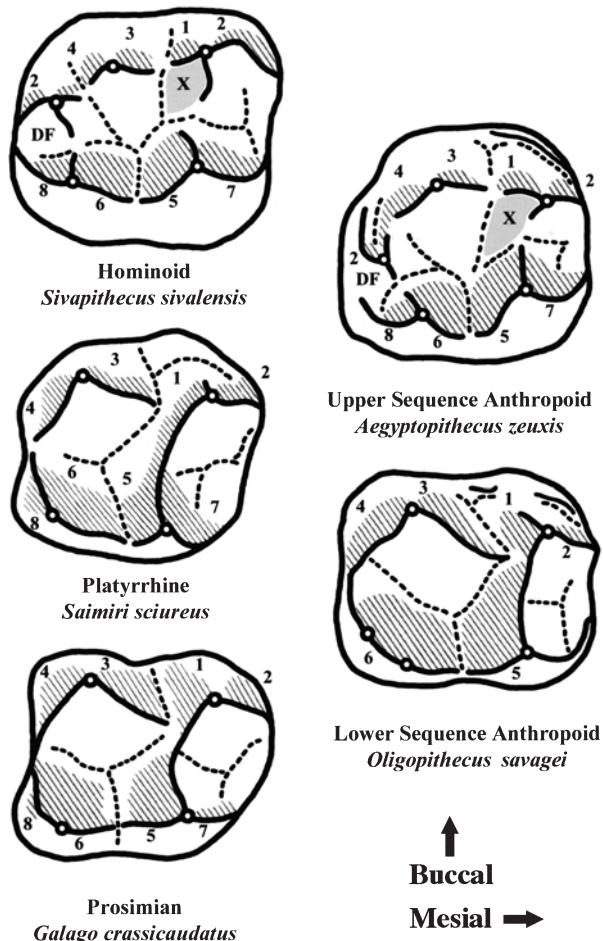


Figure 1.  $M_2$ s of representative primate species. Primary phase I wear facets indicated by slanted lines and numbered following Kay (1977). Only the shearing crests associated with wear facets 1–6 were measured for this analysis. Phase II wear facet X indicated by shading when present. DF=distal fovea. All illustrations modified after Kay & Hiemae (1974) and Kay (1977). Figures not to scale.

crest measurements (henceforth “ $M_1$  SQs”) are presented in Table 5.

## Results

### Body mass

Our estimates of body mass based on  $M_2$  area (Table 3) are in broad agreement with body mass estimates previously published for *Oligopithecus*, *Catopithecus*, *Proteopithecus*, and *Q. wingi* (Simons & Kay, 1983; Rasmussen & Simons, 1992). Quantitative

body mass estimates for other Fayum primates have not been published. Our results suggest that four taxa (*Anchomomys milleri*, *Wadilemur elegans*, *Afrotarsius chatrathi*, and *Q. wingi*) probably had body masses less than 300 g. By analogy with living primates, these species could have been primarily insectivorous, frugivorous, or gummivorous (Kay & Covert, 1984). In spite of the wide confidence ranges for Conroy’s (1987) dental regressions L-41 *Qatrania* sp. may also be included in this group. However, if

Table 3 Estimated body mass of fossil species based on  $M_1$  area

	$n$	$M_1$ area (mm <sup>2</sup> )	All primate regression (g)	Prosimian regression (g)	Anthropoid regression (g)	Kay's Threshold
<i>Anchomomys milleri</i>	1	2.75	77 (38–157)	74 (28–196)	144 (77–268)	Below
<i>Wadilemur elegans</i>	2	3.32	108 (50–235)	100 (36–277)	194 (102–369)	Below
<i>Qatrania wingi</i>	2	3.83	139 (61–317)	126 (44–359)	242 (125–469)	Below
<i>Qatrania</i> sp. (L-41)	3	4.77	206 (84–504)	180 (60–537)	341 (172–679)	Below
<i>Afrotarsius chatrathi</i>	1	4.90	216 (88–535)	188 (63–565)	357 (179–712)	Below
<i>Qatrania fleaglei</i>	1	6.16	325 (122–866)	272 (86–858)	510 (249–1046)	??
<i>Arsinoea kallimos</i>	1	6.48	355 (131–963)	295 (92–941)	552 (268–1139)	??
<i>Proteopithecus sylviae</i>	5	8.21	542 (185–1588)	432 (128–1452)	800 (377–1699)	Above
<i>Serapia eocaena</i>	4	9.63	721 (234–2227)	559 (160–1947)	1029 (475–2226)	Above
<i>Catopithecus browni</i>	6	9.98	768 (246–2401)	592 (169–2079)	1088 (501–2364)	Above
<i>Plesiopithecus teras</i>	3	10.35	822 (260–2602)	629 (178–2229)	1155 (529–2521)	Above
<i>Oligopithecus savagei</i>	1	12.77	1193 (360–4043)	881 (238–3267)	1602 (716–3586)	Above
<i>Aframonius diedes</i>	4	13.26	1275 (372–4376)	936 (250–3499)	1699 (756–3820)	Above

All body masses calculated using least-squares regression formulae presented in Conroy (1987). Estimated body mass (bold) and 95% confidence range (parentheses) are expressed in grams.  $M_1$  Area is the mean product of  $M_1$  crown length and  $M_1$  crown width in mm;  $n$ =number of specimens; Kay's Threshold=500 g.

its estimated body mass of 341 g (based on the anthropoid regression) is accurate, L-41 *Qatrania* sp. would be near the hypothetical maximum body size at which primary<sup>7</sup> insectivory could be sustained (i.e., 350 g; Kay & Covert, 1984).

By contrast, five species (*Serapia eocaena*, *Catopithecus browni*, *Oligopithecus savagei*, *Plesiopithecus teras*, and *Aframonius diedes*) probably had body masses greater than 600 g (Table 3). *Serapia*, *Catopithecus*, *Oligopithecus*, *Plesiopithecus*, and *Aframonius* are thus the only lower sequence primates that could have been primarily folivorous (Kay & Covert, 1984). However, it is important to note that Conroy's (1987) prosimian regression equation produces body mass estimates for *Serapia* and *Catopithecus* that are below 600 g. Accordingly,

if the molar dimensions of these lower sequence anthropoids scaled with body size in a manner more comparable to extant prosimians than extant anthropoids, *Serapia* and *Catopithecus* may actually have been too small to sustain predominantly folivorous diets.

Uncertainty regarding the capacity of *Serapia* and *Catopithecus* for folivory is compounded by the fact that anthropoids and prosimians differ in the lower body size limit at which primary folivory occurs among extant taxa. Within Malagasy strepsirrhines, a number of examples may be found in which highly folivorous species demonstrate body masses well below 1 kg (e.g., *Avahi occidentalis*, *Hapalemur griseus*, and *Lepilemur leucopus*; Smith & Jungers, 1997). By contrast, the smallest anthropoid folivore (*Procolobus verus*) weighs between 4 and 5 kg, nearly an order of magnitude larger than the smallest prosimian folivore. While the cause of this disparity is not immediately obvious, these data do suggest that additional scrutiny should be given to fossil anthropoids with relatively small body

<sup>7</sup>For the purposes of this analysis, "primary" refers to the dietary item which comprises the largest part (by volume) of a species' diet. "Secondary" designates to the next largest component of a species' diet, and thus refers to the protein source (i.e., either insects or leaves) of primarily frugivorous species or the carbohydrate source (i.e., usually fruit) of primarily insectivorous or folivorous species.

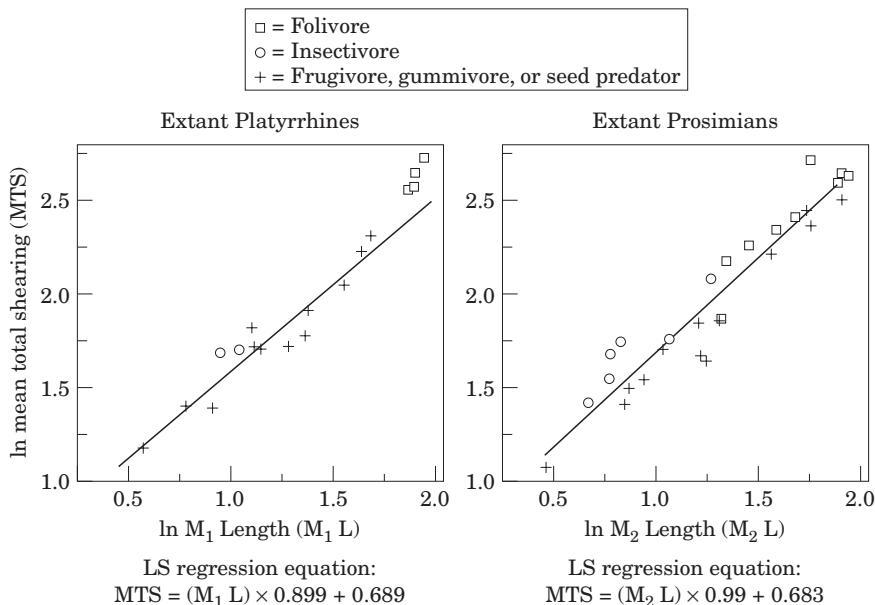


Figure 2. Regressions used to calculate shearing quotients.

masses (i.e., between 600 g and 4000 g) but high degrees of molar shearing.

The dietary implications of the body mass estimates for *Arsinoca kallimos*, *Qatrania fleaglei*, and *Proteopithecus sylviae* are similarly difficult to interpret. Estimates of body mass for *Arsinoea*, *Q. fleaglei*, and *Proteopithecus* range above and below Kay's Threshold depending on which extant group is used for comparison (Table 3). However, unambiguous findings regarding shearing crest development in *Proteopithecus* obviate concern over uncertainty in the estimated body mass of this taxon (see Discussion). Unfortunately, shearing crest measurements are not available for *Arsinoea* and *Q. fleaglei*. If one assumes that their body mass estimates based on the anthropoid regression are accurate, both taxa were probably larger than the largest living insectivorous primates (*Galago senegalensis* and *Arctocebus calabarensis*; ~300 g), but smaller than the smallest living folivorous primate (*L. leucopus*; ~600 g; Smith & Jungers, 1997). By process of elimination, these measurements

suggest that *Arsinoea* and *Q. fleaglei* were primarily frugivorous. Furthermore, because the great majority of extant frugivores under 1000 g in body mass rely on insects as a source of protein, these relatively small body mass estimates for *Arsinoea* and *Q. fleaglei* also suggest that these taxa were secondarily insectivorous. However, additional analyses of molar shearing and dental microwear will be required to confirm these hypotheses.

#### *M*<sub>2</sub> shearing quotients

**Extant prosimians.** M<sub>2</sub> SQs for extant prosimians are highly correlated with diet (Covert, 1985; Table 4). Most species that are primarily frugivorous or gummivorous have M<sub>2</sub> SQs less than -0.8, indicating relatively poor development of molar shearing crests. Conversely, most species that are primarily insectivorous or folivorous exhibit M<sub>2</sub> SQs greater than -0.8 due to the presence of relatively long and well developed molar shearing crests. The only species

Table 4 The relative development of  $M_2$  shearing crests in extant prosimians and fossil taxa

Species	n	Diet	$M_2L$	MTS	SQ
<i>Cheirogaleus major</i>	4	Fruit	3.43	5.22	- 22.12
<i>Perodicticus potto</i>	8	Fruit	3.41	5.24	- 21.44
<i>Lepilemur mustelinus</i>	4	Leaves	3.76	6.30	- 14.29
<i>Otolemur crassicaudatus</i>	6	Fruit	3.72	6.31	- 13.24
<b><i>Serapia eocaena</i></b>	4	?	<b>3.05</b>	<b>5.24</b>	- 12.41
<b><i>Qatrania</i> sp. (L-41)</b>	3	?	<b>2.42</b>	<b>4.23</b>	- 10.92
<i>Cheirogaleus medius</i>	6	Fruit	2.32	4.06	- 10.90
<b><i>Plesiopithecus teras</i></b>	2	?	<b>3.20</b>	<b>5.64</b>	- 9.90
<i>Varecia variegata</i>	5	Fruit	6.78	11.92	- 9.51
<b><i>Oligopithecus savagei</i></b>	1	?	<b>3.51</b>	<b>6.22</b>	- 9.45
<i>Allocebus trichotis</i>	1	?	1.76	3.18	- 8.22
<i>Phaner furcifer</i>	6	Gums	2.55	4.60	- 8.10
<i>Eulemur fulvus mayottensis</i>	3	Fruit	5.81	10.41	- 7.89
<i>Microcebus murinus</i>	5	Fruit	1.58	2.92	- 6.30
<b><i>Wadilemur elegans</i></b>	2	?	<b>2.28</b>	<b>4.22</b>	- 5.84
<i>Euoticus elegantulus</i>	6	Gums	2.36	4.39	- 5.20
<b><i>Proteopithecus sylviae</i></b>	4	?	<b>2.83</b>	<b>5.32</b>	- 3.99
<i>Nycticebus coucang</i>	5	Fruit	3.34	6.28	- 3.88
<i>Eulemur coronatus</i>	4	Fruit	4.78	9.03	- 3.05
<i>Galago alleni</i>	7	Fruit	2.80	5.44	- 0.80
<i>Indri indri</i>	7	Leaves	7.04	13.56	- 0.79
<b><i>Catopithecus browni</i></b>	5	?	<b>3.21</b>	<b>6.30</b>	<b>0.24</b>
<i>Propithecus verreauxi</i>	5	Leaves	6.66	13.11	1.30
<b><i>Aframomius diedes</i></b>	5	?	<b>4.52</b>	<b>9.01</b>	<b>2.18</b>
<i>Loris tardigradus</i>	6	Insects	2.88	5.78	2.39
<i>Eulemur fulvus rufus</i>	7	Leaves	5.42	10.83	2.65
<i>Eulemur macaco</i>	1	Fruit	5.63	11.27	2.88
<i>Propithecus diadema</i>	4	Leaves	6.76	13.63	3.84
<i>Lemur catta</i>	9	Leaves	4.92	10.16	5.95
<b><i>Anchomomys milleri</i></b>	1	?	<b>1.97</b>	<b>4.18</b>	<b>7.69</b>
<i>Galagoidea demidoff</i>	8	Insects	1.94	4.14	8.45
<i>Euoticus inustus</i>	5	Insects	2.15	4.72	11.83
<i>Arctocebus calabrensis</i>	6	Insects	3.56	7.79	11.88
<i>Hapalemur griseus</i>	4	Leaves	4.28	9.39	12.46
<i>Avahi laniger</i>	7	Leaves	3.84	8.61	14.73
<i>Galago senegalensis</i>	7	Insects	2.17	5.34	25.17
<i>Tarsius spectrum</i>	5	Insects	2.27	5.70	27.97
<i>Hapalemur simus</i>	2	Leaves	5.82	14.57	28.69

$M_2L$ =mesiodistal crown length of the  $M_2$  in mm; MTS=mean total shearing in mm (average sum of the lengths of  $M_2$  shearing crests 1–6); SQ=shearing quotient; n=number of specimens. Metric data for extant prosimians from Covert (1985); diets taken from Covert (1985), except *E. coronatus* (Mittermier *et al.*, 1994) and *E. macaco* (Colquhoun, 1993). Fossil taxa shown in bold.

that do not fit these generalizations are *Eulemur macaco* and *Lepilemur mustelinus*. The single measured specimen of *E. macaco* demonstrates an unusually high  $M_2$  SQ (2.9) for a frugivore. This anomaly may be the result of small sample size. Similarly, *L. mustelinus* has molar shearing crests that are very poorly developed ( $M_2$  SQ= - 14.3)

for a species whose diet is overwhelmingly composed of leaves (i.e., >90%; Russell, 1977). However, *Lepilemur* may be able to sustain a highly folivorous diet, in spite of its limited ability for mechanical comminution of fibrous foods, by practicing coprophagy (Hladik & Charles-Dominique, 1974; Covert, 1985).

**Table 5** The relative development of  $M_1$  shearing crests in extant platyrhines and fossil taxa

Species	<i>n</i>	Diet	$M_1L$	MTS	SQ
<i>Cacajao melanocephalus</i>	2	Seeds/Fruit	3.97	5.90	-14.23
<i>Chiropotes satanas</i>	5	Seeds/Fruit	3.64	5.58	-12.30
<i>Saguinus mystax</i>	5	Fruit/Insects	2.52	4.03	-11.85
<i>Cebus apella</i>	5	Fruit/Seeds	4.79	7.71	-5.33
<b><i>Plesiopithecus teras</i></b>	3	?	<b>3.45</b>	<b>5.75</b>	<b>-5.07</b>
<i>Cebuella pygmaea</i>	4	Gum/Fruit	1.78	3.26	-2.53
<i>Pithecia monachus</i>	4	Fruit/Seeds	4.00	6.78	-2.11
<b><i>Qatrania wingi</i></b>	1	?	<b>2.41</b>	<b>4.30</b>	<b>-2.00</b>
<i>Callicebus moloch</i>	10	Fruit	3.18	5.55	-1.51
<i>Callithrix argentata</i>	4	Fruit/Gum	2.22	4.08	0.01
<b><i>Serapia eocaena</i></b>	5	?	<b>3.10</b>	<b>5.54</b>	<b>0.50</b>
<i>Leontopithecus rosalia</i>	5	Fruit	3.09	5.62	2.34
<b><i>Qatrania</i> sp. (L-41)</b>	3	?	<b>2.41</b>	<b>4.50</b>	<b>2.56</b>
<i>Ateles geoffroyi</i>	10	Fruit	5.26	9.31	5.09
<b><i>Afrotarsius chatrathi</i></b>	1	?	<b>2.55</b>	<b>4.97</b>	<b>7.54</b>
<b><i>Wadilemur elegans</i></b>	2	?	<b>2.09</b>	<b>4.16</b>	<b>7.65</b>
<i>Saimiri sciureus</i>	5	Fruit/Insects	2.87	5.54	7.81
<b><i>Proteopithecus sylviae</i></b>	5	?	<b>2.98</b>	<b>5.77</b>	<b>8.47</b>
<b><i>Anchomomys milleri</i></b>	1	?	<b>1.97</b>	<b>4.01</b>	<b>9.28</b>
<i>Lagothrix lagotricha</i>	8	Fruit/Leaves	5.47	10.12	10.28
<i>Aotus trivirgatus</i>	10	Fruit/Leaves	3.06	6.16	13.16
<b><i>Catopithecus browni</i></b>	6	?	<b>3.41</b>	<b>6.91</b>	<b>15.28</b>
<i>Callimico goeldii</i>	3	Fruit/Insects	2.60	5.48	16.54
<i>Alouatta fusca</i>	6	Leaves	6.70	12.94	17.51
<i>Alouatta caraya</i>	6	Leaves	6.72	13.09	18.55
<b><i>Aframonioides diedes</i></b>	1	?	<b>4.23</b>	<b>8.69</b>	<b>19.22</b>
<i>Alouatta palliata</i>	10	Leaves	6.92	13.91	22.70
<i>Brachyteles arachnoides</i>	9	Leaves	7.22	15.19	28.97

$M_1L$ =mesiodistal crown length of the  $M_1$  in mm; MTS=mean total shearing in mm (average sum of the lengths of  $M_1$  shearing crests 1–6); SQ=shearing quotient; *n*=number of specimens. Metric data for extant platyrhines from Anthony & Kay (1993) and Meldrum & Kay (1997); diets taken from Meldrum & Kay (1997), except *Leontopithecus*, *Saimiri*, and *Callimico* (Fooden, 1964; Baldwin & Baldwin, 1981; Mittermeier & van Roosmalen, 1981; Terborgh, 1983; Rowe, 1996). Fossil taxa shown in bold.

**Fossil taxa.** Relative to the extant prosimian sample, most of the fossil taxa studied in this analysis have rather poorly developed  $M_2$  shearing crests, and therefore exhibit low  $M_2$  SQs (Table 4; Figure 3). Included within this group are *Proteopithecus* ( $M_2$  SQ=−4.0), *Wadilemur* ( $M_2$  SQ=−5.8), *Oligopithecus* ( $M_2$  SQ=−9.5), *Plesiopithecus* ( $M_2$  SQ=−9.9), L-41 *Qatrania* sp. ( $M_2$  SQ=−10.9), and *Serapia* ( $M_2$  SQ=−12.4). These findings suggest that fruit probably formed the largest component of the diets of these taxa, although gums could have been dietarily significant for small-bodied *Wadilemur* and L-41 *Qatrania*

sp. Individual frugivorous species would have supplemented their diets with insects or leaves according to body size (see Tables 3 and 7). The only genera with relatively high  $M_2$  SQs are *Aframonioides* ( $M_2$  SQ=2.2) and *Anchomomys* ( $M_2$  SQ=7.7). These two adapiforms are the largest (*Aframonioides* ~936 g) and smallest (*Anchomomys* ~74 g) fossil prosimians included in this analysis, and fall on opposite sides of Kay's Threshold. These data support the conclusion that *Aframonioides* was largely folivorous, while *Anchomomys* was predominantly insectivorous (Figure 3). Like *Aframonioides*, *Catopithecus* also demonstrates a positive  $M_2$  SQ

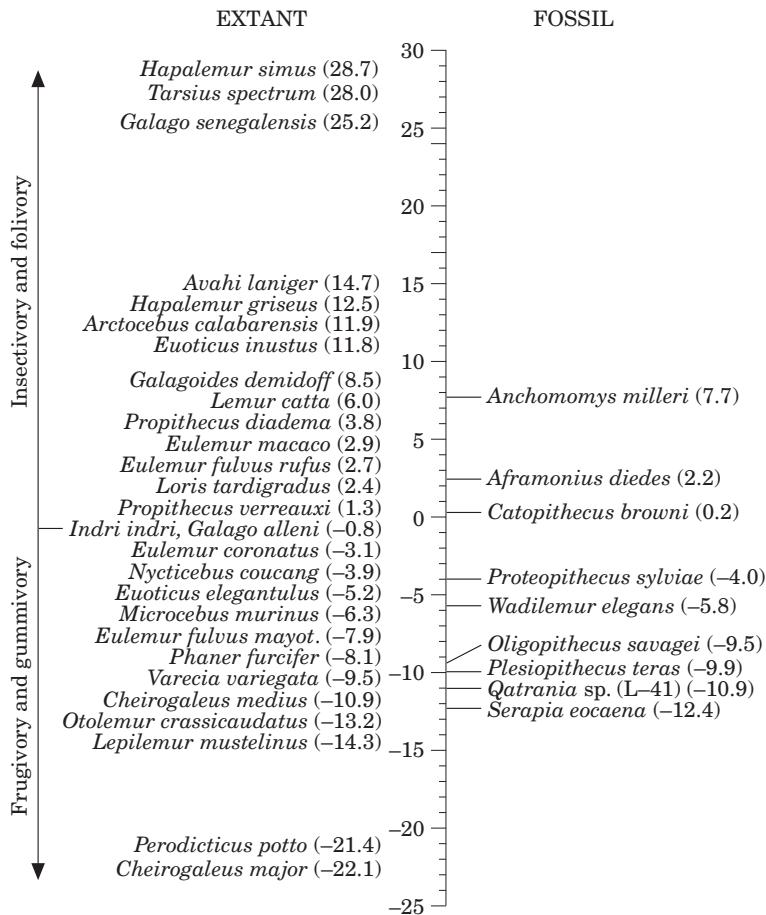


Figure 3. Comparison of  $M_2$  shearing quotients in fossil primates from the Fayum and extant prosimians.

(0.2) and a body mass ( $\sim 1088$  g) above Kay's Threshold. Though these findings are suggestive of folivory, the  $M_2$  SQ of *Catopithecus* is very close to the value that distinguishes extant frugivores from insectivores and folivores ( $-0.8$ ) (Figure 3). This relatively low  $M_2$  SQ, combined with wide confidence limits for body mass, limit the degree of certainty with which dietary assessments can be made for *Catopithecus* based on the extant prosimian sample.

#### $M_1$ shearing quotients

*Extant platyrhines.* As with the  $M_2$  SQs of extant prosimians,  $M_1$  SQs of living platyr-

rhines are strongly correlated with diet (Anthony & Kay, 1993; Meldrum & Kay, 1997; Table 5). The most frugivorous platyrhines have  $M_1$  SQs below 6.0. Primary gummivores and seed predators have even lower  $M_1$  SQs, with maximum values of about  $-2.5$  and  $-2.1$ , respectively (Figure 4). These low  $M_1$  SQs for frugivores, gummivores, and seed predators confirm expectations that the foods eaten by these species require little shearing during mastication. A middle range of shearing quotients between about 7.0 and 17.0 is occupied by species that are primarily frugivorous, but consume large secondary quantities of either insects (i.e., *Saimiri* and

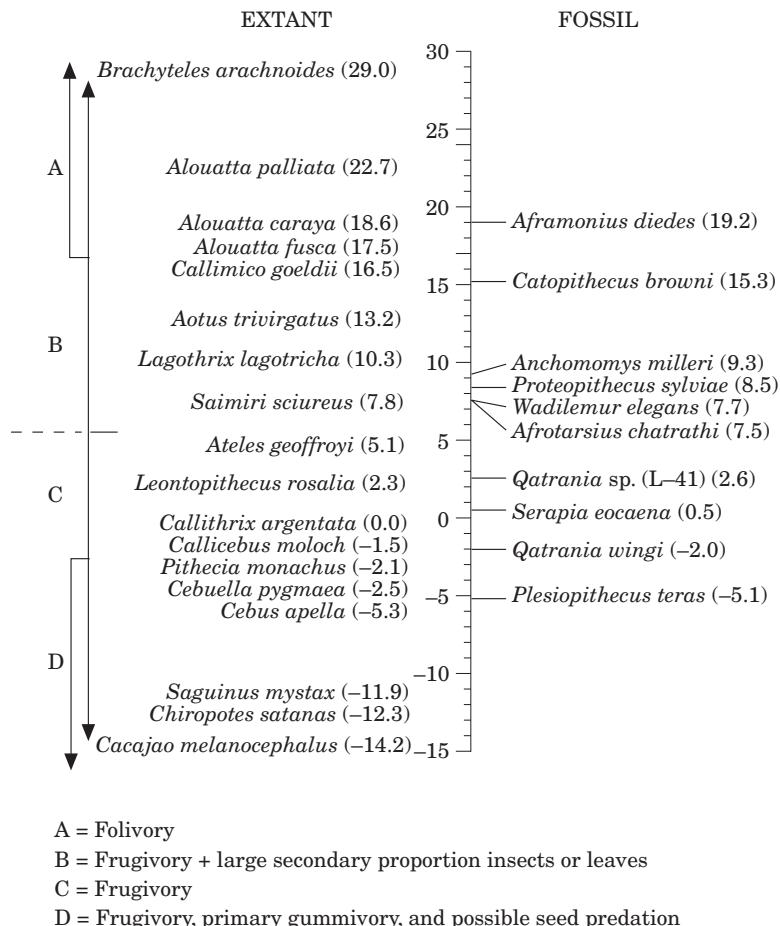


Figure 4. Comparison of  $M_1$  shearing quotients in fossil primates from the Fayum and extant platyrhines.

*Callimico*; see footnote 6) or leaves (i.e., *Lagothrix* and *Aotus*) (for dietary sources, see Wright, 1985; Anthony & Kay, 1993; Rowe, 1996; Meldrum & Kay, 1997; and Fleagle, 1999). These taxa thus help establish a range of  $M_1$  SQs within which fruits, as well as significant quantities of other food items requiring more molar shearing, may be exploited. As expected, folivorous platyrhines have the highest  $M_1$  SQs (Figure 4), with all species of *Alouatta* and *Brachyteles* exhibiting  $M_1$  SQs greater than 17.0.

**Fossil taxa.** Fossil taxa demonstrate a wide range of  $M_1$  SQ values relative to extant

platyrhines (Table 5, Figure 4). *Aframomius* has the highest  $M_1$  SQ (19.2) of all included fossil species, and falls well within the range of extant folivores. *Catopithecus* ( $M_1$  SQ=15.3), *Anchomomys* ( $M_1$  SQ=9.3), *Proteopithecus* ( $M_1$  SQ=8.5), *Wadilemur* ( $M_1$  SQ=7.7), and *Afrotarsius* ( $M_1$  SQ=7.5) also have relatively high degrees of molar shearing that are suggestive of frugivory with a large secondary component of insects or leaves. By contrast, L-41 *Qatrania* sp. ( $M_1$  SQ=2.6), *Serapia* ( $M_1$  SQ=0.5), *Q. wingi* ( $M_1$  SQ=-2.0), and *Plesiopithecus* ( $M_1$  SQ=-5.1) demonstrate very low  $M_1$  SQs that place them unambiguously in the range

Table 6 Inferred diets of fossil species

	Previous dietary assessment	Diet based on prosimian SQ ( $M_2$ )	Diet based on platyrhine SQ ( $M_1$ )	Final dietary assessment
<i>Anchomomys milleri</i>	None	Insects	Fruit+insects	Insects+fruit
<i>Wadilemur elegans</i>	None	Fruit or gums	Fruit+insects	Fruit or gums+insects
<i>Qatrania wingi</i>	Fruit or gums	N/A	Fruit or gums	Fruit or gums
<i>Qatrania</i> sp. (L-41)	None	Fruit or gums	Fruit or gums	Fruit or gums
<i>Afrotarsius chatrathi</i>	None	N/A	Fruit+insects	Fruit+insects
<i>Qatrania fleaglei</i>	None	N/A	N/A	Fruit (see text)
<i>Arsinoea kallimos</i>	Seeds	N/A	N/A	Fruit (see text)
<i>Proteopithecus sylviae</i>	Fruit and insects	Fruit	Fruit+insects	Fruit+insects
<i>Serapia eocaena</i>	None	Fruit	Fruit	Fruit
<i>Catopithecus browni</i>	Fruit and insects	Ambiguous	Fruit+insects or leaves	Fruit+insects or leaves
<i>Plesiopithecus teras</i>	Seeds and nuts	Fruit	Fruit or seeds	Fruit or seeds
<i>Oligopithecus savagei</i>	Fruit and insects	Fruit	N/A	Fruit
<i>Aframomius diedes</i>	Leaves	Leaves	Leaves	Leaves

Previous dietary assessments taken from literature cited in the Introduction. Final dietary assessment lists only the primary component of the diet unless the platyrhine data indicate significant exploitation of a secondary food source in addition to fruit (i.e., a “borderline  $M_2$  SQ”, as found in *Catopithecus*, *Proteopithecus*, *Afrotarsius*, *Wadilemur*, and *Anchomomys*).

of strict frugivores or frugivore/gummivores. Of these four taxa, only *Plesiopithecus* exhibits  $M_1$  SQs that are low enough to potentially be indicative of hard seed predation (Figure 4).

## Discussion

### Comparison of extant samples

Table 6 presents a summary of the dietary hypotheses for fossil taxa generated by this analysis. These new assessments of diet are largely in accord with those of previous authors. Furthermore, most dietary assessments based on the prosimian and platyrhine comparative samples are also congruent. However, in one case (*Anchomomys*), the  $M_1$  SQ favors a slightly different dietary interpretation than the  $M_2$  SQ. In this instance, we regard the food item favored by both comparative data (i.e., insects) as the most likely major dietary component of the species in question.

### Diets of fossil species

**Prosimians.** *A. milleri* has an  $M_2$  SQ that places it firmly within the range of insectivorous and folivorous prosimians, and an  $M_1$  SQ indicative of frugivory with a large secondary component of insects or leaves (henceforth termed a “borderline  $M_1$  SQ”). Given the very small body mass estimates for this species, we conclude that *Anchomomys* relied on insects as its primary food source, and that fruit formed a lesser but significant component of its diet. *W. elegans* also demonstrates a borderline  $M_1$  SQ, but has an  $M_2$  SQ suggestive of frugivory or gummivory. Small body mass estimates for *Wadilemur* favor the conclusion that this prosimian was primarily frugivorous or gummivorous, but supplemented its diet with a large quantity of insects.

*A. chatrathi* is known from a single mandibular specimen with a damaged  $M_2$ . As a result, it is presently only possible to measure  $M_1$  shearing crests for this species. These measurements reveal that *Afrotarsius*

has a borderline  $M_1$  SQ. Body mass estimates for *Afrotarsius* fall well below Kay's Threshold, leading to the conclusion that although this species was primarily frugivorous, insects formed an important secondary component of its diet.

*P. teras* has an  $M_2$  SQ falling within the range of frugivorous prosimians, and the lowest  $M_1$  SQ of all fossil taxa measured. Large body mass estimates for *Plesiopithecus* rule out the possibility that this species was primarily gummivorous. These data indicate that *Plesiopithecus* was a frugivore with the potential for hard seed predation. Because the estimated body mass of *P. teras* is below 1000 g, this species probably relied secondarily on insects rather than leaves as a source of dietary protein. By contrast, *A. diedes* exhibits the highest  $M_1$  SQ of all fossil taxa measured, and has an  $M_2$  SQ within the range of insectivorous and folivorous prosimians. The relatively large body mass estimates for this species thus suggest that *Aframomius* was highly folivorous.

*Anthropoids*. *Q. wingi* from quarry E is the smallest anthropoid included in this analysis. Its  $M_1$  SQ is very low, and approaches the range of platyrhine seed predators such as *Pithecia*. These data suggest that *Q. wingi* could have been frugivorous or gummivorous. However, we consider the possibility that this species was a seed predator unlikely due to its small body size (~242 g; Table 3). Similarly, the geologically older unnamed species of *Qatrania* from quarry L-41 demonstrates  $M_1$  and  $M_2$  SQs that are both indicative of frugivory or gummivory. As with *Q. wingi*, exudates cannot be eliminated as a potential major food item for L-41 *Qatrania* sp. due to the very small body size of this species. Small body mass estimates for both species further suggest that *Q. wingi* and L-41 *Qatrania* sp. relied secondarily on insects as a protein source.

As noted previously, shearing crest measurements are unavailable for the

geologically youngest *Qatrania* species, *Q. fleaglei*. However, the close resemblance in molar morphology between all species of *Qatrania* suggests that *Q. fleaglei* was also primarily frugivorous or gummivorous and secondarily insectivorous. This conclusion is corroborated by an estimated body mass for this species (~510 g) that falls between the ranges of extant primary folivores and insectivores.

*A. kallimos* is known from a single hemimandible with teeth that are too worn to permit shearing crest analysis on either the  $M_1$  or  $M_2$ . However, like *Q. fleaglei*, *Arsinoea* was probably too large (~550 g) to have been primarily insectivorous, and too small to have been primarily or secondarily folivorous. Accordingly, we suggest that *Arsinoea* was a frugivore that supplemented its diet with insects.

*P. sylviae* has an  $M_2$  SQ that is within the range of prosimian frugivores and a borderline  $M_1$  SQ. Because its body mass was probably above Kay's Threshold but below 1000 g, it is unlikely that *Proteopithecus* was primarily gummivorous or secondarily folivorous. These data favor the conclusion that the main component of *Proteopithecus*' diet was fruit, supplemented by a significant quantity of insects. *S. eocaena* and *O. savagei* also have estimated body masses above Kay's Threshold. However, the  $M_1$  and  $M_2$  SQs of these species unambiguously indicate that *Serapia* and *Oligopithecus* were frugivores. While the estimated body mass of *Serapia* cannot resolve the question of whether it was secondarily insectivorous or folivorous, *Oligopithecus* was almost certainly secondarily folivorous due to its large body mass.

Perhaps the most surprising SQs are those of *C. browni*. All body mass estimates (range=592 g–1088 g) place *Catopithecus* above Kay's Threshold, and the All-Primate and Anthropoid regressions place *Catopithecus* within the size range of prosimian folivores (Table 3). Furthermore, both the

Table 7 Comparison of diets of upper and lower sequence fossil primates

Dietary category	Upper sequence 33.1–34.0 Ma (early Oligocene) quarries I, M, V, G	Lower sequence 34.0–35.9 Ma (late Eocene) quarries E, L-41
Frugivores or gummivores with insect protein source	<i>Afrotarsius chatrathi</i> (P) <i>Apidium moustafai</i> (A) <i>Qatrania fleaglei</i> (A)	<i>Arsinoea kallimos</i> (A) <i>Proteopithecus sylviae</i> (A) <i>Qatrania wingi</i> (A) <i>Qatrania</i> sp. (L-41) (A) <i>Wadilemur elegans</i> (P) <i>Plesiopithecus teras</i> (P)
Frugivores with leaf protein source	<i>Aegyptopithecus zeuxis</i> (A) <i>Propriopithecus chirobates</i> (A) <i>Propriopithecus markgrafi</i> (A)	<i>Oligopithecus savagei</i> (A)
Indeterminate frugivores	<i>Apidium phiomense</i> (A) <i>Parapithecus fraasi</i> (A)	<i>Catopithecus browni</i> (A) <i>Serapia eocaena</i> (A)
Folivores	<i>Parapithecus grangeri</i> (A)	<i>Aframomius diedes</i> (P)
Insectivores		<i>Anchomomys milleri</i> (P)

Dietary assessments for upper sequence anthropoids taken from Kay & Simons (1980). Final dietary determinations assume that Conroy's (1987) prosimian equation produces the most accurate body mass estimates for fossil prosimians, and that Conroy's (1987) anthropoid equation produces the most accurate body mass estimates for fossil anthropoids. (P)=prosimian; (A)=anthropoid.

$M_1$  and  $M_2$  SQs of *Catopithecus* are relatively high, falling at or near the low end of the ranges for extant folivores and insectivores. One possible interpretation of these data is that *Catopithecus* was an exceptionally small anthropoid folivore. However, because extant folivorous anthropoids tend to be much larger than *Catopithecus*, we feel that it is more likely that *Catopithecus* was a primary frugivore that supplemented its diet with significant quantities of either insects or leaves (e.g., as in *Saimiri* or *Aotus*). This interpretation is well in accord with *Catopithecus'* borderline  $M_1$  SQ, although it is not currently possible to determine whether *Catopithecus* was secondarily insectivorous or folivorous due to its intermediate size.

#### *A comparison of the Fayum's upper and lower sequences*

Prior to the current analysis, the only quantitative assessments of molar shearing crest development in Fayum primates were those of Kay & Simons (1980). These authors measured molar shearing crests of 7 upper

sequence anthropoid species, and concluded that all but one (*Parapithecus grangeri*) were highly frugivorous (Table 7). To date, *P. grangeri* is the only upper sequence primate thought to have included a significant quantity of leaves in its otherwise frugivorous diet (Kay & Simons, 1980; Teaford *et al.*, 1996). Though fossil samples from the upper sequence are biased in favor of larger taxa, one small-bodied prosimian (*A. chatrathi*) has also been recovered from this horizon. According to our analysis, *Afrotarsius* was probably a frugivore-insectivore. As the only upper sequence primate that included a significant quantity of insects in its diet, *Afrotarsius* represents a previously unappreciated element of the trophic structure of early Oligocene Fayum primate communities.

Relative to known upper sequence species, lower sequence Fayum primates demonstrate greater dietary diversity (Table 7). *A. milleri*, the most diminutive Fayum prosimian, is also the most insectivorous primate yet recovered from the lower sequence. At the opposite end of the trophic

spectrum is *Aframomius diedes*, the largest known Fayum prosimian and a highly specialized folivore. The remaining lower sequence primates, including two prosimians and seven anthropoids, were all primarily frugivorous. At least six of these lower sequence frugivores probably relied on insects as a source of dietary protein, while only one lower sequence frugivore (*O. savagei*) may be securely considered secondarily folivorous. This distribution contrasts with what is known of upper-sequence frugivores, which were evenly divided between frugivory supplemented by insectivory and frugivory supplemented by folivory (Kay & Simons, 1980).

Although size bias at upper sequence localities warrants caution in interpreting these data, several important contrasts between the upper and lower sequence primate samples probably reflect real ecological differences. Lower sequence prosimians are taxonomically diverse (five genera), span a wide range of estimated body masses, and form a major element of the lower sequence fauna. Lower sequence prosimians also occupied a variety of dietary niches, including strict folivory (*Aframomius*), generalized frugivory (*Plesiopithecus*), frugivory+insectivory (*Wadilemur*), and insectivory (*Anchomomys*). Lower sequence anthropoids demonstrate even greater taxonomic diversity (six genera from four families) than lower sequence prosimians, but were all primarily frugivorous.

In strong contrast to the Fayum's lower sequence, over 90 years of collection at upper sequence quarries has yielded only one substantial prosimian fossil—the type specimen of *Afrotarsius chatrathi*<sup>8</sup> (Simons &

<sup>8</sup>The only other possible prosimian specimen from the upper sequence is an M<sup>3</sup> allocated by Simons *et al.* (1986) to the Lorisidae. However, Godinot (1994) and Gheerbrant *et al.* (1995) have noted that this tooth bears strong resemblance to specimens of *Oligopithecus* (especially the Omani species *O. rogeri*). Furthermore, Ross *et al.* (1998) have questioned the prosimian status of *Afrotarsius chatrathi*, suggesting that this species may

Brown, 1985). Markedly lacking from the upper sequence are folivorous prosimians like *Aframomius* and large frugivorous prosimians like *Plesiopithecus*. This absence is probably not due to taphonomic or collection biases because *Aframomius* and *Plesiopithecus* are comparable in estimated body mass to several well-represented upper sequence anthropoid species. Anthropoids are by far the dominant element of the upper sequence primate fauna, exhibiting generic diversity (n=5) similar to that of lower sequence anthropoids. Although most Fayum anthropoids were primarily frugivorous, the estimated body masses of upper sequence anthropoids (range=680–5875 g; Kay & Simons, 1980) are somewhat larger as a group than those of lower sequence anthropoids (range=240–1600 g; Table 3). As a result, a large proportion of upper sequence anthropoid frugivores probably relied on leaves as a source of dietary protein. By contrast, most lower sequence frugivorous anthropoids appear to have been secondarily insectivorous (Table 7).

#### *Changes in feeding ecology across the Eocene–Oligocene boundary in Afro-Arabia*

Early Oligocene localities of the Fayum's upper sequence provide evidence of the existence of primate communities that were broadly similar in trophic structure<sup>9</sup> to most extant Old World primate communities. Upper sequence anthropoids dominated the mid- to large-sized feeding niches, and constituted the only folivorous and highly frugivorous primate species. Conversely, the only known upper sequence primate that probably included a significant proportion

be an African eosimiid (and thus a stem anthropoid according to their phylogeny). These taxonomic questions are beyond the scope of the present paper, but should be borne in mind as possible alternatives to the views presented here.

<sup>9</sup>When referring to a primate community's trophic structure, we are primarily concerned with the manner in which dietary niches are distributed among anthropoid and prosimian taxa.

of insects in its diet was a prosimian. This partitioning of dietary niches between anthropoids and prosimians in the upper sequence is thus reminiscent of primate communities in modern continental Africa and Asia, in which anthropoids are predominantly large and folivorous or frugivorous, while prosimians (in this case, lorisiform strepsirrhines) are much smaller and insectivorous or frugivorous. By contrast, in the Fayum's lower sequence, prosimians filled a much greater diversity of dietary niches. The most insectivorous and folivorous lower sequence primates were prosimians, while frugivorous niches were occupied jointly by prosimians and anthropoids. In these respects, the late Eocene primate communities represented in the Fayum's lower sequence were unlike any modern primate fauna.

Evidence that sympatric prosimians and early anthropoids jointly occupied frugivorous feeding niches during the late Eocene reinforces the conclusion that changes in diet did not form the primary ecological impetus for the origin of anthropoids (Rasmussen & Simons, 1992; Kay *et al.*, 1997). Though most Fayum anthropoid lineages appear to have increased in body mass through time, *P. grangeri* represents the only likely deviation from the basic anthropoid pattern of frugivory seen in both the upper and lower sequences. Moreover, the simultaneous presence in the lower sequence of oligopithecids, parapithecids and proteopithecids that were primarily frugivorous suggests that diet was not a prime factor driving the early divergence of these anthropoid clades.

From the middle Eocene to the early Oligocene, dramatic changes in world climate led to a fundamental reorganization of the terrestrial biotas of North America, South America, Europe, and Asia (Prothero & Berggren, 1992; Prothero, 1994; Prothero & Heaton, 1996; Beard, 1998; Meng & McKenna, 1998; Kay *et al.*, 1999). The

most notable climatic change was an episode of severe cooling that took place just after the Eocene/Oligocene boundary (Prothero & Heaton, 1996). Although this deterioration in mean global temperature may have been related to the final extinction of primates in North America,<sup>10</sup> Europe, and much of Asia (Prothero & Berggren, 1992; Beard, 1998; Fleagle, 1999), primate faunas of Afro-Arabia continued to flourish throughout the Oligocene (Thomas *et al.*, 1991; Rasmussen *et al.*, 1992; Gheerbrant *et al.*, 1993, 1995; Simons & Rasmussen, 1994a). Nonetheless, it is interesting to note that the shift from archaic to essentially modern trophic structures in Fayum primate communities may have immediately preceded the marked faunal changes that occurred in Eurasia shortly after the Eocene/Oligocene boundary (Prothero & Berggren, 1992; Meng & McKenna, 1998). In spite of the similar timing of these events, evidence that these changes in primate community structure at the Fayum are a direct result of the global environmental factors responsible for the Mongolian Remodeling in Asia and the Grand Coupure in Europe is currently lacking (Prothero & Berggren, 1992; Meng & McKenna, 1998). Indeed, denser sampling of this time period in Afro-Arabia is necessary to rule out the possibility that local environmental effects are responsible for the patterns of faunal change evident in the Fayum fossil record.

In addition to the Fayum, Taqah in Oman is the only other Paleogene Afro-Arabian fossil locality that has yielded both anthropoid and prosimian species (Thomas *et al.*, 1989, 1991; Gheerbrant *et al.*, 1993, 1995). Taqah thus provides an important comparative test of the uniqueness of the sequence of faunal turnover seen at the Fayum. Four primate species are currently documented from Taqah, including two anthropoids (*Oligopithecus rogeri* and *Propithecus*

<sup>10</sup>Except possibly *Ekgmowechashala*, which has doubtful primate affinities (McKenna, 1990).

*markgrafi*) and two cercamoniine adapiforms (*Omanodon minor* and *Shizarodon dhofarensis*). Body mass estimates for these taxa demonstrate that the two prosimians are the only species that were small enough to have been insectivorous, while the two anthropoids are the only species large enough to have been folivorous (either primarily or secondarily; Thomas *et al.*, 1989, 1991; Gheerbrant *et al.*, 1993, 1995; Fleagle, 1999). Accordingly, the Taqah primate community was probably more similar in trophic structure to the primate communities of the Fayum's upper sequence than the lower sequence. This finding is consistent with studies of faunal correlation and charophytes that favor an early Oligocene age for Taqah (Thomas *et al.*, 1989, 1991; Gheerbrant *et al.*, 1993, 1995).

However, several additional factors suggest that the fossil-bearing strata at Taqah may date to the latest Eocene, and hence be most comparable in age to quarry E of the Fayum's lower sequence (Rasmussen *et al.*, 1992). The presence of tribe Anchomomyini and genus *Oligopithecus*, which are both known only from the lower sequence at the Fayum, is the strongest evidence in favor of a latest Eocene age for Taqah. This interpretation would be further strengthened if Thomas *et al.* (1991) are correct in suggesting that *P. markgrafi* (of unknown provenance at the Fayum) was initially recovered from the Fayum's lower sequence. Additionally, the slightly older Omani site of Thaytiniti has been dated to 35.8 Ma (late Eocene) on the basis of paleomagnetic correlation (Thomas *et al.*, 1989). The Taqah fossil locality is located only about 50 m higher than Thaytiniti in the Ashawq Formation, but unfortunately, similar paleomagnetic studies have not been published for Taqah. If Taqah is most comparable in age to Fayum quarry E, then the changes in primate community structure at the Fayum described herein may have predated the Eocene/Oligocene boundary by as

much as 1.5 Ma. We eagerly await the publication of more precise dates for Taqah so that Paleogene Afro-Arabian fossil localities may be compared in the appropriate context.

#### *Implications for Asian paleobiogeography*

Recent discoveries of the putative anthropoids *Amphipithecus mogaungensis* and *Pondaungia cotteri* from the later middle Eocene (40–37 Ma) of Myanmar (Maw *et al.*, 1979; Ciochon *et al.*, 1985; Jaeger *et al.*, 1998b; Chaimanee *et al.*, 2000a), and *Siamopithecus eocaenus* from the late Eocene (37–35 Ma) of Thailand (Chaimanee *et al.*, 1997, 2000b; Ducrocq, 1999) have led to renewed speculation that southern Asia was an important site of diversification for the Anthropoidea during the Eocene (Ducrocq, 1998; Jaeger *et al.*, 1998a). However, many of the derived morphological characters used to identify these species as anthropoids do not appear among Fayum anthropoids until the early Oligocene (ca. 34 Ma). Such features include advanced bunodonty (*Amphipithecus*, *Pondaungia*, *Siamopithecus*), large body size (*Amphipithecus*, *Pondaungia*, *Siamopithecus*), deep mandibles (*Amphipithecus*, *Pondaungia*, *Siamopithecus*), trigonids and talonids of similar height (*Amphipithecus*, *Pondaungia*, *Siamopithecus*), and the presence of wear facet X (*Amphipithecus*, *Pondaungia*). Other characteristics of these taxa, such as the presence of paraconids on the M<sub>2</sub>–M<sub>3</sub> (*Amphipithecus* and *Pondaungia*), indicate that they are in some ways dentally more primitive than undisputed anthropoids of similar age (~36 Ma) from Fayum quarry L-41.<sup>11</sup> Furthermore, *Siamopithecus* exhibits a highly derived suite of features in the upper dentition (e.g., the

<sup>11</sup>*Arsinoea kallimos* is the only lower sequence anthropoid that exhibits paraconids on all lower molars. *Proteopithecus*, *Catopithecus*, *Serapia*, *Oligopithecus*, and L-41 *Qatrania* sp. retain small paraconids only on the M<sub>1</sub>. The lower sequence prosimians *Aframomius*, *Plesiopithecus*, *Wadilemur*, and *Anchomomys milleri* lack molar paraconids entirely.

presence of a distinct mesial fovea on the M<sup>1</sup> and a crest on the M<sup>2</sup> connecting the metacone and hypocone in place of the cristid obliqua; see Ducrocq, 1999) that are not seen in any Fayum anthropoid. This unusual mosaic of primitive and derived characters relative to the earliest known Fayum anthropoids casts uncertainty on the proposed anthropoid status of *Amphipithecus*, *Pondaungia* and *Siamopithecus*.

The fact that most of the derived dental features shared by putative large-bodied anthropoids from the Eocene of Asia and undoubtedly anthropoids from the early Oligocene of the Fayum are lacking in late Eocene Fayum anthropoids has significant paleobiogeographic implications. The only two possible explanations for the observed temporal and geographic distribution of such advanced “anthropoid-like” dental characters are migration and convergence. According to the former hypothesis, dentally “derived” anthropoids could have evolved in Asia and migrated to Africa in the earliest Oligocene. In this case, they would have replaced the dentally more primitive late Eocene African anthropoids seen in the Fayum’s lower sequence. We regard this scenario as unlikely for several reasons. Foremost, most lines of evidence suggest that there was little faunal interchange between Africa and other biogeographic provinces throughout the Eocene and Oligocene (Gheerbrant, 1990). The apparent migration into Africa of certain semi-aquatic anthracotheriids (Ducrocq, 1995, 1997) and the marsupial genus *Peratherium* are isolated events that stand in sharp contrast to the otherwise highly endemic nature of African faunas from this period (Gheerbrant, 1990). Second, there is a large body of anatomical evidence which suggests that late Eocene Fayum parapithecids and propliopithecids are closely related to early Oligocene Fayum representatives of these anthropoid families (Simons, 1989, 1992; Simons & Rasmussen, 1994a; Fleagle,

1999; Seiffert *et al.*, 2000). Morphological similarity between early and late-occurring members of the Parapithecidae and Propliopithecidae (respectively) suggests that these exclusively Afro-Arabian lineages have phyletic continuity across the Eocene–Oligocene boundary.<sup>12</sup> Finally, a hypothesis of anthropoid migration into Africa from Asia fails to explain why derived anthropoids did not persist in Asia past the Eocene–Oligocene boundary, while adapiforms and tarsiids did (Beard, 1998; Fleagle, 1999).

An alternative and more likely explanation for the advanced “anthropoid-like” features shared by early Oligocene Fayum anthropoids and *Amphipithecus*, *Pondaungia* and *Siamopithecus* is convergence due to similar diet and body size. Most of the dental characters that have been used to support the anthropoid status of these Asian taxa have significant functional and dietary implications (Maw *et al.*, 1979; Ducrocq *et al.*, 1995; Chaimanee *et al.*, 1997, 2000a,b; Jaeger *et al.*, 1998b; Ducrocq, 1999). For instance, lowering of the trigonid relative to the talonid, the presence of wear facet X, paraconid loss, and advanced bunodonty are all characters associated with a reduction of molar shearing and an increase in crushing and grinding during mastication (Kay, 1977). Although quantitative dietary study of the Asian taxa has not yet been undertaken, it seems likely that the common occurrence of these dental features in large putative Asian anthropoids and early Oligocene African anthropoids could easily be accounted for by a common dietary emphasis on frugivory.

Because most of the morphological features that have been used to ally *Amphipithecus*, *Pondaungia* and *Siamopithecus*

<sup>12</sup>However, this argument would be weakened if Kay *et al.* (1997) are correct in suggesting that oligopithecines (herein considered propliopithecid catarrhines) are not crown anthropoids (see also Ross *et al.*, 1998).

with later occurring known anthropoids are likely the product of convergence, we are left with no firm foundation for attributing these Asian forms to the Anthropoidea. It is possible that “derived” dentitions and large body mass were acquired separately in Paleogene Afro-Arabian and Asian anthropoid populations, and that the Asian clade subsequently became extinct. According to this scenario, large putative Asian anthropoids could be recognized as derived representatives of an early (Eocene) radiation within the anthropoid stem lineage (Kay *et al.*, in prep.). If this hypothesis is correct, *Amphipithecus*, *Pondaungia* and *Siamopithecus* need not demonstrate all of the derived cranial features shared by crown anthropoids (e.g., postorbital closure) in order to be recognized as sharing a close phyletic relationship with undisputed anthropoids from the Fayum (Kay *et al.*, in prep.).

However, given what is known unequivocally of anthropoid evolution and the timing of key anthropoid dental character changes from the African fossil record, it is equally parsimonious to conclude that most large-bodied Paleogene Asian primates had no special phyletic relationship to the Anthropoidea. Accordingly, the phylogenetic affinities of *Amphipithecus*, *Pondaungia* and *Siamopithecus* may either lie with the Adapiformes or an as-yet unnamed group of primates (Godinot, 1998). In the Eocene of North America, Europe, Africa, and Asia, it is primarily adapiforms which filled the large-bodied folivorous and frugivorous niches that are most often associated with modern anthropoids (Beard *et al.*, 1994; Covert, 1997; Godinot, 1998; Qi & Beard, 1998; Fleagle, 1999). In Asia, such adapiforms (i.e., the Sivaladapidae) persisted even as late as 10 Ma (Gingerich & Sahni, 1984; Pan, 1988). The final disappearance of the Sivaladapidae may have been related to the arrival of cercopithecoid monkeys from Africa that were more successful as

medium-sized arboreal folivores and frugivores (Gingerich & Sahni, 1979, 1984; Qi & Beard, 1998).

The basic similarities between the dietary habits of anthropoids and adapiforms have produced (via convergence) or maintained (via heritage and stabilizing selection) a degree of dental resemblance in these clades that is at the heart of ongoing controversy regarding anthropoid origins (see Fleagle & Kay, 1994). Indeed, Gingerich & Schoeninger (1977:494) note that it is “sometimes difficult to distinguish advanced adapoid primates from primitive anthropoids” on the basis of dental material alone. The truth of this statement is borne out by previous uncertainty regarding the anthropoid or adapiform affinities of *Oligopithecus savagei* (Simons, 1971; Szalay, 1971; Gingerich, 1977). Similarly, *Plesiopithecus teras* was initially described as an anthropoid due to its general resemblance in molar morphology to known anthropoids such as *Catopithecus* and *Proteopithecus* (Simons, 1992). It was not until a single crushed cranium of *Plesiopithecus* was recovered that this species was correctly recognized as phyletically unrelated to the Anthropoidea (Simons & Rasmussen, 1994b). More recently, *Wailekia orientale* from the late Eocene of Thailand was described as an anthropoid on the basis of dental features shared with *Oligopithecus* (Ducrocq *et al.*, 1995). However, Godinot (1998) and Qi & Beard (1998) have since presented convincing morphological evidence that *Wailekia* is instead a sivaladapid adapiform.

The early misidentifications of *Oligopithecus*, *Plesiopithecus* and *Wailekia* should serve as cautionary examples to those authors who would assign fossil taxa known only from dental material to the Anthropoidea. The origin and diversification of anthropoids, once thought to be associated with a shift to larger body size and a frugivorous–folivorous diet, is now known to have occurred within the size range and

broad dietary niche (i.e., insectivory and frugivory) characteristic of extant non-Malagasy prosimians (Rasmussen & Simons, 1992; Kay *et al.*, 1997). Accordingly, it is also now known that the earliest anthropoids had dentitions that were phenetically quite different from those of modern anthropoids and that the list of dental characters distinguishing early anthropoids from prosimians is more subtle than was previously appreciated (see Ross *et al.*, 1998).

We continue to believe that the best interpretation of the available fossil evidence is that crown anthropoids did not reach Asia from Afro-Arabia until these land masses made contact in the Miocene (Andrews *et al.*, 1996; Harrison & Gu, 1999; for an opposing point of view, see Jaeger *et al.*, 1998a). If the Fayum fossil record faithfully records both the timing and direction of character state changes in anthropoid dental evolution, the only putative anthropoids from the Paleogene of Asia that are primitive enough to have been stem anthropoids are *Eosimias* (40–45 Ma; Beard *et al.*, 1994, 1996) and *Bahinia* (approx. 37–42 Ma; Jaeger *et al.*, 1999). However, the older (46–50 Ma) African species *Algeripithecus minutus* and *Tabelia hammadae* much more closely resemble late Eocene Fayum anthropoids in the general morphology of their molars (Godinot & Mahboubi, 1992, 1994). Enhanced bunodonty, lowering of the trigonid relative to the talonid, and loss of the paraconid on the  $M_3$  are derived features that *Algeripithecus*, *Tabelia* and most early Fayum anthropoids share to the exclusion of *Eosimias* and *Bahinia*.<sup>13</sup> As noted previously,

phylogenetic inferences based on these characters should be made with caution due to the potential for functional convergence. However, unlike large-bodied Asian taxa (e.g., *Amphipithecus*, *Pondaungia* and *Siamopithecus*) which share similar features, *Algeripithecus* and *Tabelia* are not too dentally derived to have been broadly ancestral to later-occurring Fayum anthropoids. *Algeripithecus* and *Tabelia* further resemble the earliest Fayum anthropoids in exhibiting relatively small body sizes (i.e., 150–450 g; Fleagle, 1999). This size range (which overlaps the 340–1090 g size range of anthropoids from Fayum quarry L-41; Table 3) is similar to that of *Eosimias* and *Bahinia* (100–400 g), but differs greatly from that of *Amphipithecus*, *Pondaungia* and *Siamopithecus* (6·8–8·6 kg) (Fleagle, 1999; Jaeger *et al.*, 1999).

These similarities between *Algeripithecus*, *Tabelia* and Eocene Fayum anthropoids, combined with the patently omomyiform-like morphology of the Shanghuang petrosal (MacPhee *et al.*, 1995) and the suite of derived dental characters linking *Eosimias* to tarsiids like *Xanthorhysis* and *Tarsius eocaenoides* (Beard, 1998), cast uncertainty on the phylogenetic position of the Eosimiidae. If *Eosimias* and *Bahinia* are stem anthropoids, as suggested by numerous dental, mandibular, and tarsal features (Beard *et al.*, 1994, 1996; Kay *et al.*, 1997; Ross *et al.*, 1998; Jaeger *et al.*, 1999; Gebo *et al.*, 2000), these genera are most likely late-surviving representatives of a very early stage in the evolution of the Anthropoidea that is currently not represented in the African fossil record. Furthermore, if large-bodied stem anthropoids were widespread in Asia during the Eocene, the course of anthropoid evolution

<sup>13</sup>These derived features may also be shared by the poorly known species *Biretia piveteaui* from the late middle Eocene (~40 Ma) of Algeria (de Bonis *et al.*, 1988). This species is known from an isolated lower molar and was originally described as a catarrhine on the basis of derived dental characters including paraconid loss, the “probable” presence of wear facet X, and a “distinct” posterior fovea (de Bonis *et al.*, 1988). However, the published photograph of the type speci-

men suggests that *Biretia* lacked wear facet X and did not demonstrate a posterior fovea similar to those seen in early Oligocene Fayum anthropoids (de Bonis *et al.*, 1988). Furthermore, the absence of a paraconid in *Biretia* could be a shared derived resemblance with late Eocene Fayum anthropoids (excluding *Arsinoea*) if the type specimen is actually an  $M_2$  rather than an  $M_1$ .

in Asia must have been radically different from that seen in Africa.

### Summary and conclusions

Anthropoids from late Eocene Fayum localities were predominantly frugivorous. Late Eocene Fayum prosimians exhibited a diverse array of dietary habits, including specialized insectivory (*Anchomomys*), generalized frugivory (*Plesiopithecus*), frugivory+insectivory (*Wadilemur*), and strict folivory (*Aframomius*). By contrast, early Oligocene Fayum localities are overwhelmingly dominated by frugivorous anthropoids, and appear to have lacked large-bodied prosimians that occupied frugivorous and folivorous niches. These differences between the dietary specializations of anthropoids and prosimians in the Eocene and Oligocene Fayum samples probably reflect the modernization of continental Afro-Arabian primate communities across the Eocene–Oligocene boundary.

Undoubted late Eocene anthropoids from the Fayum were relatively small (i.e., less than 2 kg) and lack many of the dental specializations for an increase in Phase II crushing during mastication seen in early Oligocene anthropoids. Derived features shared by large Eocene Asian primates (e.g., *Amphipithecus*, *Pondaungia* and *Siamopithecus*) and dentally advanced early Oligocene Fayum anthropoids are therefore probably the result of convergence in body mass and diet. In the absence of more definitive cranial evidence, hypotheses that *Amphipithecus*, *Pondaungia* and *Siamopithecus* are anthropoids must be considered tentative.

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