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Molar microwear of subfossil lemurs: improving the resolution of dietary inferences

In this study we use molar microwear analyses to examine the trophic distinctions among various taxa of Malagasy subfossil lemurs. High resolution casts of the teeth of *Megaladapis*, *Archaeolemur*, *Palaeopropithecus*, *Babakotia*, and *Hadropithecus* were examined under a scanning electron microscope. *Megaladapis* was undoubtedly a browsing folivore, but there are significant differences between species of this genus. However, dietary specialists appear to be the exception; for example, *Palaeopropithecus* and *Babakotia* probably supplemented their leaf-eating with substantial amounts of seed-predation, much like modern indrids. *Hadropithecus* was decidedly *not* like the modern gelada baboon, but probably did feed on hard objects. Evidence from microwear and coprolites suggests that *Archaeolemur* probably had an eclectic diet that differed regionally and perhaps seasonally. Substantial trophic diversity within Madgascar's primate community was diminished by the late Quaternary extinctions of the large-bodied species (>9 kg).

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Introduction

Giant lemurs were part of Madagascar's unique fauna until very recent times, perhaps surviving into the 17th century or later (Simons *et al.*, 1995*a*; Burney, 1999). The Holocene extinction of 16 or more "subfossil" species greatly reduced the adaptive diversity of the entire lemuriform clade, and many of their econiches have remained unoccupied since the time of their demise (Godfrey *et al.*, 1997*a*, 1999). Although most of the recognized subfossil taxa were discovered long ago (Szalay & Delson, 1979; Tattersall, 1982; Godfrey & Jungers, 2002), two new species have been recovered from the Ankarana Massif in the extreme north, *Babakotia radofilai* (Godfrey *et al.*, 1990) and *Mesopropithecus dolichobrachion* (Simons *et al.*, 1995*b*). The majority of the large-bodied (>9 kg) subfossil lemurs are believed to have been arboreal, although the archaeolemurids were no doubt more terrestrial than any extant strepsirrhine (Walker, 1974; Godfrey *et al.*, 1997*b*; Jungers *et al.*, 2002). With the possible exception of the giant aye-aye, the activity cycles of most extinct lemurs have been reconstructed as diurnal (e.g., Godfrey *et al.*, 1997*a*). Many of the subfossils appear

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to have been folivores (e.g., *Megaladapis* species; sloth lemurs), but this category conceals considerable diversity in feeding preferences (Jungers *et al.*, 2002). Some species were probably more frugivorous (e.g., *Pachylemur*, *Archaeolemur*), whereas *Hadropithecus* has often been likened to the grass-eating geladas (Jolly, 1970; Tattersall, 1973). Dietary reconstructions to date have been based for the most part on gross craniodental morphology and analogies to extant mammals.

Attempts to capture and describe fully this impressive adaptive diversity (e.g., the heuristic, quantitative "ecospace" of Godfrey *et al.*, 1997*a*) are hampered greatly by the relatively coarse resolution of existing dietary inferences. Although dental microwear has been used recently to identify those giant lemurs that maintained a functional toothcomb for grooming (Jungers *et al.*, 2002), the potential of this analytical tool for refining and/or correcting dietary reconstructions has yet to be adequately explored. Accordingly, the purpose of the present study is to re-evaluate and expand upon some of the previously published conclusions about the diets of the subfossil lemurs via dental (molar) microwear analyses.

Archaeolemur and Hadropithecus

The dentitions of the archaeolemurids are highly derived in comparison to living lemurs and converge to varying degrees on cercopithecines. The upper incisors of *Archaeolemur* are large, spatulate and contact stout lower teeth (i.e., there is no toothcomb). Taken as a unit, the premolars form a long shearing blade mesial to the bunodont, bilophodont and quadrate molars. These features have invoked a frugivorous, baboon-like feeding analogy (Jolly, 1970; Tattersall, 1973, 1982) that includes substantial incisal and premolar preparation of tough-skinned fruits prior to mastication. Recent analyses of dental and mandibular development, and dental microstructure, have refined these interpretations, suggesting a higher proportion of hard objects in the diet of *Archaeolemur* (King *et al.*, 2001; Schwartz *et al.*, 2002). Fecal pellets ascribed recently to *Archaeolemur* suggest a rather more generalized, perhaps omnivorous diet that included small vertebrates (Burney *et al.*, 1997). In contrast, the anterior dentition of *Hadropithecus* is relatively small, the premolars are "molarized", and the molars themselves have complex occlusal surfaces. These features and the cranial architecture of *Hadropithecus* formed the basis of a gelada-like, graminivorous/granivorous dietary reconstruction (Jolly, 1970; Tattersall, 1973). Presumably, rhizomes and grass seeds would require little incisal preparation prior to forceful grinding by the molars and distal premolars.

Palaeopropithecus and Babakotia

The palaeopropithecids include four genera—*Palaeopropithecus*, *Archaeoindris*, *Babakotia* and *Mesopropithecus*. This clade has been dubbed the "sloth lemurs" (Simons *et al.*, 1992) because of remarkable postcranial convergences with South American sloths. The postcanine teeth of sloth lemurs are similar in number (two premolars, three molars) and general design to living indrids (Tattersall, 1982). *Babakotia* and *Mesopropithecus* preserve the typical indrid-like toothcomb, but *Palaeopropithecus* and *Archaeoindris* have replaced it with four short and stout teeth of unknown functional significance. On the basis of high robusticity of the mandibular corpus, Ravosa (1991) argued that these latter two genera were highly folivorous. The molars of *Palaeopropithecus* and *Babakotia* sport more shearing crests per unit tooth than do any of the extant indrids, an observation that is also compatible with reconstructions of specialized folivory (Covert, 1986; Jungers *et al.*, 2002). However, field observations of diet in living indrids (summarized in Hemingway, 1996; Godfrey *et al.*, 1997*a*; Yamashita,

1996) suggest the notions of folivory and frugivory are overly simplistic. Seed predation via consumption of fruits is an important component of the indrid diet, if only seasonally, and mastication of seeds is handled well by teeth thought to be designed for leaf-eating (Lucas & Teaford, 1994). It is reasonable to suspect that the sloth lemurs were also mixed-feeders rather than specialized browsers (Jungers *et al.*, 2002).

Megaladapis

Megaladapis shares with its extant sister genus *Lepilemur* (Montagnon *et al.*, 2001) a suite of craniodental features that is associated with specialized folivory. These characteristics include the loss of upper incisors and posteriorly expanded temporomandibular joint surfaces (Thenius, 1953; Wall, 1997). *Megaladapis* also shares a number of craniodental features with browsing mammals, particularly ungulates (a large postcanine diastema, elongated ventrally flexed nasal bones) and the koala (caudally directed foramen magnum, pronounced airorhynchy) (Tattersall, 1972). While the term browsing is frequently used to distinguish selective leaf-eating from grass grazing in ungulates, we retain its use here for historical reasons, and because it highlights the remarkable anatomical convergences between *Megaladapis* and these nonprimate taxa. Together, these features suggest that *Megaladapis* used its head as a functional extension of the neck, its elongated face ending in a mobile snout capable of efficiently harvesting leaves and cropping them against a horny maxillary pad before they were transported to a battery of molars with well-developed shearing crests (high shearing ratios; see Jungers *et al.*, 2002; also see Seligsohn, 1977). Despite fundamentally similar Bauplans, it seems likely that there were ecogeographic differences among the recognized species of *Megaladapis* (Vuillaume-Randriamanantena *et al.*, 1992; Wunderlich *et al.*, 1996), some of which might have been reflected in diet.

Expected microwear patterns

The brief dietary sketches offered above suggest a broad range of possible feeding behaviors and diets in subfossil lemurs. Finer scale distinctions might be possible given certain patterns of differences in dental microwear. The basis for more detailed dietary interpretation derives from anatomical and behavioral analyses of living and subfossil taxa, in conjunction with findings from previous microwear analyses on primate and nonprimate taxa.

If *Megaladapis* was indeed a specialized folivore or browser, then we expect to observe microwear that is dominated by fine scratches, although the number of scratches may vary depending on additional factors such as the amount of tooth–tooth wear (Teaford, 1994; Solounias & Semprebon, 2002). In marked contrast, the proposed tough and/or hard-object feeding adaptations of archaeolemurids (*Archaeolemur* and *Hadropithecus*) are expected to lead to larger, coarser microwear features, especially pits (Teaford & Walker, 1984; Teaford, 1985, 1988; Strait, 1993; Teaford, 1994).

Beyond this marked dichotomy in browsing *vs.* hard object feeding, we expect that some similarities and perhaps some subtle differences in microwear will be apparent between taxa. For example, as members of a folivorous guild, *Megaladapis*, *Palaeopropithecus*, and *Babakotia* should exhibit somewhat similar microwear patterns. All three genera possess molars with extremely high shearing quotients and ratios (Jungers *et al.*, 2002), an observation believed to signal folivory (Kay, 1975; Covert, 1986; Yamashita, 1998). Alternatively, if sloth lemurs are indeed the sister clade of living indrids (Jungers *et al.*, 1991; Yoder *et al.*, 1999), their diets may have also been more mixed with substantial amounts of seed

Table 1 Specimens used in this study

Taxon	Specimen numbers
Archaeolemur cf. *edwardsi* (*n*=10)	DPC7849, DPC7927, DPC7928, DPC7943, DPC7970, DPC9104, DPC9106, DPC9890, DPC10903, DPC11830
Archaeolemur edwardsi (*n*=8)	AMNH15869,BM9909, BM9965, BM9966, BM9968, BM9969, BM9970, BM9972
Archaeolemur majori (*n*=2)	AMNH30007, BM13923
Palaeopropithecus (*n*=5)	AMNH15872, AMNH93826, MM N, MM R, MM 2A
Megaladapis edwardsi (*n*=11)	AMNH15870, AMNH30024, AMNH30025, AMNH30027, AMNH30028, BM7370, BM7438, BM13912, BM13916, BM13917, MM V
Megaladapis grandidieri (*n*=14)	BM9917, BM9918, BM9919, BM9920, BM9921A, BM9921B, BM9921C, BM9922A, BM9922B, BM9922E, BM9922F, BM9975, BM9976, BM9977
Megaladapis madagascarensis (*n*=2)	BM4848, BM4849
Babakotia (*n*=2)	DPC11300, DPC11799
Hadropithecus (*n*=2)	MM DP, MM Q

predation and frugivory (Godfrey *et al.*, 1997*a*). If this is the case, then one might expect a higher incidence of pitting (and/or larger scratches) on the molars of sloth lemurs than on those of *Megaladapis*.

Given species differences in body size, ecogeography, and perhaps sympatry, we might also expect to observe differences in molar microwear between species within a genus. For example, it has been suggested that members of the subgenus *Megaladapis* (*M. madagascariensis* and *M. grandidieri*) were smaller-bodied and perhaps more arboreal than *M. edwardsi* (subgenus *Peloriadapis*) (Vuillaume-Randriamanantena *et al.*, 1992; Wunderlich *et al.*, 1996). *M. madagascariensis* and *M. edwardsi* are found together at many southern and southwestern subfossil localities and were probably broadly sympatric (Wunderlich *et al.*, 1996). Possibly the larger *M. edwardsi* was a more specialized browser (strictly folivorous) compared to *M. madagascariensis*. Similarly, *Archaeolemur majori*, from mostly southern and southwestern localities, was substantially smaller in body size than *A. edwardsi* from the high central plateau and *A.* cf. *edwardsi* from the caves of the north and northwest (Godfrey, 1997*b*). These body size and ecogeographic differences might be associated with dietary differences, although it is uncertain, *a priori*, how these species differed. We suggest that the species with a higher percentage of pits and/or more variations in scratch size might have had a more variable diet.

Materials

Samples

The subfossil lemur specimens used in this study derive from the collections of the American Museum of Natural History (AMNH), the Natural History Museum of London (BM), the Duke University Primate Center (DPC), and the Academie Malgache in Antananarivo (MM). Table 1 specifies the taxa and specimens included in the analyses.

All three species of *Megaladapis* are represented in the samples, although our sample of useable *M. madagascariensis* molars is quite small (*n*=2). The larger members of the genus *Archaeolemur* are relatively well sampled, but only two individuals of

A. majori were judged to be suitable for microwear analysis. We have pooled specimens of *Palaeopropithecus* into a single sample (n=5); although two species are often recognized, *P. maximus* from the high plateau and *P. ingens* from the south and southwest (Godfrey & Jungers, 2002), a species level distinction is hard to sustain on morphological and metric criteria (Walker, 1967; Szalay & Delson, 1979; Tattersall, 1982). *Hadropithecus* and *Babakotia* are quite rare fossils, and our sample sizes for them are correspondingly small (n=2 for each).

Methods

Data collection

As in previous studies of dental microwear (e.g., Teaford & Robinson, 1989; Teaford & Runestad, 1992), the second maxillary molar was used whenever possible. However, in some cases, particularly with the rarest subfossil material, mandibular second molars were substituted when maxillary second molars were not available, thereby maximizing the sample size. Similarity in microwear patterns between upper and lower molars has been previously demonstrated (e.g., Teaford & Walker, 1984). After careful cleaning with acetone, dental impressions were taken using the polysiloxane impression material "President Jet Regular" by Coltene-Whaledent. High-resolution casts were made from "Araldite" (Ciba-Geigy) or "Epotek" (Epoxy Technology) epoxy using the techniques described by Rose (1983) and Teaford & Oyen (1989). The casts were sputter-coated with gold (200Å) and examined in an Amray 1810 scanning electron microscope in secondary emissions mode. For each specimen, two representative micrographs were taken at a magnification of 500×, using every precaution to minimize the effects of potentially complicating factors such as working distance, excessive tilt, etc. (Gordon, 1988). As the teeth of some taxa had very different morphologies (e.g., molars of *Megaladapis* and *Archaeolemur*), extra care had to be taken to insure that images were collected from homologous areas on the occlusal surfaces. Standard procedure is to use Kay's system of numbered wear facets (Kay, 1977) to monitor the location of surfaces recorded via the S.E.M. However, those facets are not always found on all molars. Thus, to aid in the standardization of data collection, all micrographs were taken from wear surfaces along the lingual half of the central basin of maxillary molars, or the buccal half of the central basin of mandibular molars—with the intention of monitoring areas used in the crushing phase at the end of the power stroke.

All of the microwear features on each micrograph were measured in microns using a computer-controlled digitizer. The semi-automated program *Microware 4.0* (Ungar, 2001) has recently become the method of choice in dental microwear analyses, but comparisons of measurements from that technique and the one used here have revealed that both approaches yield the same patterns of microwear differences between populations (Grine *et al.*, 2002).

The total number of features and the maximum length and width of each feature were recorded for each micrograph. A 4:1 length to width ratio was used to distinguish between pits and scratches. For each individual, data from both micrographs were pooled to yield the following information: (1) average number of features per micrograph, (2) percentage of pits (vs. scratches), (3) average width of pits, and (4) average width of scratches.

Data analysis

As noted above, prevailing ideas about the dietary habits of the subfossil lemurs leave a number of hypotheses to be tested using these data. The microwear measurements of the subfossil primates were first compared via one way analyses of variance using either

Table 2 Dental microwear measurements for subfossil *Genera*

Genus	Sample size	Pit width	Scratch width	#Features per micrograph	% Pits
Palaeopropithecus	5	$4·4 \pm 0·74^{a}$	$1·24 \pm 0·066^{c,d}$	$113 \pm 7·5$	$18·4 \pm 5·4$
Archaeolemur	20	$4·1 \pm 0·33^{b}$	$0·81 \pm 0·052^{c}$	$129 \pm 6·3$	$21·5 \pm 2·7$
Megaladapis	27	$2·8 \pm 0·2^{a,b}$	$0·92 \pm 0·059^{d}$	$116 \pm 11·1$	$15·9 \pm 2·7$
Babakotia	2	$3·5 \pm 0·41$	$1·19 \pm 0·14$	65 ± 17	$35·2 \pm 12·3$
Hadropithecus	2	$5·0 \pm 0·64$	$1·47 \pm 0·17$	$85 \pm 6·8$	$31·6 \pm 4·8$

*Not included in statistical analyses (taxa with matched superscripts differ at a significance level indicated below).
[a]Significantly different, $P<0·016$.
[b]Significantly different, $P<0·01$.
[c]Significantly different, $P<0·009$.
[d]Significantly different, $P<0·036$.

genus or species as factors. A nested analysis of variance, with species nested within genera, was judged inappropriate because not all genera had more than one species, and those that did had dramatically different sample sizes. When significant differences were found within the samples, the Tukey Highly Significant Difference Test was used to pinpoint differences, post-hoc, between specific taxa. To determine the most appropriate statistical treatments, all data were run through the Bartlett's test (for homogeneity of variance) and the Lilliefors test (for normality of distributions). If the distributions differed significantly from normality, or if they showed significant differences in variance, the data were then transformed, either via arcsine transformation (for the ratios), log transformation (for other measurements), or rank transformation in order to meet or approximate the assumptions of parametric statistics (Conover & Iman, 1981; Zar, 1984). Obviously, there are other methods of analysis that could be used with these data—most notably multivariate techniques such as discriminant functions or cluster analyses. However, while these techniques often yield interesting illustrations of the patterns of variation in given samples, they are not as easy to interpret as are direct comparisons of measurements.

Results

Comparisons of genera

Descriptive statistics for the microwear measurements for each genus are presented in Table 2, where taxa with matched superscripts differ at a significance level indicated at the bottom of the table. Given the dramatic differences in sample size among genera, *Babakotia* and *Hadropithecus* were not included in statistical analyses. Similarly, *Archaeolemur majori* and *Megaladapis madagascarensis* were not included in the comparisons between subfossil species. However, summary measurements for all of these taxa are presented in Table 3 for the qualitative insights they might provide into the dietary adaptations of these species.

There are no significant differences in the incidence of pitting or in the number of microwear features per micrograph. *Megaladapis* does show a smaller average pit size than did *Archaeolemur* and *Palaeopropithecus,* and both *Archaeolemur* and *Megaladapis* show relatively narrow scratches compared with *Palaeopropithecus*.

Comparisons of species

As can be seen in Table 3, when the samples are split into species, a number of additional differences appear. As for Table 2, taxa with matched superscripts in

Table 3 Dental microwear measurements for subfossil *species*

Genus	Sample size	Pit width	Scratch width	#Features per micrograph	% Pits
Palaeopropithecus	5	4·4 ± 0·74[a]	1·24 ± 0·066[c,d]	113 ± 7·5	18·4 ± 5·4
A. cf. *edwardsi*	10	3·6 ± 0·31	0·74 ± 0·077[c,e]	122 ± 7·1	21·4 ± 4·6[g]
A. edwardsi	8	4·3 ± 0·39[b]	0·91 ± 0·077	140 ± 12·7	22·8 ± 3·8[h]
A. majori	2	6·3 ± 2·43	0·81 ± 0·11	119 ± 1·0	16·9 ± 0·3
M. edwardsi	11	3·0 ± 0·34	0·68 ± 0·046[d,f]	107 ± 17·3	5·1 ± 1·2[g,h,i]
M. grandidieri	14	2·6 ± 0·28[a,b]	1·07 ± 0·075[e,f]	119 ± 16·5	22·6 ± 3·7[i]
M. madagascarensis	2	3·2 ± 0·15	1·19 ± 0·19	143 ± 25·5	29 ± 0·5
Babakotia	2	3·5 ± 0·41	1·2 ± 0·14	65 ± 17	35·2 ± 12·3
Hadropithecus	2	5·0 ± 0·64	1·48 ± 0·175	85 ± 6·8	31·6 ± 4·8

*Not included in statistical analyses (taxa with matched superscripts differ at a significance level indicated below).
[a]Significantly different, $P<0\cdot036$.
[b]Significantly different, $P<0\cdot021$.
[c]Significantly different, $P<0\cdot002$.
[d]Significantly different, $P<0\cdot000$.
[e]Significantly different, $P<0\cdot009$.
[f]Significantly different, $P<0\cdot001$.
[g]Significantly different, $P<0\cdot023$.
[h]Significantly different, $P<0\cdot019$.
[i]Significantly different, $P<0\cdot006$.

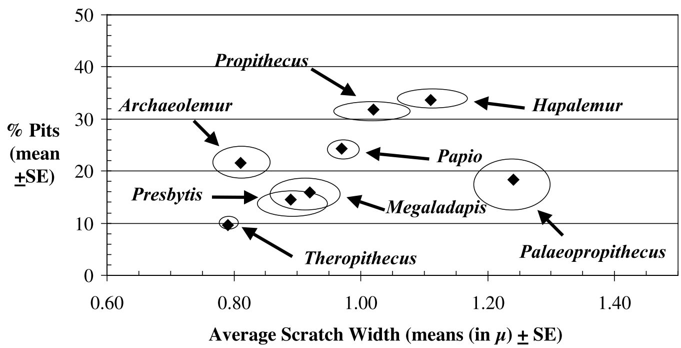

Figure 1. Comparison of dental microwear in modern and subfossil genera. Average scratch width and percentage of pits per micrograph (means surrounded by ellipses for which the long axes are the standard error of the mean for each variable).

Table 3 differ at a significance level indicated at the bottom of the table. Most notably, *Megaladapis edwardsi* emerges with the lowest incidence of pitting yet recorded for a primate, while the smaller species of *Megaladapis* shows a much higher incidence of pitting, analogous to that shown by *Archaeolemur*, and wider scratches more akin to those in *Palaeopropithecus*. The taxa of *Archaeolemur* show no significant differences in molar microwear. All species of *Archaeolemur* have relatively narrow scratches on their molar wear surfaces. Other differences suggested by the data, albeit by small samples, include the relatively low amount of microwear and high incidence of pitting in *Babakotia*, and the wide features on the teeth of *Hadropithecus*.

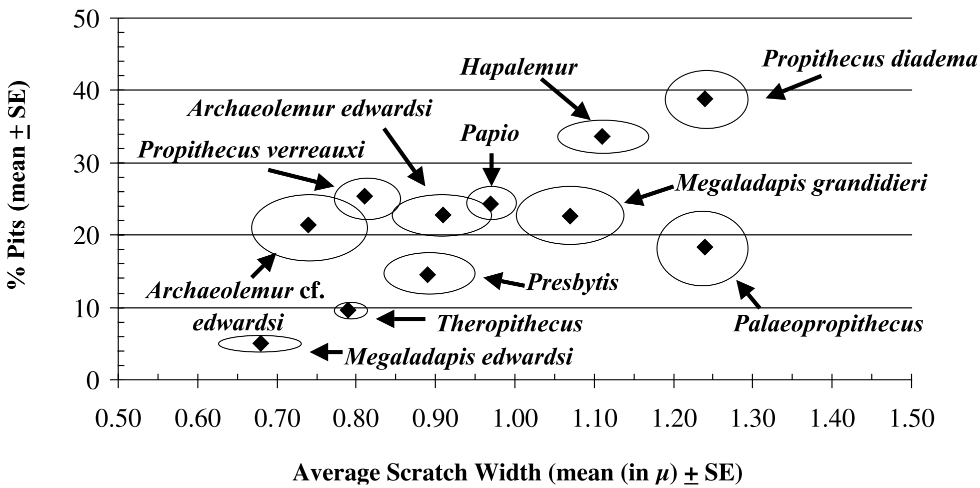

Figure 2. Comparison of dental microwear in modern and subfossil species. Average scratch width and percentage of pits per micrograph (means surrounded by ellipses for which the long axes are the standard error of the mean for each variable).

Discussion

Some of the results of this study were hindered by small sample sizes. Thus, any difference between the small samples (i.e., *Babakotia*, *Hadropithecus*) and the larger samples are merely suggestive at best. Regardless, the relatively wide scratches on the teeth of *Hadropithecus*, and the relatively high incidence of pitting on the teeth of *Babakotia*, are intriguing and perhaps functionally significant (e.g., suggesting that hard objects, such as some seeds were consumed).

Other results of this study corroborate prior speculations and inferences and offer some support for the basic expectations outlined above. In particular, the place of *Megaladapis* as a dedicated leaf-eater is certainly reaffirmed by its narrow pits, narrow scratches, and low incidence of pitting. The difference *between* species of *Megaladapis* is also noteworthy, because the smaller species show trends away from folivory, while *M. edwardsi* appears to have been a ''hyperfolivore'', with the lowest incidence of pitting yet seen in primates and very narrow scratches too. Previous analyses of *Megaladapis* have suggested that the smaller species might have had a more varied diet than did *M. edwardsi* (Godfrey *et al.*, 1997*a*; Vuillaume-Randriamanantena *et al.*, 1992), and the results of this study support this interpretation.

To gain better insight into the microwear differences within the genus *Megaladapis*, comparisons were also made with a sample of modern taxa—chosen because they have been mentioned as possible dietary analogues for the subfossils. Those comparisons yield some additional insights. As can be seen in Table 4 and Figure 1, *Hapalemur* and *Propithecus* have a relatively high incidence of pitting, in contrast to *Presbytis*. *Papio* has relatively large pits, whereas *Theropithecus* has relatively narrow scratches. *Papio* and *Theropithecus* also have fewer features per micrograph. Interestingly, when the sample of *Propithecus* is examined more closely, its two species, *P. diadema* and *P. verreauxi*, exhibit some significant differences, with *P. diadema* showing more pitting and significantly wider scratches on its molars (see Table 5 and Figure 2). The relatively high incidence of pitting for both species of *Propithecus*, however, suggests that

Table 4 Dental microwear measurements for modern *Genera*

Genus	Sample size	Pit width	Scratch width	#Features per micrograph	% Pits
Papio	12	$6·32 \pm 0·4^{a,b,c}$	$0·97 \pm 0·027$	$91 \pm 6^{f,g,h}$	$24·3 \pm 1·7^{l,o}$
Propithecus	21	$3·37 \pm 0·19^{a}$	$1·02 \pm 0·06^{d}$	$151 \pm 12^{f,i}$	$31·8 \pm 2·8^{m,n}$
Hapalemur	17	$4·14 \pm 0·28^{b}$	$1·11 \pm 0·057^{e}$	$166 \pm 17^{g,j}$	$33·7 \pm 1·5^{o,p,q}$
Presbytis	9	$4·93 \pm 0·9$	$0·89 \pm 0·057$	$157 \pm 10^{h,k}$	$14·5 \pm 2·6^{m,p}$
Theropithecus	17	$4·28 \pm 0·44^{c}$	$0·79 \pm 0·016^{d,e}$	$94 \pm 7^{i,j,k}$	$9·7 \pm 1·2^{l,n,q}$

Taxa with matched superscripts differ at a significance level indicated below.
[a]Significantly different, $P<0·000$.
[b]Significantly different, $P<0·003$.
[c]Significantly different, $P<0·006$.
[d]Significantly different, $P<0·008$.
[e]Significantly different, $P<0·000$.
[f]Significantly different, $P<0·007$.
[g]Significantly different, $P<0·001$.
[h]Significantly different, $P<0·018$.
[i]Significantly different, $P<0·004$.
[j]Significantly different, $P<0·000$.
[k]Significantly different, $P<0·015$.
[l]Significantly different, $P<0·000$.
[m]Significantly different, $P<0·000$.
[n]Significantly different, $P<0·000$.
[o]Significantly different, $P<0·036$.
[p]Significantly different, $P<0·000$.
[q]Significantly different, $P<0·000$.

Table 5 Dental microwear measurements for modern *species*

Species	Sample size	Pit width	Scratch width	Features per micrograph	% Pits
Papio cynocephalus	12	$6·3 \pm 0·4$	$0·97 \pm 0·027$	91 ± 6	$24·3 \pm 1·7$
Propithecus verreauxi	11	$3·53 \pm 0·27$	$0·81 \pm 0·049^{a,b,c}$	162 ± 13	$25·4 \pm 2·5^{f}$
Propithecus diadema	10	$3·19 \pm 0·27$	$1·24 \pm 0·054^{a}$	139 ± 19^{d}	$38·8 \pm 4·2^{f}$
Hapalemur griseus	13	$4·28 \pm 0·34$	$1·1 \pm 0·07^{b}$	$146 \pm 15^{d,e}$	$34·8 \pm 1·6$
Hapalemur simus	4	$3·68 \pm 0·43$	$1·14 \pm 0·09^{c}$	231 ± 41^{e}	$30·1 \pm 4$
Presbytis entellus	9	$4·93 \pm 0·9$	$0·89 \pm 0·057$	157 ± 10	$14·5 \pm 2·6$
Theropithecus gelada	17	$4·28 \pm 0·43$	$0·79 \pm 0·016$	94 ± 7	$9·7 \pm 1·2$

Significance levels are only presented among those genera that have been split into two species.
Taxa with matched superscripts differ at a significance level indicated below.
[a]Significantly different, $P<0·000$.
[b]Significantly different, $P<0·001$.
[c]Significantly different, $P<0·011$.
[d]Significantly different, $P<0·011$.
[e]Significantly different, $P<0·018$.
[f]Significantly different, $P<0·003$.

neither was as dedicated a leaf-eater as *Presbytis entellus*; rather, the microwear signature is that of a seed predator, such as *Pithecia pithecia* (Teaford & Runestad, 1992).

From this perspective, the differences between *M. edwardsi* and *M. grandidieri* (see Figure 2) suggest that the latter included a wider range of foods in its diet, including perhaps some tough seeds. Modern analogues for this type of diet might include primates such as *Propithecus diadema* and some of the seed-eating langurs of

Southeast Asia (Davies & Oates, 1994), but also some nonprimates with diets including leaves and seeds, such as the tapir (Janzen, 1981).

Microwear data for *Palaeopropithecus* (Figure 2) also support previous interpretations, in that its wider scratches and slightly elevated incidence of pitting suggest it was not a specialized browser. As was suggested by Godfrey *et al.* (1997*a*), it was probably a "folivorous seed-predator", much like *Propithecus diadema*.

In contrast to the findings for *Megaladapis* and *Palaeopropithecus*, the position of *Archaeolemur* in these analyses was not as expected. If it was indeed adapted for eating tough foods, or even hard foods, why would it exhibit average to small-sized pits, narrow scratches, and only an average incidence of pitting? In essence, nothing in its molar microwear pattern is exceptionally noteworthy or clearly diagnostic. Its only microwear similarity with modern *Papio* (the incidence of pitting) (Figure 2), may well indicate that *Archaeolemur* had an eclectic diet, as suggested by analyses of its fecal pellets (Burney *et al.*, 1997*a*). However, the small size of its microwear features complicate such interpretations. It is possible that *Archaeolemur* was indeed adapted to a varied diet, with different individuals in different geographical areas feeding on different foods (Godfrey *et al.*, 1997*a*). There is a suggestion of larger features on the molars of *A.* cf. *edwardsi* and *A. majori* in comparison to *A. edwardsi* (Table 3 and Figure 2). This is ultimately due to differences between micrographs from individual specimens, with some showing relatively large pits, and others showing relatively small pits (see Figure 3). As it happens, the specimens with larger pits are categorized as *Archaeolemur* cf. *edwardsi*, while those with only smaller pits are *A. edwardsi*. Those labeled *A.* cf. *edwardsi*, are from northern Madagascar, while those labeled *A. edwardsi* are from the high plateau. Perhaps then, the molar microwear may be reflecting ecogeographic variations within this genus (Godfrey *et al.*, 1997*a*).

If there *were* ecogeographic differences within the genus *Archaeolemur*, how might we explain some of its craniodental adaptations (e.g., patterns of dental and mandibular development, and dental microstructure)—which are fairly consistently indicative of a diet of tough, hard foods (King *et al.*, 2001; Schwartz *et al.*, 2002)? To answer this question, we must remember that adaptations for tough or hard-object feeding may not have been required to process all types of ingested foods. If the survival and reproduction of certain individuals depended upon frequent processing of hard or tough objects, then associated adaptations would be maintained within the population. Or, if these foods were critical "fall-back foods" at certain times of the year, or in certain habitats (Conklin-Brittain et al, 1998; Lambert *et al.*, 1999), then this too may have led to the maintenance of associated traits as a complex within a species. In other words, *Archaeolemur* may well have acquired the facultative *ability* to feed on hard or tough objects. Similarly, its dental and mandibular development may have facilitated feeding on hard or tough objects (King *et al.*, 2001). But it did not have to be strictly dedicated or limited to a diet of those food items. This basic idea forms a crucial link and caveat between modern analyses of functional morphology and paleobiological inferences. The former are always demonstrating the complexities of everyday life for modern organisms, whereas the latter are often forced to rely upon over-generalizations—e.g., categorizing animals as frugivores or folivores—because paleobiological analyses usually cannot reach the level of resolution seen in studies of modern organisms.

Nevertheless, and within the limits of the resolution seen here, we believe our results allow us to improve upon overly simplistic dietary categories for subfossil lemurs.

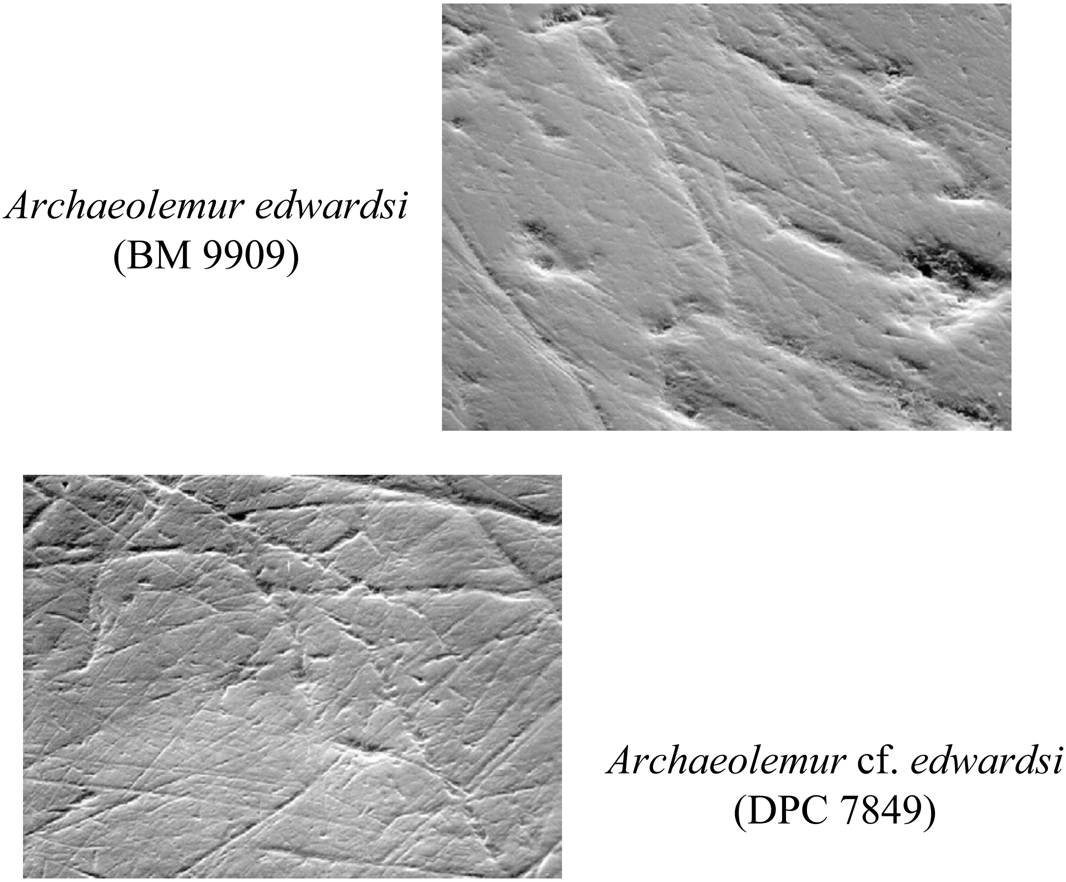

Figure 3. Scanning electron micrographs showing differences in molar microwear between specimens of *Archaeolemur* collected from different geographic regions on Madagascar.

Megaladapis was a highly specialized folivore; both microwear and shearing capabilities corroborate this inference. There is also the possibility that the largest species, *M. edwardsi*, was the most specialized or dedicated leaf-eater in this folivorous genus. Despite very high shearing quotients (Jungers *et al*., 2002), the sloth lemurs were probably folivores of a different ilk. Not unlike their extant indrid relatives, leaf-eating was probably supplemented by frequent seed-predation (perhaps seasonally). *Archaeolemur* apparently had an eclectic diet that may have differed regionally and/or seasonally. With a higher incidence of features and wider scratches, *Hadropithecus* exhibits no special resemblance to the gelada baboon, and the reconstruction of a grass-eating specialization is unlikely. The folivore guild in Madagascar was large and diverse until recently (Godfrey *et al*., 1999), but there were also dietary generalists among the subfossils. The Great Red Island still offers an enormous range of habitats, and it remains to be explained why only the largest members of this adaptively broad radiation were driven to extinction in historical times.

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