The Ecology of Oligocene African Anthropoidea

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African anthropoids are first recorded in Early Oligocene deposits of the Fayum Province, Egypt. Six genera and nine species are recognized. Estimated body weights for these taxa are based on the regression equation $log_{10}(B) = 2.86\ log_{10}(L) + 1.37$, where B is the body weight in grams, and L is the M_2 length in millimeters. The equation is derived from 106 species of living primates. Fayum species range in body weight from about 600 g (Apidium moustafai) *to about 6000 g* (Aegyptopithecus zeuxis). *A similar range of body weight is found among extant Cebidae. The Fayum primates are larger than any extant insectivorous primates; this fact probably rules out a predominantly insectivorous diet. Extant frugivorous hominoids can be separated from folivorous hominoids on the basis of molar morphology. Folivorous apes (gorilla and siamang) have proportionately more shearing on their molars than do frugivorous species. Based on the hominoid analogy, the molar morphology of the Fayum species is consistent with a frugivorous diet.* Parapithecus grangeri *stands apart from other Fayum species in having better developed molar shearing, possibly indicating that it had more fiber in its diet. Terrestrial species of Old World monkeys tend to have significantly higher molar crowns than do more arboreal species. This difference may relate to an increased amount of grit in the diet of the more terrestrial species, selecting for greater resistance to wear. Oligocene primates have molar crown heights consistent with q primarily arboreal mode of existence. However, the particularly high molar crowns of* Parapithecus grangeri *suggest that this species may have foraged on the ground to a considerable degree. Other evidence is advanced suggesting that* Apidium *may have had a diurnal activity pattern.*

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INTRODUCTION

The earliest African record of Anthropoidea comes from deposits of Early Oligocene age in the Fayum Depression, Egypt. Finds from the first decade of this century included single specimens of four species of primates, but it was not until recently that substantial dental samples and other cranial and postcranial remains were accumulated, allowing ecological interpretations based on morphology. The purpose of this work is to review the available cranial and dental evidence on ecological specializations of the Fayum anthropoids.

Fayum primates come from the Jebel el Qatrani Formation, composed of variegated sands, gravels, and sandstones with interbedded layers of siltstone and claystone. At frequent intervals in the upper levels, lacustrine limestones occur. The formation is entirely continental in deposition, representing rivers, streams, and lakes in an area of low relief. The climate is thought to have been humid, and subtropical to tropical, with dense forests, at least along the major streams, but with the possibility of savannas in the interstream areas (Simons, 1968).

The Jebel el Qatrani Formation conformably overlies the Qasr el Sagha Formation, which is thought to be of Late Bartonian age, perhaps 37–40 million years old (Late Eocene), and it is overlain unconformably by a basalt layer radiometrically dated at both 24.7 ± 0.4 and 27 ± 2 million years before present (Simons, 1967). The duration of the erosional event prior to the deposition of the basalt is unknown but lengthy.

The Fayum primates collected in the early part of this century— *Parapithecus fraasi, Propliopithecus haeckeli,* and *"Moeripithecus"* (= *Propliopithecus*) *markgrafi*—are represented by single specimens of uncertain horizon. *Apidium phiomense,* described in 1908, is known to have come from the Upper Fossil Wood Zone, high up in the section.

The Yale and Duke expeditions of the 1960s and 1970s have collected primates from three levels in the Jebel el Qatrani Formation. From the Lower Fossil Wood Zone comes the oldest Fayum primate, *Oligopithecus savagei,* known from a single left lower jaw. About 50 yd up-section, at Quarry G, comes the type, and numerous specimens of, *Apidium moustafai,* as well as some fragmentary ape teeth of the appropriate size and morphology to belong to either or both described *Propliopithecus* species. A third group of fossils comes from the Upper Fossil Wood Zone, about 50 yd above Quarry G, at Quarries I and M, including *Apidium phiomense, Parapithecus grangeri, Aegyptopithecus zeuxis,* and *Propliopithecus* (= *Aeolopithecus*) *chirobates* (Simons *et al.,* in preparation).

The Fayum primates appear to fall into two natural groups. One group, the Parapithecidae, includes *Apidium* and *Parapithecus.* A second, dentally ape-like, group includes *Aegyptopithecus* and *Propliopithecus.*

The affinities of *Oligopithecus savagei* are poorly understood, although it has the same dental formula as the fossil apes.

BODY SIZE OF FAYUM SPECIES

Estimation of Body Size

Dental, especially molar, remains are the most commonly recognized fragments of Fayum anthropoids. In fact, more than half of the recognized species are represented by dental fragments alone. For this reason it has been necessary to rely on dental dimensions to estimate the body weights of these species. A regression equation was formulated to express log body size (body weight) as a function of log second lower molar length for 106 species of living primates including lemurs, lorises, tarsiers, hominoids, cerco-pithecoids, and cebids. The New World monkey family Callitrichidae was not sampled because of extreme molar reduction in that group. The equation is $\log_{10}(B) = 2.86 \log_{10}(L) + 1.37$, where B is the body mass in grams, and L is the second lower molar length in millimeters. The coefficient of correlation for the equation is 0.949. Thus, body weight alone accounts for 90% (i.e., 0.949^2) of the variance in second molar length among extant primates. This regression equation is very close to one reported by Gingerich (1977) for extant Hominoidea, where $\log_{10}(B) = 2.99(L) + 1.46$, with a coefficient of correlation of 0.942. Table I provides information on the second lower molar length of samples of 10 species of Fayum anthropoids, together with an estimate of their body mass, in grams, on the basis of our regression equation. The body size estimates

Table I. Second Lower Molar Length and Estimated Body Mass

	M_2 length			Estimated body mass (g)	95% Confidence range of body mass (g)
	$\bar{X}$	SD	N		
Apidium phiomense	3.92	0.16	13	1177	1051–1318
Apidium moustafai	3.24	0.25	12	682	596– 781
Parapithecus grangeri	4.55	0.18	7	1802	1632–1990
Parapithecus fraasi	3.94	—	1	1194	1067–1337
Oligopithecus savagei	3.38	—	1	763	668– 872
Propliopithecus chirobates	5.43	0.33	4	2951	2698–3228
Propliopithecus markgrafi[a]	4.48	0.07	3	1724	1561–1903
Propliopithecus haeckeli	5.00	—	1	2360	2147–2594
Aegyptopithecus zeuxis	6.90	0.47	12	5876	5346–6450

[a]Here, as in Tables V and VII, two isolated teeth from Quarry G have been assigned tentatively to *Propliopithecus markgrafi* Schlosser, although the type comes from an uncertain horizon.

provided here should be used with great caution. Even with the very high coefficients of correlation in the log–log regression equations, the 95% confidence intervals of estimated body size are extremely large.

Body size estimates for *Aegyptopithecus* can also be obtained from the dimensions of a nearly complete skull in the Cairo Geological Museum (Table II, Fig. 1). The mean estimated body weight for *Aegyptopithecus*, based on cranial dimensions, is about 5300 g, with a 95% confidence interval of 935 g. This estimate of *Aegyptopithecus* body size is virtually identical to that estimated from molar length.

Generally, parapithecids tend to be smaller than the apes at any given stratigraphic level. For example, *Parapithecus grangeri* and *Apidium phiomense* from the Upper Fossil Wood Zone are smaller than *Aegyptopithecus zeuxis* and *Propliopithecus chirobates*. From geologically older Quarry G, *Apidium moustafai* is smaller than contemporary *Propliopithecus* sp.

Similarly, there is a tendency for earlier (geologically older) species to be smaller than their closest later (geologically younger) relatives. Thus, *Apidium moustafai* from Quarry G is smaller than *Apidium phiomense* from Quarries I and M, higher in the section. The same is true for ape material from Quarry G in comparison with Quarries I and M ape species.

Aspects of the Adaptive Significance of Body Size

Among living primate species, body sizes are broadly correlated with what a species eats and where it eats it. Thus, insectivorous species tend to

Table II. *Aegyptopithecus zeuxis:* Cranial Dimensions and Estimated Body Mass[a]

Cranial dimension	Value (mm)	Body mass (g) = slope in (dimension) and constant	R for equation	Estimated body mass (g)
(A) Orbital diameter	18.0	5.55(A) − 8.21	0.89	2,558
(B) Interorbital breadth	8.5	2.54(B) − 3.32	0.79	6,420
(C) Prostion–nasion	38.5	2.14(C) + 0.36	0.92	3,545
(D) Maximum dental arcade width	33.6	3.68(D) − 4.29	0.96	10,038
(E) Anterior orbital edge to anterior point on maxillary –premaxillary suture	20.6	1.61(E) + 3.95	0.91	6,705
(F) Prostion–inion	101.8	3.07(F) − 5.85	0.94	4,149
(G) Maximum dental arcade length	39.4	2.58(G) − 1.10	0.96	2,850
			Mean estimated mass:	5,281
			Standard error:	382
			95% Conf. interval:	±935

[a]Regression equations are derived from 16 Old and New World monkey species. The cranial dimensions are identified and defined by Cartmill (1970).
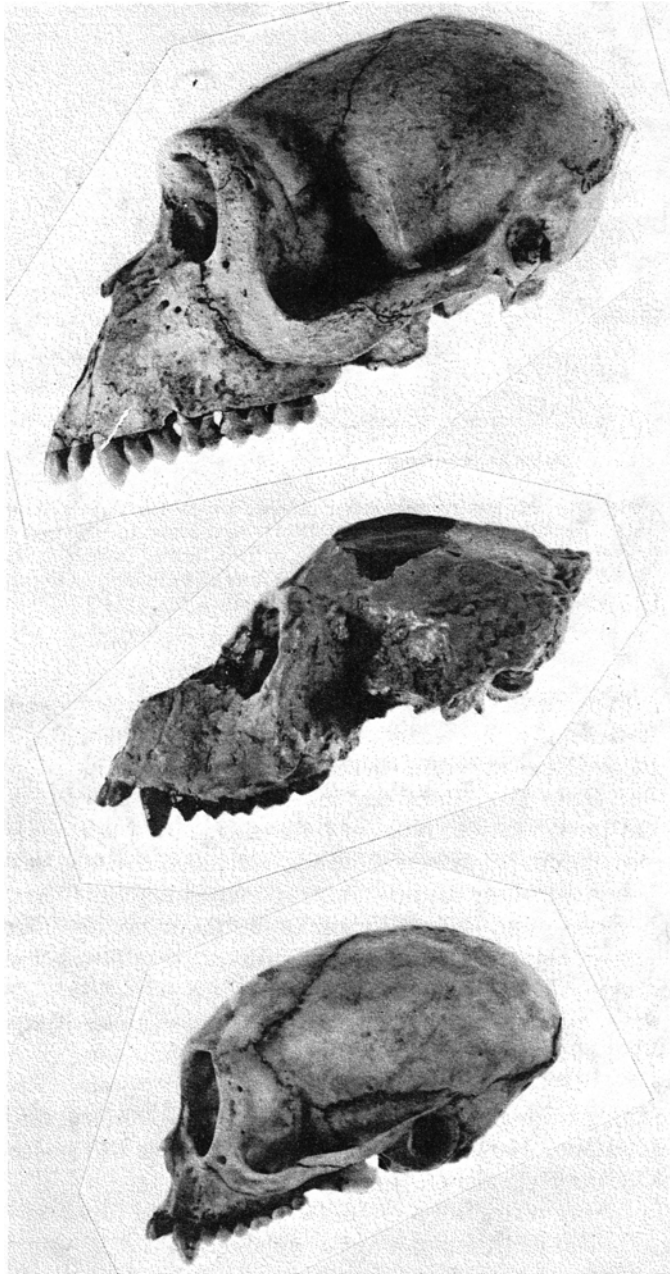
Fig. 1. Comparison of the skulls of *Macaca sylvanus* (USNM 398445) (top), *Cebus albifrons* (AMNH 19014) (bottom), and *Aegyptopithecus zeuxis* (cast of CGM40237) (center) to illustrate the approximate size of this skull.
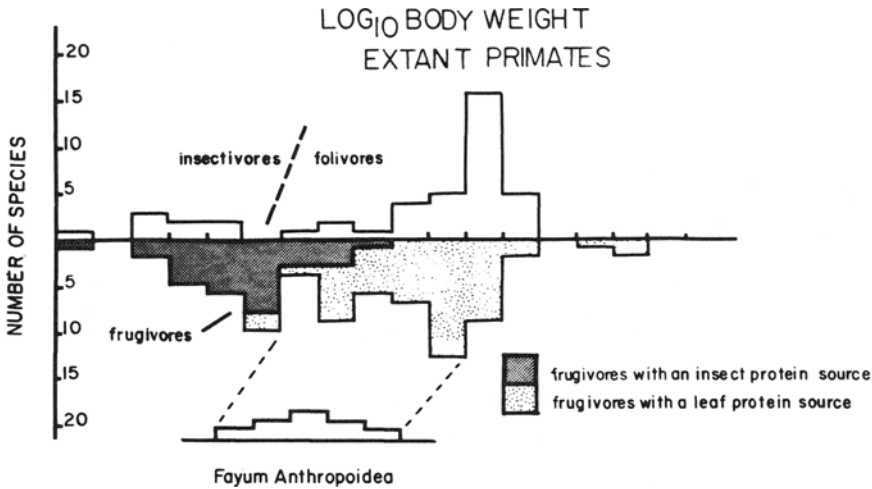
Fig. 2. Histograms of $\log_{10}$ body weight for extant primate species. Each species is assigned to a dietary category—frugivory, insectivory, or folivory—according to the best behavioral evidence. Frugivorous species are assigned to one of two further categories according to whether they eat large additional amounts of leaves or insects. Each interval in the histogram represents a 0.2 $\log_{10}$ interval. Fayum taxa are shown separately.

be smaller than folivorous species. (Fruit-eating species overlap both groups.) Furthermore, terrestrially or semiterrestrially adapted primates tend to be larger than their closest arboreal relatives.

Body Size and Diet. Body size may be viewed as part of a species' adaptation to exploit various types of food (Kay, 1973). Histograms of the body size distribution of arboreal species with insectivorous, folivorous, and frugivorous diets are shown in Fig. 2. (As used here, the terms "insectivore," "folivore," and "frugivore" are a shorthand notation for whether a species' diet is dominated by invertebrate foods, plant foods containing a high percentage of fiber, or plant foods low in fiber, respectively. Each term refers to the most common kind of food within each category.) Insectivorous primate species, with the doubtful exception of *Daubentonia* (Kay and Hylander, 1979), are smaller than folivorous species. Thus, it is possible to distinguish all extant primate insectivores from extant folivores by body size alone. The adaptive reasons for this size difference are discussed by Kay and Hylander (1979).

The body size distribution of fruit-eating arboreal primates has three peaks (Fig. 2). This distribution may be explained by the limitation of fruit as a protein source. According to Hladik *et al.* (1971) and Hladik (1977), the fruits eaten by some groups of primates contain large amounts of readily available carbohydrates, but small amounts of protein. Primate fruit-eaters

must eat other kinds of foods to get their protein. Two such protein sources are leaves and insects, each of which contains more than 20% protein by dry weight (Hladik *et al.*, 1971; Hladik, 1977; Boyd and Goodyear, 1971). The choice of leaves or insects as a source for protein in the diet of frugivorous primates is an important element in selection for body size. Frugivores which concentrate on insects as a source for their protein tend to be relatively small, whereas frugivores which obtain their protein from leaves tend to be relatively large. The intermediate peak in the histogram for frugivores in Fig. 2 is made up of fruit-eaters with a secondary specialization in insects and fruit-eaters with a secondary specialization in leaves.

The body size distribution among the Fayum species (Fig. 2), as estimated from their second lower molar lengths, tends to rule out insectivory as a plausible feeding strategy for these species. On the basis of body size, a leaf- or fruit-eating diet is indicated. The larger species, *Parapithecus grangeri, Oligopithecus, Propliopithecus,* and *Aegyptopithecus,* would most likely have used leaves as a source for their protein. The smaller species, *Apidium moustafai* and *Parapithecus fraasi,* could equally well have utilized insects as a source for protein.

Body Size and Terrestriality. Among extant primates, the Old World monkeys serve as the only available model for comparison of body size among closely related arboreally and semiterrestrially adapted species, since each of the major taxonomic groups of Old World monkeys contains species with both lifestyles. (As used here, the term "semiterrestrial" is intended to refer to a species which spends a considerable portion of its foraging time on the ground, even though it may be quite at home in an arboreal setting.)

Although arboreal and terrestrial Old World monkeys overlap in size to a considerable degree (Table III, Fig. 3), terrestrial species tend to be larger than arboreal species. This phenomenon is especailly marked when each subgroup of Old World monkeys is considered separately (Table III). Arboreal members of the tribes Cercopithecini and Papionini, and the subfamily Colobinae, are smaller than their more terrestrially adapted close relatives. Some overlap in body size occurs within the cercopithecins and the colobines, but none is found within African or Asian papionins. However, it should be noted that terrestrially adapted cercopithecins are smaller on average than terrestrially adapted papionins or colobines. Thus, while there is a tendency for arboreal species to be smaller than their close terrestrial relatives, body size, taken by itself, does not completely separate the groups.

Several possible reasons may be suggested for the size disparity between arboreal and terrestrial members of the major groups of Cercopithecidae. One possibility is that, for some reason, an upper body size limit is selectively maintained for arborealists. Such a limit might be related to a limited food supply or to the increased difficulty in locomotion in an

Table III. M_2 Length of Arboreal and Terrestrial Old World Monkeys[a]

	Number of species of uncertain habitus	Arboreal species		Terrestrial species	
		N	$\log_{10} M_2$ length range	N	$\log_{10} M_2$ length range
Cercopithecini (tribe)	3	18	0.60 to 0.83	4	0.81 to 0.88
African Papionini (tribe)	0	2	0.83 to 0.86	11	0.90 to 0.98
Asian Papionini (tribe)	2	4	0.83 to 0.88	7	0.90 to 0.98
Colobinae	3	19	0.74 to 0.91	1	0.91

[a]Within each group the more terrestrially adapted species tend to be larger than the more arboreally adapted species.

arboreal setting for large animals. The removal of this limit may lead to evolutionary increases in body size. Thus, when any arboreal species becomes adapted to a more terrestrial habitus, body size increase will be favored. Accordingly, more terrestrially adapted species will tend to be larger than their arboreal close relatives, but not necessarily larger than arboreal members of more distantly related taxa. Another possibility could be that body size increase is favored in terrestrial species in response to increased predator pressure.

Fayum primates fall well within the body size range of arboreal anthropoids and outside the range of extant terrestrial anthropoids, suggesting an arboreal adaptation for the group (Fig. 3).
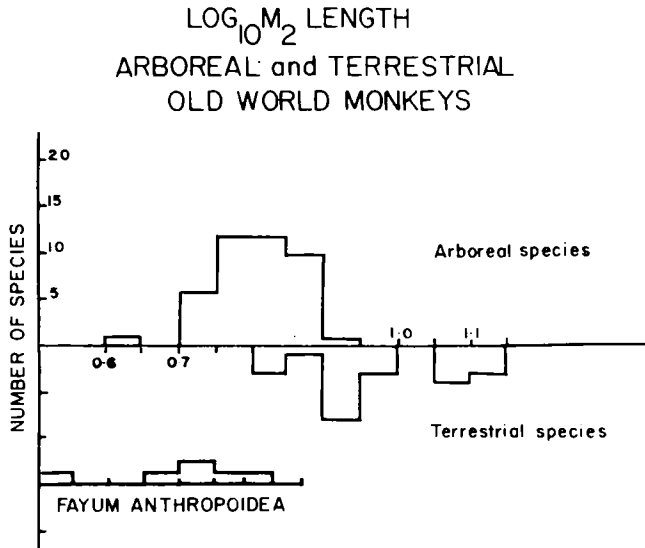

Fig. 3. Histograms of $\log_{10}$ second lower molar length (as a measure of size) for arboreal species (above the line) and terrestrial species (below the line), with the size distribution of Fayum species shown separately.

DENTAL MORPHOLOGY

The details of the functional adaptations of the molars of Fayum primates and the phylogenetic implications of these findings have been dealt with in detail elsewhere (Simons, 1967; Kay, 1977a). We will concern ourselves here with the adaptive significance of the dental morphology of Fayum species, using the habits and morphology of living primates as a model.

Incisor Morphology

Recent studies of catarrhine incisor morphology have shown that the more frugivorous species have relatively larger incisors than do the more folivorous or graminivorous species (Hylander, 1975). This difference may be related to the extent of incisal preparation prior to mastication. Certain foods, including leaves, stems, berries, grasses, seeds, buds, and flowers, may not ordinarily require any extensive preparation prior to mastication. In contrast, large, tough-skinned fruits may require a considerable amount of incisor handling prior to mastication. A great deal of food preparation leads to a large amount of incisor wear. Thus, enlarged incisors may be an adaptive response to delaying the time when the incisors wear out.

The relative size of the incisors of any anthropoid may be expressed in relation to a regression equation of incisor size versus body weight for anthropoid species as a whole. Knowing the body weight, we can estimate the incisor size for an "average" anthropoid of that size. This estimate can be compared with the actual incisor dimension by means of a ratio. Hylander (personal communication) has kindly provided a regression equation to express maxillary incisor size as a function of body mass. Among Cercopithecidae, $\log_e$ (incisor size) = 0.31167 $\log_e$ (body mass in grams) + 0.09762, where maxillary incisor size is the maximum linear distance between the distal cemento–enamel junction of the left and right lateral incisors (e.g., a chord dimension) in millimeters.

A maxillary incisor dimension of 17.8 mm may be estimated for *Aegyptopithecus,* represented by a skull (Fig. 1) which preserves undamaged incisor sockets. The estimated body size of this individual is 5281 g, with a 95% confidence interval of 932 g. From these estimates, an average cercopithecid should have a maxillary incisor dimension of 15.95 mm, with a 95% confidence range of 15.01–16.78 mm. *Aegyptopithecus* resembles Old World monkeys which use considerable incisor preparation prior to mastication. Such a morphology is often associated with a frugivorous diet, and never found among catarrhine folivores. By inference from Hylander's model, *Aegyptopithecus* was probably frugivorous.

Molar Shearing

Recent studies have explored the relationship between dietary habits and molar structure, especially the relative length of the shearing crests on the second lower molar. Within various taxonomic groups, including strepsirhines, New World monkeys, Old World monkeys, and apes, more folivorous and insectivorous species have relatively longer molar shearing crests proportionate to molar length than do frugivorous and guminivorous species (Kay *et al.*, 1978; Kay, 1977c; Kinzey, 1978; Rosenberger and Kinzey, 1976; Seligsohn, 1977).

Because of their overall functional similarity to Fayum primate molars, the molars of extant Hominoidea were chosen as a model on which to base hypotheses concerning the diets of Fayum primates. Ten species of extant hominoids were studied: Eight are predominantly frugivorous (species of *Hylobates, Pongo,* and *Pan*) and two are more folivorous [species of *Gorilla* and *Hylobates (Symphalangus)*] (Kay, 1977b). A regression equation was calculated to express the summed length of eight shearing crests (see Kay, 1977b, for details) as a function of the second lower molar length for the eight frugivorous species: S_E = 2.46 (M_2 length)$^{0.95}$, where S_E is the expected summed shearing blade length. From this equation, the relative amount of shearing development (*SQ*, or shearing quotient) may be expressed by the equation $SQ = [S_O - S_E(100)]/S_E$, where S_O is the observed summed shearing blade length. As expected from the way this equation is formulated, frugivorous hominoids have *SQ*'s clustering around zero (mean = +0.23, SD = 3.40). The two folivorous hominoids *Gorilla gorilla* and *Hylobates (Symphalangus) syndactylus* have mean *SQ*'s of 7.06 and 9.04, respectively, exceeding the range of mean *SQ*'s for frugivorous hominoids (Table IV). This indicates that folivorous hominoids have proportionately more molar shearing than do frugivorous species. To test the validity of this model for estimating dietary adaptations, *SQ*'s were calculated for samples of *Cebus capucinus,* a small frugivorous New World monkey, and *Alouatta seniculus,* a more folivorous New World monkey. The *SQ*'s are −2.00 and +11.16, respectively: These species would be correctly assigned to the frugivorous and folivorous categories on the basis of the hominoid model.

SQ's were calculated for the Fayum anthropoids (Table V). With the exception of *Parapithecus grangeri,* all Fayum species fall well within the cluster of extant frugivorous hominoids, suggesting a diet dominated by fruit. The relatively well-developed shearing crests on the M_2 of *Parapithecus grangeri* are suggestive of a more folivorous diet for this species (but not approaching that of folivorous extant hominoids). A shearing quotient of −14.01 is calculated for *Oligopithecus savagei,* extremely low for a hominoid species. We are not confident that our model is a realistic standard of

Table IV. Total Shearing Capacity of the M_2 Among Extant Hominoidea

Species	N	Shearing quotient (SQ)[a]	Range	SD
Hylobates lar	5	−0.69	−10.31 to 2.62	5.47
H. klossi	5	−2.28	−8.90 to 2.36	4.44
H. moloch	5	−1.31	−4.66 to 2.50	2.72
H. agilis	5	−0.14	−10.31 to 7.04	8.35
H. hoolock	2	6.76	3.74 to 9.78	4.74
H. syndactylus	3	9.04	7.82 to 11.37	2.02
Pan paniscus	11	−1.08	−8.91 to 5.86	4.09
P. troglodytes	10	−3.37	−9.94 to 1.79	3.99
Pongo pygmaeus	5	3.95	−3.86 to 11.20	5.46
Gorilla gorilla	14	7.06	1.52 to 16.70	4.50

[a]Shearing quotient (SQ) is expressed as $SQ = 100 (S_T - S_E)/S_E$, where S_T is the summed length of shearing blades 1–8 for each species, and S_E is the shearing "expected" for a frugivorous hominoid based on the equation $S_E = 2.46 (M_2 \text{ length})^{0.9531}$. See text for further discussion.

comparison for *Oligopithecus;* the second lower molar of *Oligopithecus* lacks two shearing crests found in other catarrhines, the premetacristid (7) and postentocristid (8), rendering suspect the significance of the low *SQ* of *Oligopithecus savagei.*

Crown Height

Two aspects of terrestrial feeding may subject the dentitions of primates to a degree of wear not found among arboreal species. First, grasses

Table V. Total Shearing Capacity of the M_2 Among Oligocene Anthropoidea[a]

Species	N	Shearing quotient (SQ)	Range	SD
Lower Fossil Wood Zone species				
Oligopithecus savagei[b]	1	−14.01	—	—
Quarry G species				
Apidium moustafai	12	−3.80	−9.03 to 1.39	3.51
cf. *Propliopithecus markgrafi*[c]	3	−1.06	−3.67 to 0.64	2.29
Quarries I, M species				
Apidium phiomense	11	+1.50	−9.73 to 11.78	6.16
Parapithecus grangeri	4	5.73	1.65 to 8.02	2.82
Aegyptopithecus zeuxis	3	−3.64	−6.14 to 0.86	3.91
Propliopithecus chirobates	2	−3.86	−5.67 to 2.05	2.56
Species of uncertain horizon				
Parapithecus fraasi	1	1.79	—	—

[a]See text and Table IV for further discussion. *Propliopithecus haeckeli* is represented only by single, heavily worn specimen.
[b]This species has only six shearing blades, rather than the eight always found among living and fossil catarrhines.
[c]The type of *Propliopithecus (= Moeripithecus) markgrafi* is from an uncertain horizon. Two isolated M_2's from Quarry G are tentatively assigned to this species. The *SQ* of the type is 0.64; those of the Quarry G specimens are −3.67 and −0.16.

provide a major potential food source available to terrestrial primates but unavailable to arboreal species. Grasses contain relatively large amounts of highly abrasive silica in their stems and leaves, whereas the same parts of trees and shrubs contain relatively small amounts of silica (Eisenberg, 1978). Thus, the dentitions of grass-eating species are subjected to a relatively large amount of wear.

Second, one would expect to find more dust and other gritty substances on foods found near the ground than on foods taken from the forest canopy. This dust could have a highly abrasive effect on the dentitions of terrestrial herbivores.

Either or both of the above possibilities may explain why there is a general tendency for more terrestrial Cercopithecoidea to have considerably higher crowns than their more arboreal close relatives (Table VI). (Similar cross-species comparisons are not possible for other primate groups, since they are virtually all arborealists.) In separate comparisons, when allowance is made for differences in tooth size, primarily terrestrial-adapted species of the tribes Papionini and Cercopithecini have relatively higher crowns than their more arboreal relatives. Relative crown height (C_R) is expressed as C_R = $100 (C_T - C_E)/C_E$, where C_T is the sum of the hypoconid height and the metaconid height, and C_E is the summed crown height "expected" for a terrestrial cercopithecin from the empirically derived regression equation $C_E = 1.63 (M_2$ length$)^{0.92}$. For both tribes of cercopithecins, terrestrial species have relatively larger C_R's than arboreal species at the $p < 0.01$ level.

Relative crown height is not a very reliable indicator of the degree of arboreality or terrestriality in primates that lack close extant relatives, since

Table VI. Relative Crown Heights of Arboreal and Terrestrial Cercopithecidae[a]

Species group	Terrestrial species			Arboreal species		
	N	X	SD	N	X	SD
Macaca spp.	5	2.38	4.51	2	−5.17	0.12
Cercopithecus spp., *Miopithecus* spp., *Erythrocebus* sp.	3	−4.26	1.03	16	−9.91	3.07
Cercocebus spp.	3	3.74	1.77	2	−5.60	2.15
Papio spp., *Mandrillus* spp., *Theropithecus* sp.	6	0.11	2.97	—	—	—
Colobinae (except *Presbytis entellus*)	—	—	—	19	−4.59	3.18
Presbytis entellus	—	0.71	—	—	—	—
Totals for all species	17	0.78	3.92	39	−6.85	3.92

[a]"Relative" crown height (C_R) is expressed as C_R = $100 (C_T - C_E)/C_E$, where C_T is the sum of the hypoconid height and the metaconic height, and C_E is the summed crown height "expected" for a terrestrial cercopithecin from the regression $C_E = 1.63 (M_2$ length$)^{0.92}$. For each group, and for all species combined, the crown height of terrestrial species is higher than that for arboreal species at the $p < 0.01$ level.

Table VII. Relative Crown Height for Fayum Species[a]

Species	N	Mean relative crown height	Standard error of mean
Oligopithecus savagei	1	− 19.93	—
Apidium moustafai	12	− 9.24	1.79
Apidium phiomense	11	− 8.93	1.11
Propliopithecus markgrafi	3	− 0.13	5.57
Aegyptopithecus zeuxis	3	− 17.14	6.89
Propliopithecus chirobates	2	−21.21	2.95
Parapithecus grangeri	4	0.66	3.42
Parapithecus fraasi	1	− 14.36	—

[a]See text and Table VI for clarification of the "relative crown height" measure.

it cannot be applied confidently in between-group comparisons. For example, although the more terrestrial species of the tribe Cercopithecini have higher crowns than the arboreal species, they tend to have lower crowns than terrestrial papionins. Similarly, the molar crowns of arboreal papionins are higher in some cases than those of terrestrially adapted cercopithecins. Thus, the only conclusion which can be made is that, in a group of extinct species, the more terrestrial members might be expected to have relatively higher crowns.

One species of Fayum primates, *Parapithecus grangeri,* stands out as having high crowns, by comparison with both other Fayum primates and the relatively higher-crowned papionins (Table VII). Thus, *Parapithecus* seems likely to have been more terrestrially adapted than its contemporaries.

CRANIAL MORPHOLOGY

From the skull of *Aegyptopithecus zeuxis* and a reconstruction of the face of *Apidium phiomense* presented by Simons (1970), we can get some idea of the relative size of the orbits of Fayum species. Using cranial length as a standard of comparison, it has been shown that *Aegyptopithecus zeuxis* had relatively small orbits by comparison with those of living cercopithecoids (Kay and Cartmill, 1977). Although it is not possible to make more than a rough guess, visual inspection suggests that *Apidium* has very small orbits as well. The presence of small orbits tends to be a relatively good indicator of activity pattern among small primates. Nocturnal species have relatively larger orbits than diurnal species. Among living mammal species with skull lengths greater than 75 mm, orbit size is a less reliable indicator of activity pattern (Kay and Cartmill, 1977). Unfortunately, *Aegyptopithecus* falls somewhat above the size range where relative orbit size yields useful

information about activity pattern. *Apidium's* small orbits suggest a diurnal mode of existence similar to that found among almost all extant anthropoids.

The relative size of the infraorbital foramen provides information about the vascularization and innervation of the snout. This foramen transmits the infraorbital branches of the maxillary nerve and vessels which supply the upper lip, rhinarium, and vibrissae. Among extant mammals, a relatively small foramen indicates that these snout structures are poorly developed (Kay and Cartmill, 1977). This is always the case among living anthropoids, for which these sensory modes are relatively unimportant. *Aegyptopithecus* and *Apidium* have very small infraorbital foramina, implying an anthropoid grade of organization.

BRAIN SIZE AND MORPHOLOGY

Radinsky (1973) estimated an overall cranial capacity of between 30 and 34 cm^3 for the skull of *Aegyptopithecus*. More recently, on the basis of Jerison's (1973, p. 50) "double integration" method, Radinsky revised this estimate downward to 27 cm^3 (Radinsky, 1977).

Given Radinsky's brain size estimates and our body size estimates, it is possible to calculate Jerison's encephalization quotient *(EQ),* an expression of the relative brain size of a mammalian taxon, by comparison with that of an "average" living mammal. (An *EQ* of 1.0 would indicate a brain comparable in size to that of an average living mammal.) If *Aegyptopithecus* had a 32-g brain (the midpoint of Radinsky's early estimates), body size estimates based on M_2 length would yield a mean *EQ* of 0.82, with a range of 0.43 to 1.53; an *EQ* of 0.87 would be predicted from body size estimates based on cranial dimensions. The *EQ*'s for *Aegyptopithecus* would be somewhat lower given Radinsky's more recent brain size estimate of 27 cm^3: M_2-estimated body weight yields a mean *EQ* of 0.69 (a range of 0.36 to 1.29); weight estimates from cranial dimensions would yield an *EQ* of 0.73. These estimates are in agreement with those of Gingerich (1977), who estimated body weight based on a regression equation of M_2 length against body weight for seven species of hominoids and used Radinsky's earlier estimates of brain size.

Based on any set of the foregoing brain and body size estimates, the brain of *Aegyptopithecus* is very small for an anthropoid. Jerison (1973) provides *EQ*'s for 46 anthropoid species. All species, with the exception of two species of *Presbytis,* have *EQ*'s exceeding 1.43. The most liberal estimate of relative brain size in *Aegyptopithecus* is smaller than that of all but one living anthropoid. On the other hand, *Aegyptopithecus* had a brain size

well within the limits of those of living strepsirhines, which range from 0.60 to 1.73.

Radinsky (1973) studied the incomplete endocasts of the brain of *Aegyptopithecus*. He concluded that *Aegyptopithecus* had a brain with a relatively larger visual cortex and a relatively smaller olfactory bulb than is the case for most prosimians. However, *Aegyptopithecus* was more primitive than modern anthropoids in having a smaller frontal lobe. He concluded from this that *Aegyptopithecus* had developed an increased emphasis on vision, and a decreased emphasis on smell, in a fashion similar to that seen among living Anthropoidea.

INFERRED HABITS OF FAYUM SPECIES

The following points have been established about the Fayum primates.

(a) Fayum primates were primarily frugivorous. *Parapithecus grangeri* may have been somewhat more folivorous than the other Fayum primates. There is no evidence that any of these species were primarily insectivorous or primarily folivorous in their diet.

(b) A predominantly arboreal habitus is suggested for most species. *Parapithecus grangeri* is a possible exception; the high crowns of its molars are suggestive of semiterrestrial habits.

(c) The relatively small orbits inferred from the reconstruction by Simons (1970) suggest that *Apidium* was diurnal, similar to extant anthropoids. Because of the large body size of *Aegyptopithecus*, its comparatively small orbits warrant no interference concerning its activity pattern.

(d) The small infraorbital foramina of *Apidium* and *Aegyptopithecus* show that they had a poorly developed tactile sensory apparatus in the snout, a feature similar to extant Anthropoidea.

Probably the closest living ecological analogues of the Fayum species are found among living New World cebids. The latter are similar in their range of body size and have diurnal habits and a predominantly frugivorous diet. Our inference of a slightly more folivorous and slightly more terrestrial habitus for *Parapithecus grangeri* is particularly intriguing, since in this combination of features, *Parapithecus* may come closest among the Fayum species to filling the ecological niche predicted by Kay (1977c) for the ancestral Old World monkey.

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