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Diet, Species Diversity and Distribution of African Fossil Baboons

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Based on measurements of molar features shown to be functionally correlated with the proportions of fruits and leaves in the diets of extant monkeys, Plio-Pleistocene papionin baboons from southern Africa are shown to have included more herbaceous resources in their diets and to have exploited more open country habitats than did the highly frugivorous forest dwelling eastern African species. The diets of all species of fossil Theropithecus *are reconstructed to have included more fruits than the diets of extant* Theropithecus gelada. Theropithecus brumpti, T. quadratirostris *and* T. darti *have greater capacities for shearing, thinner enamel and less emphases on the transverse component of mastication than* T. oswaldi, *and are therefore interpreted to have consumed leaves rather than grass. Since these species are more ancient than the grass-eating, more open country dwelling* T. oswaldi, *the origin of the genus* Theropithecus *is attributed to folivorous adaptations by large papionins in forest environments rather than to savannah adapted grass-eaters. Reconstructions of diet and habitat are used to explain differences in the relative abundance and diversity of fossil baboons in eastern and southern Africa.*

INTRODUCTION

Interpretations of the dietary habits of fossil Old World monkeys have been based largely on analogies to extant mammals with lophodont teeth (Jolly 1970; Napier 1970; Delson 1975; Andrews 1981; Andrews and Aiello 1984; Temerin and Cant 1983). With the exception of Jolly's (1972) study of *Theropithecus oswaldi,* such interpretations have focused on the origins of Cercopithecoidea with relatively little attention given to more recent dietary diversification within the superfamily.

In this study the dietary habits of Plio-Pleistocene cercopithecine monkeys from fossil sites in eastern and southern Africa are reconstructed on the basis of dental features shown to be functionally correlated to diet among extant cercopithecoids (Kay 1977, 1978, 1981, 1984; Kay and Covert 1984; Kay and Hylander 1978; Benefit 1987). A major concern of the study is to better understand the differences in the patterns of species diversity and the relative abundance of cercopithecine monkeys which existed in the eastern and southern regions of the African continent during the Plio-Pleistocene.

In cave deposits of southern Africa *Theropithecus* is rare, comprising 7% of the total cercopithecoid fauna collected prior to 1976 (Freedman 1976). In contrast, 84% of the monkeys collected at the Omo and 85% of those collected at Koobi Fora, both in eastern Africa, prior to the same date belong to the genus *Theropithecus* (Eck 1976; Leakey 1976). In addition, *Theropithecus* is more diverse in deposits from eastern Africa, with five species occurring in the fossil deposits, as opposed to only two in southern Africa. The opposite pattern of diversity and abundance between eastern and southern Africa is observed for members of the Papionina *(Papio, Cercocebus, Parapapio, Gorgopithecus,* and *Dinopithecus).* [We follow Szalay and Delson (1979) in recognizing two tribes of cercopithecines, Cercopithecini and Papionini, and three subtribes of the Papionini: Theropithecina (geladas, fossil and modern), Macacina (macaques, fossil and modern) and Papionina (baboons, drills, mandrills and mangabeys, fossil and modern)]. Eighty-four percent of the fossil monkeys in southern Africa are papioninans (Freedman 1976), while only 10% of those in eastern Africa are members of this subtribe. In southern Africa at least nine species of papioninan monkeys have been recovered, but only three species are known to have occurred in eastern Africa (although the actual number is presently indeterminable due to the fragmentary and incomplete nature of the material). Reconstructions of the dietary habits of these extinct animals, in combination with information about the habitats in which they lived and studies of food consumption and habitat use by living mammals, are used to describe a new scenario about the evolution, diversity, distribution and relative abundance of fossil *Theropithecus* and other baboons during the Plio-Pleistocene.

MATERIALS AND METHODS

Fossil cercopithecine monkeys were sampled from Plio-Pleistocene deposits in southern Africa (Sterkfontein Member 4, Kromdraai Members A and B, Taung, and Swartkrans Member 1) and eastern Africa (Laetoli and Olduvai, Tanzania; Olorgesailie and Koobi Fora, Kenya -- Areas 1-203; Omo, Ethiopia -- Usno Formation, Shungura Formation Members B-H, and Kalam Area). Species sampled are listed by deposit in Table 1. [A complete list of specimens sampled is given in Benefit (1987).] Taxonomic identifications for the southern African fossils are largely based on Freedman (1957, 1961a, 1961b, 1965, 1976), Freedman and Brain (1972), Freedman and Stenhouse (1972), Maier (1971a, 1971b) and Eisenhart (1974). Identification of fossil monkeys from eastern Africa are based on descriptions by R.E. Leakey (1969), Jolly (1970, 1972), M.G. Leakey (1976, 1982), Leakey and Leakey (1973a, 1973b, 1976), Eck (1977), Eck and Howell (1982), Eck and Jablonski (1984) and Leakey and Delson (1987).

Biostratigraphic dating of the southern African cave deposits indicates that Makapansgat is the oldest site at approximately 3.0 million years (my), followed by Sterkfontein (3.2-2.5 my and 1.75-1.4 my), Kromdraai (2.7-1.8 my), Taung (2.3-1.0 my) and Swartkrans (1.8-1.6 my and 1.25-0.9 my) (Vrba 1982). Eastern African deposits are more securely dated on radiometric grounds. Laetoli is considered to be 3.8-3.5 my (Leakey *et al.* 1976; Leakey and Hay 1982), the Usno and Shungura Formations at the Omo range in age from 2.9-1.3 my (Shuey *et al.* 1974; Brown and Nash 1976; Brown *et al.* 1985), Koobi Fora and Ileret Formations range in age from 3.3-1.5 my (Feibel *et al.* 1989), Olduvai from 2.2-0.6 my (Leakey and Hay 1982) and Olorgesailie from 1.3-0.5 my (Potts 1989). Because of the long

Table 1. Numbers of fossil cercopithecine molars measured. L = Lower, U = Upper.

EAST AFRICA

	LM1	LM2	LM3	UM1	UM2	UM3
Cercocebus sp., KOOBI FORA	5	10	9	7	11	5
Cercocebus ado, OLDUVAI	1	1	1			
Parapapio ado, LAETOLI	5	8	10	4	8	5
Parapapio jonesi, KANAPOI	1	1	1			
Parapapio sp., KOOBI FORA	2	3	6	2	2	2
Papionini indet, BARINGO			1			
Papio sp., OLDUVAI		2	3	1	2	
Theropithecus oswaldi,						
KOOBI FORA & ILERET (combined)	13	61	40	12	44	17
AREA 1 (1.5-1.6 my)		3	1		1	
AREA 8 (1.5-1.6 my)		8	1	2	8	1
AREA 103 (1.6-1.7 my)		5		1	1	1
AREA 10 (1.7-1.9 my)		3		1	1	
AREA 123 (1.7-1.9 my)		3	5			
AREA 130 (1.8-1.9 my)	3	8	5	1	4	2
AREA 104 (1.7-2.0 my)	2	4	3		1	1
AREA 106 (2.0 my)		1				
AREA 116 (2.0 my)	1	2		1	1	1
OMO SHUNGURA FORMATION						
Member G		4				
Member H		1				
Kalam area (Members J-L)		1				
OLDUVAI	2	11	12	4	8	8
OLORGESAILIE	39	35	23	35	25	14
Theropithecus brumpti						
KOOBI FORA/TULU BOR						
AREA 117 &204 (3.3 my)	4	2	6	1	2	3
AREA 203 (3.3 my)	2	6	6	1		
OMO, SHUNGURA FORMATION						
Member C		9				
Member D		2				
Theropithecus quadratirostris						
OMO USNO FORMATION						
Member 11		1				

SOUTHERN AFRICA

	M1	LM2	LM3	UM1	UM2	UM3
Dinopithecus ingens, SWARTKRANS	3	5	7	4	7	5
Gorgopithecus major, KROMDRAAI	1	3	4	3	4	5
Papio angusticeps, KROMDRAAI	2	2	2	1	2	2
TAUNG		3	1		2	2
Papio robinsoni, SWARTKRANS	6	10	10	5	15	10
Parapapio jonesi, SWARTKRANS	2	1	2	1	2	2
STERKFONTEIN	3	7	3	1	4	5
Parapapio whitei, STERKFONTEIN	2	4	4	2	2	2
Parapapio broomi, STERKFONTEIN	3	4	3	2	5	3
Theropithecus darti, SWARTKRANS		2	4	2	3	

time ranges represented at most of the deposits, samples of monkeys were examined according to their stratigraphic unit of provenience whenever possible.

Dietary estimates for the fossil species are based on the relationship between molar morphology and diet in nine extant species which have been studied extensively in the wild and for which the proportions of leaves and fruits in the annual diet are known (Table 2). The species considered were *Colobus badius* (n=33), *Colobus guereza* (n=22), *Colobus satanas* (n=2), *Presbytis melalophos* (Kay and Covert 1984), *Presbytis obscura* (Kay and Covert 1984), *Cercocebus galeritus* (n=20), *Cercocebus albigena* (n=25), *Macaca nemestrina* (n=6) and *Macaca fascicularis* (n=34). Additional comparative data were taken from Kay (1978, 1981; Kay and Covert 1984) and Benefit (1987). Dental terminology and measurements used in this paper follow Jolly (1972), Delson (1973), Kay (1978, 1981) and Benefit (1987).

Folivorous monkeys use their molars to puncture and shear leaves while frugivorous monkeys crush and grind harder, more fibrous fruits and seeds (Walker and Murray 1975). Folivores emphasize the shearing or first phase of molar occlusion as the mandible moves upward and medially, while frugivorous crushing and grinding takes place during the second phase of occlusion as the jaw moves lingually and mesially, with the protoconid and hypoconid coming into direct contact with the protocone and hypocone as a result (Crompton and Hiiemae 1970; Kay and Hiiemae 1974; Kay 1975, 1978). The tendency for monkeys that include large amounts of leaves in their diets to have longer shear crests than monkeys which eat greater amounts of fruits and seeds has been demonstrated by Kay (1975, 1978, 1981; Kay and Covert 1984).

Table 2. Average percentages of fruits and leaves in the annual diets of the extant cercopithecoid species sampled.

	FRUIT	LEAVES
Colobus badius	7.6	74.7
Colobus guereza	13.6	68.3
Colobus satanas	58.0	37.0
Presbytis melalophos	58.0	39.0
Presbytis obscura	44.0	36.0
Cercocebus galeritus	77.0	13.0
Cercocebus albigena	71.0	2.6
Macaca nemestrina	74.2	13.0
Macaca fascicularis	62.5	20.0

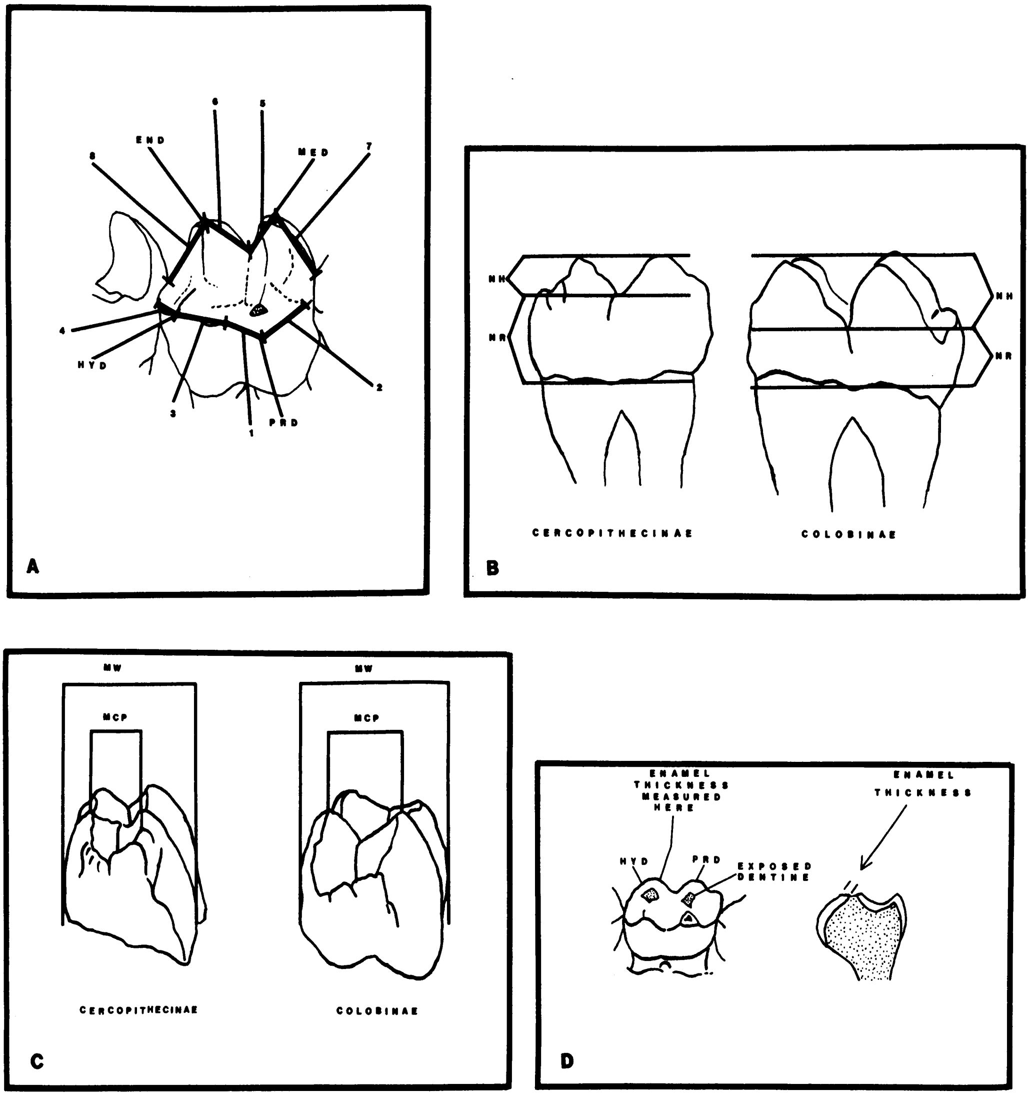
Data taken from Struhsaker (1975, 1978), Marsh (1981), Clutton-Brock (1975), Gatinot (1975), Oates (1977), Gautier-Hion (1978,1980), McKey (1978), Homewood (1978), Waser (1977, 1984), Quris (1975), Freeland (1979), Caldecott (1986), Aldrich-Blake (1980), MacKinnon and MacKinnon (1978), Mah (1980), Wheatly (1980) and Raemakers and Chivers (1980).

In this study eight shear crest lengths for each upper and lower molar were measured using an ocular micrometer mounted in a stereoscopic microscope (Figure 1A). Shearing crest development was then appraised in four ways: 1) from calculation of Kay's (1984) shear quotient (SQ) for lower second molars; 2) from the sum of shear crests gauged against molar length (abbreviated PERS); 3) from the sum of lingual (for lower molars) or buccal (for upper molars) shear crests relative to molar length (PERLS); and 4) from the sum of shear crests bordering the lingual and buccal notches relative to molar length (PERMS). The shear quotient is calculated using the formula $SQ = 100(So-Se/Se)$, with So (observed shear) equal to the sum of the lengths of the eight shear crests, and Se (expected shear) equal to 2.79 (lower second molar length) to the 0.982 exponent. Because the shear quotient exaggerates variation in the observed sum of shear, the simple indices (PERS, PERLS, PERMS) were also used. Unworn molars were measured for calculations of SQ, PERS and PERMS. Since the lingual cusps of lower molars and the buccal cusps of upper molars wear less rapidly than cusps on the opposite side of the tooth, PERLS has the advantage of being measurable on both unworn and moderately worn molars. PERMS is especially useful for the measurement of lower molars with hypoconulids or accessory cuspules on the posthypocristid, such as the third molars of all species and the first and second molars of *Theropithecus*.

For each of the extant species listed above, the average shear quotient was plotted against the average proportion of fruits and leaves consumed annually (Figure 2). Shear quotient was found to be significantly correlated to diet (Table 3). The same procedure was used for the shear indices of each upper and lower molar (Benefit 1987). For those indices found to be significantly correlated to diet, regression equations best describing the relationship (Table 4) were used to estimate the proportions of fruits and leaves eaten by the extinct monkeys.

Greater shear crest length on the molars of folivorous colobine monkeys is accomplished by

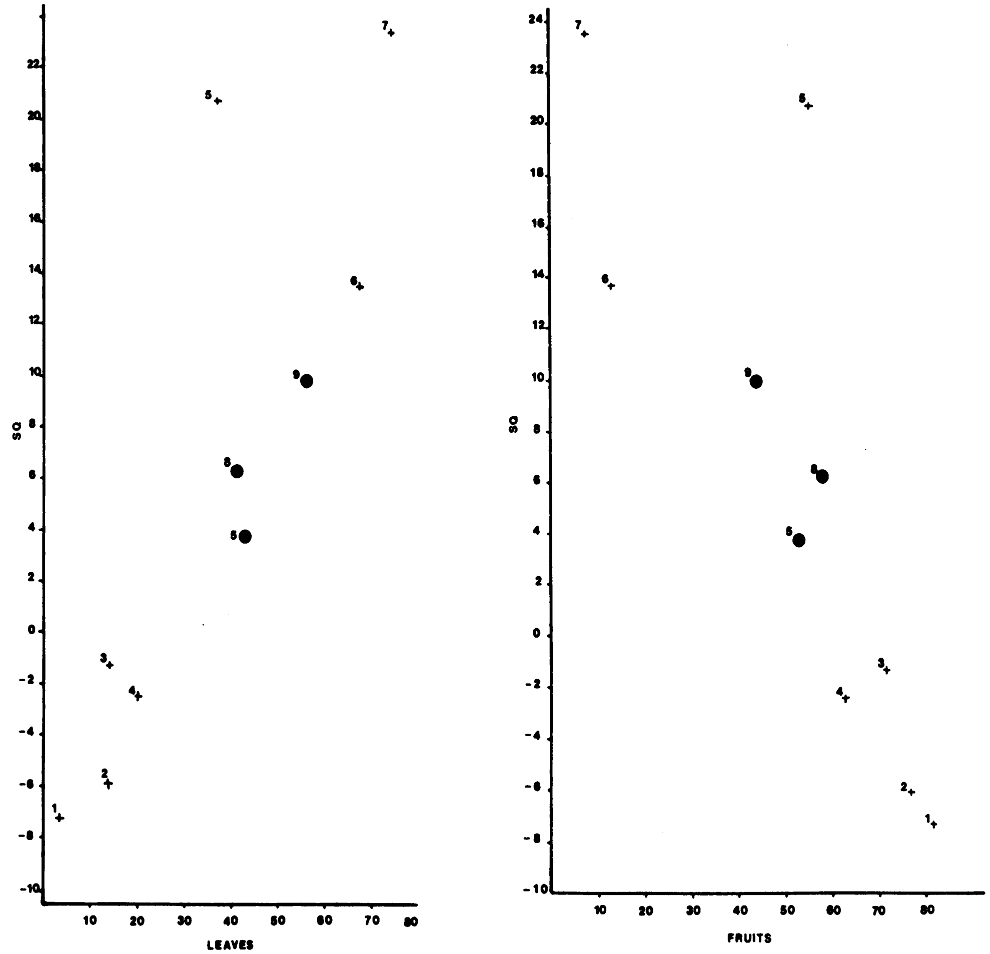
Figure 1. Measurements of molar features functionally correlated to diet among extant cercopithecoids. A. Lengths of shear crests, numbers 1-8; END = entoconid, MED = metaconid, HYD = hypoconid, PRD = protoconid. B. Lingual notch height; NH = vertical height from the notch to the base of the lingual notch, NR = vertical height from the base of the notch to the cervix below. C. Proximity between mesial pairs of cusps; MW = mesial width, MCP = distance between mesial cusp tips. D. Enamel thickness.



a decrease in the heights of the central basin, mesial fovea and distal fovea above the cervix, rather than through an increase in absolute cusp height (Benefit 1987). As a result the lingual notch on lower molars (buccal notch on upper molars) is significantly taller and the height of the crown from the base of the notch to the cervix is significantly lower on colobine than on frugivorous cercopithecine molars (Delson 1973; Benefit and Pickford 1986; Benefit 1987) (Figure 1B).

As for the shear indices, index NHNR (height of the crown above the notch/height of the crown below the notch x 100) was plotted against the proportions of fruits and leaves eaten annually by the extant species and found to be significantly correlated to diet for the lower second and third molars as well as for the upper second molar (Table 3). Regression equations based on NHNR (Table 4) are used in addition to the shear indices to reconstruct the diets of the fossils papionins.

Figure 2. Bivariate plots of shear quotient values against percentages of food items in the annual diets of extant monkeys.



1 = *Cercocebus albigena;* 2 = *Cercocebus galeritus;* 3 = *Macaca nemestrina;* 4 = *Macaca fascicularis;* 5 = *Colobus satanas;* 6 = *Colobus guereza;* 7 = *Colobus badius;* 8 = *Presbytis melalophos;* 9 = *Presbytis obscura.*
● Kay 1984; + Benefit 1987

The emphasis colobine and cercopithecine monkeys place on shearing and grinding is apparent not only from the lengths of the shear crests and notch heights but also from the manner and rate at which the teeth wear. Although the enamel is thick, the molars of cercopithecine monkeys are adapted to wear flat rapidly, while the cusps of thin enamelled colobine monkeys maintain their height and integrity even when large areas of dentine are exposed (Figure 3). The rapid rate at which cercopithecine teeth wear is probably related to the significantly closer proximity of their cusp tips and loph(id)s than is observed for colobines (Benefit 1987), and the resulting constriction of the central basin. The space in which occluding cusps and basins can interdigitate is extremely limited on cercopithecine molars. Consequently, the chance that opposing cusps will rub against each other is enhanced, as is the rate at which the crown wears. The cusp tips of colobine molars are set much further apart than those of cercopithecines (Benefit 1987). The wide distance between the cusps and the subsequently large size of the central basin allows the occluding cusps to interdigitate more freely, leading to a decrease in the rate at which the molars wear.

The combination of low cusp relief and close cusp proximity causes cercopithecine molars to wear flat rapidly. The shearing capacity of the molar is lost as wide enamel rims, created by the merging together of worn grinding facets, form around circular and concave patches of dentine on

Table 3. Pearson correlation coefficients for dental indices significantly correlated to the average proportions of fruits and leaves included in the annual diets of nine extant monkey species.
L = Lower, U = Upper.

INDEX	FRUIT	LEAVES
LM2 SQ	-0.9450	0.9710
LM2 PERS	-0.9642	0.9766
LM2 PERLS	-0.9738	0.9855
LM2 PERMS	-0.9599	0.9773
UM2 PERS	-0.9882	0.9806
UM2 PERLS	-0.9815	0.9743
UM2 PERMS	-0.9744	0.9751
LM2 FL	-0.9302	0.9149
LM3 FL	-0.9087	
LM2 NHNR	-0.9648	0.9682
LM3 NHNR	-0.9828	0.9695
UM2 NHNR	-0.9506	0.9593

the flat cusp tips (Figure 3). Because cercopithecine crowns are flared, with greater width at the cervix than between mesial and distal pairs of cusps, the perimeter of the enamel rim and the surface area that can be devoted to grinding increases as the crown wears. On colobine molars, which experience little change in cusp relief as they wear, elongated areas of dentine surrounded by thin enamel rims occur along the crests of lophs, providing little surface area for crushing and grinding.

For the extant species sampled, significant correlations were found between proportions of fruits and leaves consumed and the degree to which the lower second and third molars and upper second molars were flared (mesial crown width at the apex of cusps/mesial width x 100) (Figure 1C; Table 3). As for cusp relief and shear indices, regression equations based on these measurements were used to estimate the diets of fossil species.

In addition to the dental indices mentioned above, enamel thickness was also measured on the extant and fossil teeth (Figure 1D). Because there was little variation in enamel thickness within each subfamily for the extant sample, correlations between a simple enamel index relating enamel thickness to molar length and diet was not found to be significant, and no regression equation was computed. However, the relationship between enamel thickness and diet was demonstrated by Kay (1981; Kay and Covert 1984) on the basis of logarithm-transformed measurements. Enamel thickness is therefore referred to in this paper as a general indicator of frugivory and folivory.

One of the inherent problems in reconstructing the diets of extinct monkeys based on dental morphology is that the dental indices alone do not differentiate grass-eating from leaf-eating. The molars of extant grass-eating *Theropithecus gelada* are unique among cercopithecids in that they combine characteristics of both folivorous colobine and frugivorous cercopithecine molars. From the lingual perspective, the lower molars of *T. gelada* resemble colobine monkeys with high occlusal relief, low crown height below the lingual notch and long shear crests. From buccal and occlusal perspectives, *Theropithecus* lower molars resemble cercopithecines with close cusp proximity, small central basins, short shear crests and a high position of the lowest point of the lophids above the cervix. As might be expected from consideration of the cercopithecine characteristics of the molars, the cusp tips wear flat rapidly with flat enamel rims quickly forming on the molars. As noted by Jolly (1972), the pattern of enamel ridges is more elaborate on *Theropithecus* than other monkeys due to the presence of additional ridges, clefts and infoldings of enamel along the mesial and distal shelves. Grasses are milled between the teeth as occluding molars scrape transversely against each other in a manner similar to that of grazing ungulates. The enamel rims differ from those of other Cercopithecinae in being positioned well above the occlusal basin. The height of the wear surface is thought to maintain the lifetime of the crown as the teeth are subjected to rapid wear resulting from abrasion by the grasses and soil particles that adhere to plants (Jolly 1972).

From consideration of *Theropithecus* molars it is surmised that either the consumption of abrasive silicaceous grasses and/or the cercopithecine characteristic of close cusp proximity are responsible for the rapid rate of cusp deformation. We conclude that if a species has long shear crests, colobine-like cusp proximity and thin enamel, but a rapid rate of cusp deformation, it may have eaten grass rather than leaves. Patterns of wear are therefore considered together with dental indices in reconstructing the diets of fossil species. However, differentiating grass-eating from leaf-eating molars, given a combination of colobine and cercopithecine characteristics (as in *Theropithecus),* presents an extremely difficult and perhaps unresolvable situation.

RESULTS

Papionina

Dietary estimates for fossil Cercopithecinae are presented in Table 5. In general, southern African papioninans were found to be less committed to frugivory than their eastern African counterparts, the average diet of the former consisting of 56% fruits and 27% leaves (range: 50-66.5% fruits, 16-33% leaves) and the latter 61% fruits and 22.5% leaves (range: 52-83% fruits, 0-31.5% leaves). Among the southern African species only the diet of *Dinopithecus ingens* (66.5% fruits) was found to be highly frugivorous. Otherwise, three of the southern species were reconstructed as having consumed 58-60% fruits and five as 50-55% fruits. In eastern Africa, fossil *Parapapio jonesi* (83% fruits), *Cercocebus* (74% fruits) and *Papio* (67% fruits) were found to be the most committed to frugivory (74% fruits, on average), while *Parapapio ado* and *Parapapio spp.* were found to be the least frugivorous (52-53% fruits).

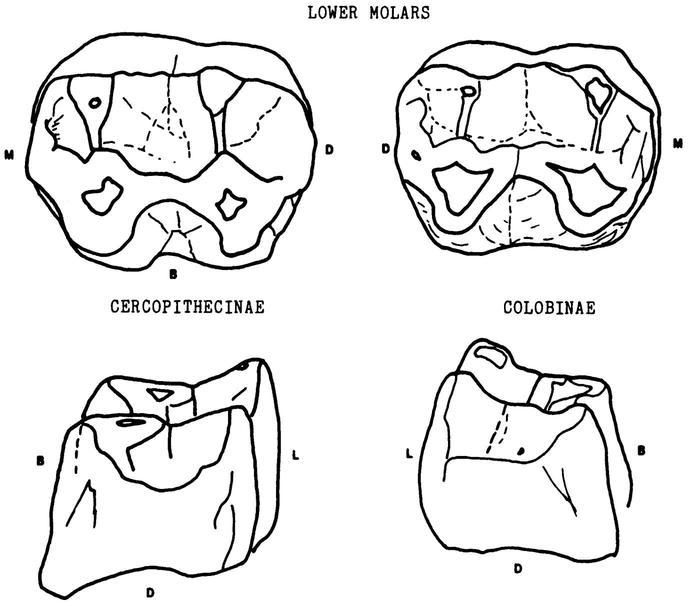
Theropithecus

The dietary habits of fossil *Theropithecus* are more difficult to assess than those of other baboons due to their unusual molar morphology which includes the presence of accessory cuspules along shear crests bordering mesial and distal shelves. The accessory cuspules make it

Table 4. Linear regression equations used to reconstruct the proportions of fruits and leaves consumed by fossil species. L = Lower, U = Upper.

	R-squared	Std. Err. Estimate
Fruit=62.53 - (2.37139 * LM2SQ)	0.89304	8.887
Leaves=24.67 + (2.48568 * LM2SQ)	0.94290	6.625
Fruit=57.77 - (-0.97320 * LM2SQW)	0.94712	8.1536
Leaves=25.25 + (0.97424 * LM2SQW)	0.94914	7.8701
Fruit=236.59 - (3.0471 * LM2FL)	0.86529	11.6888
Leaves=-145.70 + (2.94397 * LM2FL)	0.86370	12.6289
Fruit=95.24 - (0.55408 * LM2NHNR)	0.93086	9.3229
Leaves=-145.70 + (0.5472 * LM2NHNR)	0.93739	8.7323
Fruit=301.29 - (0.8998 * LM2PERS)	0.92977	9.3967
Leaves=-217.57 + (0.89692 * LM2PERS)	0.95370	7.5092
Fruit=203.04 - (1.20434 * LM2PERMS)	0.92131	9.9461
Leaves=-159.24 + (1.50747 * LM2PERMS)	0.95507	7.3971
Fruit=102.79 - (0.65061 * LM3NHNR)	0.92580	6.5573
Leaves=-18.37 + (0.63173 * LM3NHNR)	0.940	8.5481
Fruit=119.11 - (1.22808 * UM2NHNR)	0.90372	11.0018
Leaves=-35.72 + (1.21971 * UM2NHNR)	0.92026	9.8542
Fruit=318.61 - (0.97324 * UM2PERS)	0.97732	5.3396
Leaves=-229.35 + (0.95017 * UM2PERS)	0.96167	6.8321
Fruit=337.32 - (2.0863 * UM2PERLS)	0.96337	6.7857
Leaves=-247.89 + (2.0353 * UM2PERLS)	0.94983	7.8163
Fruit=265.76 - (1.77564 * UM2PERMS)	0.94946	7.9708
Leaves=-179.61 + (1.7489 * UM2PERMS)	0.95089	7.7333

Figure 3. Comparison of worn colobine and cercopithecine molars.



difficult to measure mesial and distal shear crests accurately. As a result the shear quotient, which incorporates the lengths of all crests, is highly variable. The length of shear crests bordering the central basin provide the least variable and therefore most reliable measure of shear for *Theropithecus*.

Estimated proportions of fruits and leaves consumed by fossil *Theropithecus* based on SQ, PERMS and the average of predictions of all indices are summarized in Table 6. Predictions based on index PERMS for lower second molars were found to more accurately reflect the diet of extant *T. gelada* than those based on shear quotients (Table 6). It is therefore reasonable to assume that predictions based on PERMS for fossil species are also more accurate, and greater weight is placed on these results.

All dietary predictions indicate that the southern African *T. darti* and the more ancient of the eastern African *Theropithecus*, *T. brumpti* (3.2-2.0 my) and *T. quadratirostris* (3.4-3.2 my), have had longer shear crests and a higher potential for folivory than the more recent eastern African species *T. oswaldi* (2.5-0.5 my). These results are partly corroborated by the presence of thicker enamel on the molars of *T. oswaldi* from the Omo [enamel thickness (1.5 mm)/crown length (17.3 mm) = 8.7%] than on molars of *T. brumpti* from the same site [enamel thickness (1.16 mm)/crown length (15.6 mm) = 7.4%], indicating a greater potential for frugivory for the former. According to index PERMS all fossil *Theropithecus* included more fruits in their diets than do extant geladas, which are rarely frugivorous in the wild (Dunbar 1983).

It is impossible to know whether fossil *Theropithecus* consumed leaves or grasses. Examination of wear striations under a light microscope revealed deep bucco-lingually oriented parallel striations and the relative absence of pits on the molars of *T. oswaldi* from Koobi Fora (Benefit 1987). These deep striations were probably caused by the inclusion of grit in the diet of *T. oswaldi*. They are also indicative of a heavy reliance on the transverse component of mastication, such as is associated with grass-eating in modern *T. gelada*. It is plausible that the non-fruit component of the diet of *T. oswaldi* consisted of the blades, seeds and rhizomes of grasses as suggested by Jolly (1972), rather than leaves. However, the diet of *T. oswaldi* is reconstructed here as having been more eclectic than that of *T. gelada*, counter to Jolly's (1972) suggestion that the species predominantly ate grass.

The molars of *T. brumpti* are generally more gracile than those of *T. oswaldi* with fewer accessory cuspules and infoldings of enamel. Deep transverse striations are not apparent on the worn molars of *T. brumpti*, indicating that little grit adhered to its food and that possibly the transverse component of mastication was not emphasized by the species. *Theropithecus brumpti* may have been a true papionin folivore rather than a grass-eater. A similar diet is suggested for *T. quadratirostris* and *T. darti*. The rapid rate of cusp deformation observed for the molars of *T. brumpti* can be attributed to the close proximity of the molar cusps and the consumption of fruits, rather than to a diet of abrasive grass.

Table 5. Estimated proportions of fruits and leaves consumed by fossil cercopithecines. (For Omo *Theropithecus* and *Theropithecus gelada*, s = shear crests measured in a straight line without inclusion of accessory crests and cuspules and a = additive shear crest measurements with inclusion of all features.)

EAST AFRICA

		FRUIT	LEAVES
Cercocebus sp. KOOBI FORA	LM2SQ	79.6	6.8
	LM2SQW	66.6	16.4
	LM2NHNR	65.9	17.2
	LM2PERS	84.2	0
	LM2PERMS	72.5	4.2
	LM2FL	92.4	0
	LM3NHNR	67.9	18.4
	UM2NHNR	52.3	30.6
	UM2PERS	74.9	8.5
	UM2PERLS	70.7	12.2
	UM2PERMS	71.3	11.95
	mean	74	11.5
Cercocebus ado OLDUVAI	LM3NHNR	74.6	8.9
Parapapio ado LAETOLIL	LM2SQ	60.0	27.3
	LM2SQW	56.1	26.9
	LM2NHNR	50.8	32.1
	LM2PERS	58.9	24.0
	LM2PERMS	41.4	43.1
	LM2FL	0	83.5
	UM2NHNR	82.0	1.1
	UM2PERMS	68.9	14.2
	mean	52	31.5
Parapapio jonesi KANAPOI	LM2SQW	83.1	0
Parapapio sp. KOOBI FORA	LM2SQW	58.4	24.6
	LM3NHNR	69.7	12.7
	UM2NHNR	32.3	50.0
	mean	53	29
Papionini indet. BARINGO	LM3NHNR	63.3	19.9
Papio sp. OLDUVAI	LM2FL	39.0	45.2
	LM2NHNR	61.9	21.2
	LM3NHNR	60.0	23.1
	UM2NHNR	21.0	61.7
	UM2PERS	99.5	0
	UM2PERLS	96.3	0
	UM2PERMS	90.5	0
	mean	67	13
Theropithecus brumpti KOOBI FORA/TULU BOR			
AREA 117 (3.2-3.3 my)	LM2SQ	46.1	41.7
	LM2SQW	51.0	32.0
	LM2NHNR	26.6	56.0
	LM2PERS	45.4	37.5
	LM2PERMS	26.3	62.0
	LM3NHNR	28.3	54.0
	UM2PERS	70.3	13.0
	UM2PERLS	72.2	10.7
	UM2PERMS	65.0	18.1
	mean	48	36
AREA 203 (3.3 my)	LM3NHNR	26.35	55.9
OMO SHUNGURA FORMATION			
Member unknown	LM2SQW s	61.4	21.6
	LM2FL s	13.2	70.1
	mean	37	46
Members C-G	SQ	28.8	60.1
Member C	LM2SQ s	55.4	32.1
	a	11.4	78.1
	LM2PERS s	57.0	25.9
	a	17.0	66.6
	LM2PERMS	36.8	50.1
	mean s	50	36
	mean a	22	65
Member D	LM2SQ a	0.6	89.5
	LM2PERS a	0.8	82.0
	LM2PERMS	28.4	60.4
	mean	10	77
Theropithecus oswaldi KOOBI FORA & ILERET	LM2FL	61.7	23.2
	LM2PERMS	49.8	32.5
	UM2PERS	72.7	10.7
	UM2PERLS	81.6	1.5
	UM2PERMS	58.6	24.4
	mean	53	42
AREA 1 (1.5-1.6 my)	LM2SQW	51.4	31.9
	LM2NHNR	15.4	67.3
	UM2PERS	100.0	0
	UM2PERLS	88.2	0
	UM2PERMS	81.6	1.8
	mean	67	20
AREA 8 (1.5-1.6 my)	LM2SQW	49.8	33.2
	LM2FL	48.2	36.3
	LM2NHNR	54.3	28.7
	mean	51	33
AREA 103 (1.6-1.7 my)	LM2FL	100.0	0
	LM2NHNR	43.0	39.8
	LM2PERMS	41.25	43.2
	mean	61	28
AREA 10 (1.7-1.9 my)	UM2NHNR	9.0	73.6
	UM2PERMS	33.9	48.7
	mean	21.5	61
AREA 123 (1.7-1.9 my)	LM3NHNR	26.3	55.9
AREA 130 (1.8-1.9 my)	LM2SQ	63.1	24.0
	LM2SQW	58.6	24.4
	LM2NHNR	45.6	37.3
	LM2PERS	65.0	18.0
	LM2FL	80.4	5.2
	LM3NHNR	34.3	48.1
	UM2NHNR	34.9	47.9
	UM2PERS	63.0	15.1
	UM2PERLS	71.0	11.9
	UM2PERMS	64.8	18.3
	mean	58	25
AREA 104 (1.7-2.0 my)	LM2SQ	36.1	52.4
	LM2SQW	46.9	36.1
	LM2NHNR	17.1	65.3
	LM2PERS	36.1	46.7
	LM2PERMS	40.1	44.7
	LM2FL	30.5	53.5
	mean	27.5	50
AREA 106 (2.0 my)	LM2NHNR	47.9	35.0
AREA 116 (2.0 my)	UM2PERS	82.9	0.8
	UM2PERLS	97.8	0
	UM2PERMS	38.8	43.2
	mean	73	15
OLDUVAI	LM2FL	100.0	0
	LM2PERS	72.9	10.1
	LM2PERMS	54.0	27.4
	mean	76	12
OLORGESAILIE	LM2SQW	49.2	33.8
	LM2FL	92.8	0
	LM2NHNR	22.7	59.8
	LM2PERS	55.4	27.5
	LM2PERMS	47.3	35.7
	LM3NHNR	0	99.6
	UM2PERS	87.4	0
	UM2PERLS	100.0	0
	UM2PERMS	64.9	18.2
	mean	53	30
Theropithecus quadratirostris OMO	LM2PERS a	0	83.8
	LM2PERMS	28.4	60.4
	mean	14	72
Theropithecus gelada EXTANT	LM2SQ s	60.2	27.1
	a	30.7	58.1
	LM2PERS s	43.0	39.8
	a	0	90.9
	LM2PERMS	0	86.5
	mean s	34	51
	mean a	10	78.5

Table 5, continued.

SOUTHERN AFRICA

		FRUIT	LEAVES
Dinopithecus ingens SWARTKRANS	LM2SQ	68.9	14.3
	LM2SQW	62.1	20.9
	LM2NHNR	63.8	19.3
	LM2PERS	73.1	9.9
	LM2PERMS	62.4	16.8
	LM2FL	66.0	19.2
	LM3NHNR	60.8	22.4
	UM2PERS	75.0	8.4
	mean	66.5	16
Gorgopithecus major KROMDRAAI	LM2SQ	36.7	51.8
	LM2SQW	47.5	35.5
	LM2PERS	36.9	45.9
	LM2PERMS	31.4	55.6
	LM2FL	66.3	18.9
	LM2NHNR	50.2	32.7
	LM3NHNR	28.5	27.6
	UM2PERS	100.0	0
	UM2PERLS	100.0	0
	UM2PERMS	100.0	0
	mean	60	27
Papio angusticeps KROMDRAAI	LM2SQ	58.3	29.1
	LM2SQW	58.0	25.0
	LM2NHNR	61.8	21.2
	LM2PERS	61.9	21.1
	LM2PERMS	56.1	24.7
	LM2FL	53.3	31.4
	LM3NHNR	45.9	36.9
	UM2PERS	54.0	29.0
	UM2PERLS	60.8	21.9
	UM2PERMS	65.5	17.6
	mean	58	24
Papio angusticeps TAUNG	LM3NHNR	63.3	20.0
	UM2PERS	46.8	36.0
	UM2PERLS	44.7	37.6
	UM2PERMS	45.1	37.7
	mean	50	33
Papio robinsoni SWARTKRANS	LM2SQ	58.4	29.0
	LM2SQW	58.3	24.7
	LM2PERS	57.8	25.2
	LM2PERMS	56.1	24.7
	LM2NHNR	54.1	28.9
	LM3NHNR	55.1	28.0
	UM2PERS	67.1	16.1
	UM2PERLS	68.0	14.8
	UM2PERMS	61.5	21.6
	mean	60	23
Parapapio jonesi SWARTKRANS	LM2SQW	15.9	67.1
	LM2FL	95.1	0
	LM2NHNR	53.4	29.5
	mean	55	32
STERKFONTEIN	LM2SQ	48.4	39.4
	LM2SQW	53.3	29.8
	LM2NHNR	62.2	20.8
	LM2PERS	49.8	33.2
	LM2PERMS	51.4	30.6
	LM2FL	60.3	24.6
	LM3NHNR	55.6	27.5
	UM2PERS	48.5	34.4
	UM2PERLS	40.8	41.4
	UM2PERMS	61.0	22.1
	mean	53	30
Parapapio whitei SWARTKRANS	UM2PERS	67.9	15.4
	UM2PERLS	61.1	21.6
	UM2PERMS	27.5	55.0
	mean	52	31
STERKFONTEIN	LM2SQ	46.8	41.1
	LM2SQW	51.3	31.7
	LM2NHNR	48.2	34.6
	LM2PERS	45.7	37.2
	LM2PERMS	46.6	36.6
	LM2FL	36.6	47.5
	LM3NHNR	45.2	37.5
	UM2PERS	83.5	0.2
	UM2PERLS	97.2	0
	UM2PERMS	81.6	1.7
	mean	54	27
Parapapio broomi STERKFONTEIN	LM2SQ	60.4	22.7
	LM2FL	59.6	25.3
	LM2NHNR	56.3	26.6
	LM2PERS	67.3	15.2
	LM2PERMS	45.3	38.2
	LM3NHNR	43.9	38.8
	mean	55.5	28
Theropithecus darti SWARTKRANS	LM2SQ	23.6	65.4
	LM2SQW	45.6	37.4
	LM2NHNR	12.1	70.3
	LM2PERS	33.1	41.7
	LM2PERMS	35.8	50.1
	LM2FL	95.4	0
	LM3FL	5.9	77.2
	LM3NHNR	0	84.9
	mean	31	53

DISCUSSION

The relative proportions of fruits, leaves and grasses in the diets of fossil baboons is probably related to whether or not they occupied forest or woodland habitats versus open or treeless savannahs. African grasslands are characterized by low and seasonal fruit productivity. Grasses are an important supplement to the diets of baboons living near or on the savannah during times of the year when fruits are unavailable (Dunbar 1983). Extant baboons exploiting forested habitats tend to eat higher quantities of fruits than grasses or herbs, while the opposite is true of baboons living in scrub savannah (Dunbar 1983). The diet of *Papio* baboons living in unforested (desertic) areas of Namibia consisted of 80% grasses (Hamilton *et al.* 1978). In a similar environment in Ethiopia the baboon diet consisted of 40% grasses (Dunbar and Dunbar 1974). In contrast, grass composed only 10-20% of the diet of baboons living in heavily forested areas, and 20-50% of the diet of baboons living in wooded but not heavily forested regions (Post 1978; Popp 1978; Kummer 1968; Sharman 1980; Dunbar and Dunbar 1974). Based on the principle of uniformitarianism, it is assumed that the same relationship between diet and habitat observed for extant baboons would have existed for fossil papionins.

The idea that the diets and habitats of extant species can be used to infer that highly frugivorous fossil baboons of eastern Africa occupied forest or woodland habitats has been suggested independently by Leakey (1982). It is probably more than coincidence that the least frugivorous of the eastern African baboons, *Parapapio ado,* comes from the site of Laetoli which has been reconstructed as a dry savannah environment (Leakey 1982). Indications that the southern African papioninans were less frugivorous than those from eastern Africa (Table 5) is similarly consistent with reconstructions of the southern cave deposits as representing drier, more open savannah habitats than was typical of eastern African sites such as Koobi Fora and the Omo (Boaz 1977).

In general, baboons from Sterkfontein and Taung appear to have included larger quantities of grasses or herbaceous foods in their diets than the baboons from Kromdraai and Swartkrans. The presence of the most frugivorous of the southern baboons at Swartkrans, ***Dinopithecus ingens,*** indicates that the site may have been associated with a higher degree of tree cover than Taung or Sterkfontein. This evidence contradicts interpretations of Swartkrans as representing a drier environment than was represented at Sterkfontein (Cartmill 1967; Vrba 1982).

A situation analogous to that of the baboons was discerned for australopithecines based on the study of deciduous teeth (Grine 1981). Similar to the baboons, Grine (1981) observed that *Australopithecus robustus* at Swartkrans had shorter

Table 6. Summary of dietary predictions for *Theropithecus.*

SHEAR QUOTIENT

	FRUITS		LEAVES/GRASSES	
	Mean	Range	Mean	Range
T. gelada	45.5	31-60	42.5	27-58
T. oswaldi	50	36-63	38	24-52
T. brumpti	28.5	0.5-46	60	32-89.5
T. darti	24		65	

PERMS

	FRUITS		LEAVES/GRASSES	
	Mean	Range	Mean	Range
T. gelada	0		86.5	
T. oswaldi	47	40-54	36	27-45
T. brumpti	30.5	26-37	56	50-62
T. darti	36		50	
T. quadratirostris	28		60	

MEAN OF ALL INDICES

	FRUITS		LEAVES/GRASSES	
	Mean	Range	Mean	Range
T. gelada	22	10-34	65	51-78.5
T. oswaldi	65.5	21.5-76	36	12.5-61
T. brumpti	33	10-51	53	36-77
T. darti	31		53	
T. quadratirostris	14		72	

shear crests and probably ate more hard fruits than *Australopithecus africanus* at Taung and Sterkfontein. However, Grine (1981) attributed the shorter shear crests of *A. robustus* to the consumption of small and hard, dry-adapted fruits and reconstructed Swartkrans as more xeric than Taung and Sterkfontein. It is equally possible that, as is the case for the baboons at Taung and Sterkfontein, *A. africanus* had longer shear crests than *A. robustus* because it supplemented its diet with grasses and herbs. According to Dunbar (1983), hard and small legumes are extremely scarce on the African savannah and would have proved an unlikely diet for any primate, including australopithecines. Based on this evidence, Grine's (1981) data corroborate the reconstruction of Swartkrans as having been more mesic than Taung or Sterkfontein.

The inclusion of more fruits in the diet of fossil *Theropithecus* indicates that its habitat may have been characterized by a higher degree of tree cover than that occupied by the extant species *T. gelada*. *Theropithecus oswaldi*, which probably consumed grasses rather than leaves, is likely to have occupied open country habitats adjacent to more wooded areas, such as grasslands growing along the margins of shallow lakes where seasonal flooding inhibited the growth of trees, as suggested by Jolly (1972). If the geologically more ancient of the eastern African species, *T. brumpti* and *T. quadratirostris*, consumed leaves rather than grasses as has been suggested here, it is possible that they inhabited forested environments. This reconstruction is consistent with postcranial studies by Ciochon (1986) indicating that *T. brumpti* may have been less cursorial than *T. oswaldi* and that it may have occupied a forest habitat similar to that of the extant mandrill. The occurrence of *T. darti*, which is also reconstructed as having eaten more leaves than grass, at Swartkrans provides further evidence that the site may have been more mesic than other studies have indicated. Since leaf-eating, forest adapted *Theropithecus* are more ancient than savannah dwelling species, we suggest that the origin of the genus is linked to the beginnings of leaf-eating in forest dwelling baboons, as opposed to grass-eating in open country environments as suggested by Jolly (1972).

The dietary and habitat preferences of the fossil cercopithecines almost certainly influenced the patterns of species diversity and relative abundance observed for Plio-Pleistocene *Theropithecus* and papioninans in eastern and southern Africa. If the origin of the genus *Theropithecus* is linked to the beginnings of leaf-eating in forest dwelling baboons, as suggested here, the paucity of *Theropithecus* in southern Africa may be explained by the absence of forested environments in that region. This hypothesis is consistent with the absence of leaf-eating colobine monkeys in the southern African cave deposits. The only fossil colobine found in southern Africa, *Cercopithecoides*, exhibits open country cursorial postcranial adaptations (Birchette 1981) and an unusual pattern of tooth wear that can only have resulted from the consumption of grasses (Benefit 1987). Alternatively, *Theropithecus* in southern Africa may have suffered from competition with grass-eating savannah adapted papioninan baboons. Papioninans were present in southern Africa during the late Miocene at the site of Langebaanweg (Grine and Hendey 1981), but *Theropithecus* did not occur in the area until the Middle Pliocene at the site of Makapansgat. If *Theropithecus* were endemic to eastern Africa, as seems likely, they may have arrived in southern Africa after the papioninan baboons had successfully filled the grass-eating niches available to monkeys, inhibiting *Theropithecus* from "swamping" the southern grasslands with its high population numbers, as *T. oswaldi* did in eastern Africa.

The greater diversity of *Theropithecus* in the eastern region is in part attributable to reduced competition between species of the genus as a result of differing preferences for fruits, leaves and grasses. The overwhelming abundance of *T. oswaldi* fossils in collections from eastern Africa between 2.5 my and 0.5 my may be due to its having lived closer to fluvial and lacustrine depositional environments than the more forest adapted monkeys, resulting in a higher frequency of fossilization. It is also likely that population numbers of *T. oswaldi* were absolutely greater than those of the forest cercopithecines. Population densities of extant *T. gelada* are considerably higher than those of any known population of *Papio*, presumably because dense and evenly distributed grasses can support larger numbers of animals than forest resources which are more sparsely and patchily distributed (Dunbar 1983).

The lower species diversity and rarity of papioninan fossils in eastern Africa may have resulted from their preference for forest habitats. The eastern mangabeys and baboons would have competed for forest resources with *T. brumpti* and large-bodied colobine monkeys. Plio-Pleistocene colobine monkeys seem to have been less specialized for folivory than their extant relatives. *Paracolobus* and *Rhinocolobus* have been reconstructed as including almost equal portions of fruits and leaves in their diets (Benefit 1987, 1990). Competition between the forest baboons and colobines would have been more intense during the Plio-Pleistocene than it is today. As a consequence, the diversity of forest dwelling members of both Colobinae and Cercopithecinae seems to have been effected. Since *Papio* baboons did not become the dominant savannah monkey in eastern Africa until after the demise of *T. oswaldi,* when it presumably began to exploit the grassland habitats for the first time, it is possible that competition with *T. oswaldi* prevented the papioninans from taking advantage of grassland resources at an earlier time. Competition with other forest monkeys and lack of grass-eating savannah adaptations, combined with lower population densities in forest habitats, are probably responsible for the low numbers and diversity of papioninan fossils at deposits in eastern Africa. Thus, the greater abundance and diversity of the southern papioninan baboons is attributed to the absence of, and lack of competition with, *T. oswaldi* and forest dwelling colobines, to the general tendency for grasslands to support large numbers of animals, and to a diversity of dietary preferences among the baboons themselves.

SUMMARY

Measurements of dental features shown to be functionally correlated to diet among extant monkeys were used to establish criteria from which to assess the relative proportions of fruits and leaves/grasses consumed annually by extinct baboons from Plio-Pleistocene deposits in eastern and southern Africa. The reconstructed diets of fossil papioninans from southern Africa include a generally higher percentage of herbaceous materials than do the diets of their eastern African counterparts. It is suggested that the southern baboons were savannah adapted, supplementing their diets with grasses during periods when fruits were seasonally unavailable, in a manner similar to extant *Papio* baboons (Dunbar 1983). The more frugivorous mangabeys and baboons of the eastern region probably occupied habitats with higher tree cover such as forests and woodlands. Competition from large-bodied colobine monkeys and both grass- and leaf-eating *Theropithecus,* in addition to lower population densities, may be responsible for the rarity and low diversity of eastern African papioninan baboons. The greater abundance and diversity of the southern savannah adapted baboons is attributed to the late arrival and scarcity of *Theropithecus,* as well as to the capacity for grasslands to support large numbers of animals.

Extinct species of *Theropithecus* are reconstructed to have included more fruits in their diets than do extant gelada baboons. *Theropithecus brumpti* was observed to have a greater potential for shearing and thinner enamel than *T. oswaldi.* It also placed less emphasis on the transverse component of mastication than *T. oswaldi.* This evidence indicated that *T. brumpti* may have consumed leaves rather than grasses. It is postulated that *T. brumpti* inhabited forested habitats, unlike the more recent species *T. oswaldi* which consumed grasses and occupied open country habitats such as grasslands along seasonally flooded lakes and rivers. Since the folivorous *Theropithecus* species *(T. brumpti, T. quadratirostris* and *T. darti)* are geologically older than the grass-eating species *(T. oswaldi* and *T. gelada),* the origin of the genus is attributed here to the beginnings of folivory in a large-bodied forest dwelling papionin. The paucity of *Theropithecus* in southern African deposits can be explained by the absence of forested habitats in the region, and/or by the inability of *T. darti* to successfully compete with the savannah adapted papioninan baboons. The abundance of *Theropithecus,* especially *T. oswaldi,* in eastern African deposits may be due to their occupation of habitats that were more prone to fossilization, such as the shores of lakes and rivers, as well as to their greater population numbers.

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