



Dental use wear in extinct lemurs: evidence of diet and niche differentiation

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Abstract

A new technique for molar use-wear analysis is applied to samples of all 16 species of extinct lemurs with known dentitions, as well as to a large comparative sample of extant primates. This technique, which relies on the light refractive properties of wear pits and scratches as seen under a standard stereoscopic microscope, has shown itself to be effective in distinguishing the diets of ungulates and extant primates. We draw dietary inferences for each of the 16 extinct lemur species in our database. There is a strong phylogenetic signal, with the Palaeopropithecidae showing use-wear signatures similar to those of the Indriidae; extinct lemurids (*Pachylemur* spp.) showing striking similarities to extant lemurids (except *Hapalemur* spp.); and *Megaladapis* showing similarities to *Lepilemur* spp. Only the Archaeolemuridae have dietary signatures unlike those of any extant lemurs, with the partial exception of *Daubentonia*. We conclude that the Archaeolemuridae were hard-object feeders; the Palaeopropithecidae were seed predators, consuming a mixed diet of foliage and fruit to varying degrees; *Pachylemur* was a fruit-dominated mixed feeder, but not a seed predator; and all *Megaladapis* were leaf browsers. There is no molar use wear evidence that any of the extinct lemurs relied on terrestrial foods (C4 grasses, tubers, rhizomes). This has possible implications for the role of the disappearance of wooded habitats in the extinction of lemurs.

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Introduction

The lemur communities of Madagascar have undergone remarkable changes over the past several thousand years due to the recent arrival of humans and subsequent loss of about one third of the species (Dewar, 1984; Richard and Dewar, 1991; Burney, 1997, 1999; Godfrey et al., 1997a, 1999). These extinctions were nonrandom; all of the larger-bodied species (9–200 kg) disappeared. Two of the seven families of lemurs on Madagascar—the Archaeolemuridae and Palaeopropithecidae—completely disappeared, and a third—the Megaladapidae—was severely impacted (Godfrey and Jungers, 2002). Thus, a true understanding of lemur ecology cannot be achieved without consideration of the extinct forms (Richard and Dewar, 1991; Godfrey et al., 1997a; Godfrey and Jungers, 2002). Dietary reconstruction of the extinct species offers important clues to the precise ecological changes that have occurred, and should allow us to better test competing hypotheses regarding the evolution of lemur communities, the convergence (or nonconvergence) of the primate communities on Madagascar to those on continental Africa, Asia, and the Americas, and the role of wooded habitat loss in megafaunal extinction. Of particular interest are the prevalence of tree-foliage consumption and seed predation among extinct lemurs, and the degree to which the extinct lemurs exploited terrestrial food resources (tubers, roots, grasses). Table 1 lists prior assessments of extinct lemur diets as published in the literature.

We apply a new technique for use-wear analysis (MacFadden et al., 1999; Solounias and Semprebon, 2002) to explore the diets of the extinct lemurs of Madagascar. The technique is described in detail elsewhere (Solounias and Semprebon, 2002; Semprebon, 2002, Semprebon et al., 2004). It uses a stereoscopic light microscope at low magnification (35X). Use-wear features are identified not by precise measurements but by their light refractive properties. The technique has been tested by several researchers (including two of the authors of this paper, Nikos Solounias and Gina Semprebon) and it has been found to have high reliability (low measurement error and excellent

interobserver concordance); see especially Semprebon et al. (2004) and Nelson (2004).

The goal of this paper is to reconstruct the diets of extinct lemurs. We apply the new technique to the subfossil lemurs, paying particular attention to discrepancies between the insights achieved here and earlier dietary reconstructions. We explore the ecospace occupied by extinct lemurs, asking in particular: (1) Were folivory, seed predation, and hard-object feeding in lemur communities in the recent past more prevalent than they are today? (2) Does the use-wear of the extinct lemurs suggest a dominance of terrestrial food resources (C4 grasses, tubers and roots) in at least some taxa?

Materials and methods

Samples

A total of 595 individuals comprising 16 extinct and 38 extant primate species (including 14 extant lemur species) were included in this analysis. (Data for an additional 4 lemur species were collected but they were excluded from all analyses except the genus-level discriminant function analysis and the descriptive statistics presented below because they are represented by a single individual each.) The extant sample includes representatives from 10 families with body sizes ranging from ca. 500 g (*Lepilemur leucopus*) to almost 200 kg (*Gorilla gorilla*). We excluded small-bodied, nocturnal, insectivorous or gummivorous primate species (e.g., members of the Cheirogaleidae, Galagidae, Lorisidae), but small-bodied nocturnal folivorous lemurs (*Lepilemur* spp., *Avahi* spp.; see Petter et al., 1977; Ganzhorn et al., 1985; Harcourt, 1991; Thalmann, 2001, 2002) and the largest-bodied of extant nocturnal lemurs (*Daubentonia madagascariensis*, which feeds on large, hard seeds, as well as insect larvae and other foods; see Iwano and Iwakawa, 1988; Sterling, 1994) were included in the sample. All species of extinct lemurs whose skulls are known are represented in this sample.

We limited the sample to dental adults to eliminate possible confounding effects of variation related to behavioral—ontogenetic changes in diet within species. To maximize the sample of extinct

Table 1
Prior dietary inferences for extinct lemurs

| Genus | Inferred diet | Source |
|-----------------------------------|---|--|
| <i>Hadropithecus stenognathus</i> | Open habitat foods: seeds, grass, small objects. Open habitat foods: seeds, grass, small objects. Mainly open habitat foods: hard objects, seeds, grass, some fruit and fauna Seeds, hard objects; not a grazer | Jolly (1970) Tattersall (1973, 1982) Godfrey et al. (1997a) Rafferty et al. (2002) |
| <i>Archaeolemur</i> spp. | Mainly fruit with hard pericarps Varied, primarily leaves, perhaps pliant seeds Generalist, omnivore Mainly fruit and seeds (some leaves and fauna) Varied, only facultatively a hard-object feeder; somewhat similar to <i>Papio</i> | Tattersall (1973, 1982) Rafferty and Teaford (1992) Burney et al. (1997) Godfrey et al. (1997a) Rafferty et al. (2002) |
| <i>Archaeoindris fontoynontii</i> | Mainly leaves | Godfrey et al. (1997a) |
| <i>Palaeopropithecus</i> spp. | Mainly leaves (some fruit and seeds) Leaves and seeds | Godfrey et al. (1997a) Rafferty et al. (2002) |
| <i>Mesopropithecus</i> spp. | Mainly leaves (some fruit and seeds) | Godfrey et al. (1997a) |
| <i>Babakotia radofilai</i> | Mainly leaves (some seeds and fruit) Seeds, hard objects | Godfrey et al. (1997a) Rafferty et al. (2002) |
| <i>Megaladapis</i> spp. | Terrestrial foods (tubers, rhizomes) Leaves Leaves Leaves (likely no seeds) Leaves in <i>M. edwardsi</i> , more varied (incl. tough seeds) in other species (e.g., <i>M. grandidieri</i>). | Mahé (1976) Tattersall (1982) Rafferty and Teaford (1992) Godfrey et al. (1997a) Rafferty et al. (2002) |
| <i>Pachylemur</i> spp. | Mainly fruit; harder fruits and stems than in <i>Varecia</i> More foliage than in <i>Varecia</i> Mainly fruit (some leaves, no seeds) | Seligsohn and Szalay (1974) Ravosa (1992) Godfrey et al. (1997a) |
| <i>Daubentonia robusta</i> | Termites, etc. Mainly seeds and fruit, some fauna | Simons (1994) Godfrey et al. (1997a) |

lemurs, we included lower second molars as well as upper. For each individual, we measured use-wear features on the mesialmost buccal cusp (i.e., the paracone for the uppers, protoconid for the lowers). *t*-Tests confirmed no significant differences in the use-wear signals for our samples of upper vs. lower molars of the same species (see Semperebon et al., 2004); thus, the dietary signal is apparently robust to differences in the ways in which the maxillary and mandibular molars are employed during mastication (see, for example, Kay, 1977). Association of mandibular and maxillary specimens (or of right and left fragmentary jaws) could not be ruled out for some of the subfossils in our analysis, although we tried to minimize association by selecting only one side or by selecting either the maxilla or the mandible when association was certain. For the comparative extant database, we used only upper or lower jaws of each individual.

Use-wear traits

All of the primate use-wear data were collected by GMS. Use-wear features were identified and counted on the mesiobuccal cusp of M2 (normally the paracone of M²) within a standard (0.4 mm)² area (using an ocular reticle). For each of the specimens in our sample, we collected: (1) number of pits of all types; (2) number of scratches; (3) number of large pits of all types (including all puncture pits); (4–6) numbers of small, medium, and large puncture pits; and (7) scratch texture (on a scale of 1–5 from fine to hypercoarse). The total number of puncture pits (the sum of traits 4 through 6) was also calculated. These traits were defined and measured as described in Semperebon et al. (2004). Total scratch and pit frequency counts were made at two enamel locations on the same cusp and averaged to give the mean individual values used here. Presence or absence of

gouges was also recorded but not entered into the analysis of quantitative traits, as gouges are relatively rare. Gouges are large, irregular features scooped out of the enamel band, generally along the outer edges of the band.

Statistical analysis

We used a number of statistical tools to assess the similarities and differences of use-wear patterns of extinct and extant taxa and reconstruct the diets of the extinct lemurs. SPSS (versions 10 and 11.5) was used for all analyses.

ANOVA with Tukey's HSD

First, for each use-wear trait considered separately, we ran an analysis of variance with Tukey's post hoc test for Honestly Significant Differences (HSD). Tukey's post hoc tests for HSD create "homogeneous subsets" comprised of taxa that do not differ significantly (at $\alpha = 0.05$) from the tested taxon for the trait in question. These tests allowed us to isolate extant genera with use-wear signatures similar to those of extinct lemurs, at least at the univariate level. Post hoc tests of significance of differences in use-wear traits were conducted for both genera and species, whenever needed to test particular hypotheses. We also used ANOVA with Tukey's post hoc comparisons of confamilial species pairs to test the significance of differences within families of extinct lemurs.

Principal component analysis

To explore the distribution of all taxa in the "dietary ecospace" described by variation in microscopic use-wear, and to determine the legitimacy of applying, for diagnostic purposes, discriminant functions calculated for extant genera to extinct primate species, we first ran a principal component analysis (PCA) of the trait correlation matrix for all use-wear variables of all individuals (extinct and extant) in our primate database. This allowed us to isolate the dominant use-wear signals in the data, and to assess the overall diversity of dietary niches occupied by the extinct lemurs when compared to extant primate species.

Discriminant function analysis of phylogenetic groups

Next, we ran a canonical discriminant function analysis of all primates in our database, extinct and extant, grouped at the genus level (thirty-six groups). Our purpose here was to determine whether the thirty-six genera in our database have distinctive use-wear signatures, and whether they might tend to cluster into groups that carry dietary information even when *a priori* dietary "categories" are not assigned. Given the success of this analysis (see below), and having demonstrated a consistency in the pattern of variation of use wear features (with most extinct lemurs fitting comfortably within the ordination space occupied by extant primates), we felt justified in applying the dietary diagnostic tools developed and described in our companion paper (Semperebon et al., 2004) to the large-bodied extinct lemurs.

Discriminant function analysis of dietary groups

Using dietary groups defined for extant taxa, we ran three canonical discriminant function analyses (DFA) on all primate species in our database (using the dietary group assignments and the grouped cases described by Semperebon et al., 2004). The task of the first DFA (which generated two axes) was to discriminate individuals belonging to broad dietary groups (folivores, frugivores, and graminivores). The second analysis (generating one axis) was constructed to distinguish hard-object specialists from all other primates, and the third (generating the final, fourth axis) to distinguish seed predators from species that either do not consume, or only incidentally consume, seeds. The diets of the extinct lemurs were reconstructed by treating each individual belonging to an extinct species as an ungrouped case and calculating its scores on each of four axes generated by these analyses. Predicted dietary profiles were generated for each species on the basis of the mean scores of individuals belonging to that species.

Euclidean distance analysis

Multivariate comparisons were made of the predicted dietary profiles of species generated by

discriminant function analysis. For all extinct and extant primate species in our database (with the exception of those represented by only one individual), we constructed a Euclidean distance matrix describing the spatial relationships among species' centroids. The locations of the centroids, and distances among them, were calculated on the basis of each species': (1) probabilities of grass, leaf, and mixed fruit consumption (i.e., their predicted main dietary staple); (2) probability of hard-object exploitation; and (3) probability of membership in the seed-predator category and the predicted "intensity" of seed predation (i.e., predicted seed exploitation). Using that Euclidean distance matrix, we were able to identify those extant taxa whose predicted dietary profiles most closely match those of the extinct lemurs, and who therefore might be presumed to have a similar diet.

When necessary, we compared extinct lemur use-wear patterns to those collected elsewhere for nonprimates. This allowed us to broaden our comparative baseline to species (such as rooting pigs or ungulate browsers that live in sandy environments) whose diets differ substantially from those of any extant primate. Particular attention was paid to comparisons of extinct lemur taxa to: (1) their nearest extant relatives; and (2) extant primates exploiting terrestrial food sources.

Results

ANOVA with Tukey's HSD

Table 2 provides the means and standard deviations for eight use-wear variables in the extant primates we sampled, and Table 3 provides the same data for the sixteen species of extinct lemurs. For each use-wear trait, one-way ANOVAs revealed highly significant differences among taxa ($p < 0.001$). We were able to locate the most important of these differences using Tukey's post hoc test of Honestly Significant Differences. These tests also isolated groups of species ("homogeneous" subsets) with similar values for each trait. For example, Table 4 shows clusters of genera that are

"homogeneous" with selected extinct lemurs for single use wear traits. Listed here are the three genera within each subset whose means for the trait in question are closest to that of the tested genus, and not significantly different.

Principal component analysis

Our first multivariate analysis, a principal component analysis performed on the correlation matrix for all use-wear traits, allowed us to isolate the major use-wear signal in the data. The first principal component explained about two-thirds of the total variance—more than five times the variance explained by the second component and all subsequent principal components. We therefore viewed the subsequent components as summarizing idiosyncratic contrasts in the data that could be ignored for our purposes. The mean scores and standard errors of the means for each species on the first component axis are provided in Table 5. Species with high positive scores on this axis have heavy use wear, including (in order of decreasing importance) many large pits, many pits of all sizes, thick (coarse or hypercoarse) scratches, and many puncture pits (especially small, then medium, then large). Species with high negative scores have light use wear, with no large pits, relatively few pits of any size, fine scratches, and no puncture pits. All of our original variables are significantly positively correlated with the first axis; variable loadings (or correlations) vary from 0.95 (for number of large pits) to 0.59 (for number of large *puncture* pits). The axis appears also to describe a dietary signal: extant species at the high end of the array are hard object feeders, whereas those at the low end are specialized folivores.

The extinct lemur species show an extraordinary diversity of use-wear signals, as evidenced by their scores on the first principal component axis. They occupy both extremes of the primate range, and are also distributed through the middle portion of the range. The archaeolemurids (with heavy and coarse wear) fall at the high end of the spectrum with extant hard-object feeders, and the megaladapids (with light and fine wear) fall near the low end of the array, with extant folivores.

Table 2

Use wear data for extant primates (means and standard deviations, with ANOVAs)

| Taxon | N | A | B | C | D | E | F | G | H |
|-------------------------------------|----|------------------|----------------------------|-------------------|------------------------|-------------------------|----------------------------------|-----------------------------------|----------------------------------|
| | | Scratch texture | Average # of puncture pits | Average # of pits | Average # of scratches | Average # of large pits | Average # of large puncture pits | Average # of medium puncture pits | Average # of small puncture pits |
| | | Mean (Std. Dev.) | Mean (Std. Dev.) | Mean (Std. Dev.) | Mean (Std. Dev.) | Mean (Std. Dev.) | Mean (Std. Dev.) | Mean (Std. Dev.) | Mean (Std. Dev.) |
| INDRIIDAE | | | | | | | | | |
| <i>Indri indri</i> | 12 | 2.4 (0.7) | 7.4 (5.6) | 30.0 (6.9) | 17.9 (3.5) | 11.3 (5.5) | 0 (0) | 0.3 (1.2) | 7.1 (6.0) |
| <i>Propithecus diadema</i> | 14 | 1.6 (0.5) | 5.9 (5.4) | 24.6 (8.0) | 13.2 (5.5) | 7.9 (6.0) | 0 (0) | 0.4 (1.3) | 5.6 (5.5) |
| <i>Propithecus verreauxi</i> | 40 | 2.8 (0.8) | 5.6 (5.7) | 31.5 (4.6) | 20.5 (4.6) | 12.4 (4.4) | 0 (0) | 0.3 (1.1) | 5.3 (5.6) |
| <i>Avahi occidentalis</i> | 1 | 3.0 (—) | 0 (—) | 29.0 (—) | 19.0 (—) | 12.0 (—) | 0 (—) | 0 (—) | 0 (—) |
| <i>Avahi laniger</i> | 7 | 1.1 (0.4) | 0 (0) | 15.6 (5.6) | 8.6 (4.0) | 1.0 (2.7) | 0 (0) | 0 (0) | 0 (0) |
| MEGALADAPIDAE | | | | | | | | | |
| <i>Lepilemur leucopus</i> | 13 | 1.8 (0.9) | 0 (0) | 21.8 (5.8) | 12.5 (4.2) | 3.9 (4.6) | 0 (0) | 0 (0) | 0 (0) |
| <i>Lepilemur mustelinus</i> | 6 | 1.0 (0) | 0 (0) | 15.5 (1.1) | 6.7 (2.8) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| <i>Lepilemur microdon</i> | 1 | 1.0 (—) | 0 (—) | 18.0 (—) | 8.0 (—) | 0 (—) | 0 (0) | 0 (0) | 0 (0) |
| <i>Lepilemur edwardsi</i> | 1 | 1.0 (—) | 0 (—) | 24.0 (—) | 8.0 (—) | 7.0 (—) | 0 (0) | 0 (0) | 0 (0) |
| LEMURIDAE | | | | | | | | | |
| <i>Varecia variegata</i> | 9 | 2.0 (0.5) | 0 (0) | 29.2 (7.7) | 12.6 (4.5) | 12.0 (5.2) | 0 (0) | 0 (0) | 0 (0) |
| <i>Eulemur fulvus</i> | 27 | 2.0 (0.9) | 0 (0) | 24.9 (7.1) | 14.5 (6.1) | 6.0 (5.1) | 0 (0) | 0 (0) | 0 (0) |
| <i>Eulemur mongoz</i> | 1 | 1.0 (—) | 0 (—) | 26.0 (—) | 12.0 (—) | 10.0 (—) | 0 (0) | 0 (0) | 0 (0) |
| <i>Eulemur collaris</i> | 9 | 2.3 (0.9) | 0 (0) | 30.0 (8.9) | 17.1 (1.8) | 10.7 (5.1) | 0 (0) | 0 (0) | 0 (0) |
| <i>Eulemur rubriventer</i> | 6 | 2.5 (0.8) | 0 (0) | 32.2 (11.3) | 15.3 (6.0) | 12.5 (10.2) | 0 (0) | 0 (0) | 0 (0) |
| <i>Lemur catta</i> | 6 | 2.0 (0) | 0 (0) | 30.0 (2.3) | 14.3 (3.8) | 10.5 (2.7) | 0 (0) | 0 (0) | 0 (0) |
| <i>Hapalemur griseus</i> | 20 | 1.2 (0.4) | 0 (0) | 12.6 (4.0) | 21.7 (3.1) | 1.7 (3.1) | 0 (0) | 0 (0) | 0 (0) |
| <i>Hapalemur simus</i> | 12 | 1.7 (0.9) | 0 (0) | 14.8 (5.0) | 23.4 (3.2) | 3.7 (3.3) | 0 (0) | 0 (0) | 0 (0) |
| DAUBENTONIIDAE | | | | | | | | | |
| <i>Daubentonia madagascariensis</i> | 4 | 3.5 (0.6) | 18.8 (2.8) | 39.0 (4.7) | 21.3 (5.9) | 19.5 (2.1) | 0.8 (0.5) | 3.0 (0.8) | 15.0 (2.9) |
| ATELIDAE | | | | | | | | | |
| <i>Cacajao melanocephalus</i> | 5 | 4.0 (0) | 18.6 (1.1) | 44.2 (3.7) | 23.0 (1.2) | 18.6 (1.1) | 0.6 (0.9) | 0 (0) | 15.8 (1.1) |
| <i>Chiropotes satanas</i> | 8 | 3.9 (0.6) | 18.1 (4.2) | 41.6 (3.5) | 22.1 (4.1) | 18.8 (3.9) | 0.6 (0.7) | 2.6 (1.4) | 14.9 (4.3) |
| <i>Pithecia pithecia</i> | 6 | 3.0 (0.6) | 13.0 (3.7) | 37.8 (2.3) | 20.0 (2.8) | 17.7 (1.6) | 0.8 (1.3) | 3.0 (3.0) | 9.2 (6.2) |
| <i>Pithecia monachus</i> | 3 | 3.7 (0.6) | 12.3 (4.5) | 35.3 (5.5) | 16.3 (1.2) | 15.0 (2.7) | 0.3 (0.6) | 2.3 (0.6) | 9.7 (3.5) |
| <i>Cacajao rubicunda</i> | 2 | 3.5 (2.1) | 10.5 (7.8) | 31.5 (6.4) | 23.0 (5.7) | 14.0 (2.8) | 0 (0) | 7.5 (3.5) | 3.0 (4.2) |
| <i>Ateles geoffroyi</i> | 10 | 2.5 (0.5) | 3.0 (2.7) | 34.1 (5.2) | 17.6 (3.6) | 15.9 (3.5) | 0.3 (0.7) | 2.3 (2.6) | 0.4 (1.3) |
| <i>Alouatta seniculus</i> | 4 | 1.8 (1.0) | 2.5 (5) | 18.0 (7.1) | 15.3 (7.5) | 5.0 (6.6) | 0 (0) | 0.5 (1.0) | 2.0 (4.0) |
| <i>Alouatta palliata</i> | 15 | 1.6 (0.8) | 0 (0) | 19.5 (5.4) | 11.5 (6.1) | 4.9 (4.1) | 0 (0) | 0 (0) | 0 (0) |
| <i>Alouatta pigra</i> | 3 | 1.0 (1.0) | 0 (0) | 17.3 (2.3) | 13.0 (4.4) | 5.7 (5.5) | 0 (0) | 0 (0) | 0 (0) |
| CEBIDAE | | | | | | | | | |
| <i>Cebus apella</i> | 11 | 3.9 (0.3) | 18.6 (4.1) | 39.8 (4.5) | 15.5 (4.4) | 20.1 (2.8) | 0.4 (0.7) | 5.3 (3.3) | 13.0 (4.0) |
| CERCOPITHECIDAE | | | | | | | | | |

| | | | | | | | | | |
|--|----|---------------|---------------|----------------|----------------|----------------|---------------|---------------|---------------|
| <i>Theropithecus gelada</i> | 5 | 2.2 (0.5) | 4.4 (6.1) | 15.2 (1.3) | 26.2 (3.1) | 8.2 (5.0) | 0 (0) | 0 (0) | 4.4 (6.1) |
| <i>Mandrillus leucophaeus</i> | 4 | 3.3 (0.5) | 15.5 (4.2) | 38.0 (5.9) | 18.0 (0.8) | 18.0 (4.6) | 0.5 (0.6) | 1.8 (1.5) | 13.3 (3.0) |
| <i>Papio anubis</i> | 19 | 2.7 (0.8) | 15.8 (6.4) | 35.4 (7.1) | 22.4 (3.1) | 17.4 (4.8) | 0.05 (0.2) | 1.2 (1.3) | 14.6 (6.4) |
| <i>Macaca fascicularis</i> | 17 | 2.4 (0.9) | 6.2 (4.4) | 30.5 (5.0) | 18.9 (2.5) | 11.8 (2.6) | 0 (0) | 0.5 (1.1) | 5.7 (4.1) |
| <i>Erythrocebus patas</i> | 5 | 3.0 (0) | 14.6 (3.4) | 40.2 (7.2) | 26.4 (2.0) | 16.8 (1.9) | 0 (0) | 3.0 (1.7) | 11.6 (2.5) |
| <i>Trachypithecus cristatus</i> | 11 | 1.3 (0.5) | 2.8 (4.0) | 17.5 (8.2) | 10.0 (3.8) | 4.2 (5.8) | 0 (0) | 0 (0) | 2.8 (4.0) |
| <i>Trachypithecus obscurus</i> | 26 | 1.8 (1.0) | 5.9 (6.3) | 24.1 (12.4) | 12.9 (6.1) | 7.2 (7.0) | 0 (0) | 0.8 (1.2) | 5.1 (5.4) |
| <i>Semnopithecus entellus</i> | 44 | 2.5 (1.2) | 7.8 (6.2) | 27.1 (12.6) | 18.2 (7.2) | 9.7 (6.9) | 0.2 (0.5) | 1.0 (1.2) | 6.6 (5.0) |
| <i>Nasalis larvatus</i> | 10 | 1.5 (0.5) | 4.4 (6.0) | 20.7 (10.7) | 10.7 (4.0) | 6.4 (7.7) | 0 (0) | 0 (0) | 4.4 (6.0) |
| <i>Colobus polykomos</i> | 11 | 1.7 (0.8) | 3.6 (4.3) | 20.0 (8.7) | 13.2 (5.0) | 5.9 (5.7) | 0 (0) | 0.4 (0.5) | 3.3 (4.0) |
| HYLOBATIDAE | | | | | | | | | |
| <i>Hylobates syndactylus</i> | 7 | 1.4 (0.5) | 1.6 (2.7) | 18.7 (7.6) | 11.0 (6.7) | 3.9 (4.9) | 0 (0) | 0 (0) | 1.6 (2.7) |
| PONGIDAE | | | | | | | | | |
| <i>Pongo pygmaeus</i> | 13 | 3.2 (0.9) | 17.2 (5.0) | 40.7 (7.3) | 20.8 (3.7) | 17.8 (3.6) | 0.4 (0.5) | 2.8 (1.2) | 14.0 (3.9) |
| HOMINIDAE | | | | | | | | | |
| <i>Pan paniscus</i> | 6 | 2.7 (1.0) | 16.2 (2.2) | 38.8 (4.3) | 18.8 (1.5) | 18.3 (1.2) | 0.3 (0.5) | 2.2 (1.0) | 13.7 (1.4) |
| <i>Gorilla gorilla</i> | 9 | 3.3 (1.2) | 16.0 (7.2) | 36.2 (10.7) | 20.8 (5.7) | 15.9 (7.2) | 0.4 (0.7) | 3.4 (2.4) | 12.1 (5.1) |
| ANOVA Grand mean, df (between groups, within groups) | | 2.3 (41, 401) | 6.2 (41, 401) | 27.4 (41, 401) | 17.0 (41, 401) | 10.0 (41, 401) | 0.1 (41, 401) | 0.9 (41, 401) | 5.2 (41, 401) |
| <i>F</i> , significance (<i>p</i> <) | | 8.85 (0.000) | 19.79 (0.000) | 11.26 (0.000) | 8.68 (0.000) | 11.74 (0.000) | 3.49 (0.000) | 12.22 (0.000) | 15.83 (0.000) |

Table 3
Use wear data for extinct lemurs (means and standard deviations, with ANOVAs)

| Taxon | N | A Scratch texture Mean (Std. Dev.) | B Average # of puncture pits Mean (Std. Dev.) | C Average # of pits Mean (Std. Dev.) | D Average # of scratches Mean (Std. Dev.) | E Average # of large pits Mean (Std. Dev.) | F Average # of large puncture pits Mean (Std. Dev.) | G Average # of medium puncture pits Mean (Std. Dev.) | H Average # of small puncture pits Mean (Std. Dev.) |
|---|----|--|--|---|--|---|--|---|--|
| † ARCHAEOLEMURIDAE | | | | | | | | | |
| † <i>Hadropithecus stenognathus</i> | 9 | 4.6 (0.5) | 26.4 (6.8) | 59.2 (4.9) | 21.2 (4.4) | 31.2 (7.3) | 2.7 (1.2) | 3.9 (2.9) | 19.9 (4.0) |
| † <i>Archaeolemur majori</i> | 16 | 4.3 (0.8) | 20.3 (6.0) | 46.3 (5.7) | 20.9 (3.2) | 22.8 (5.0) | 1.5 (1.4) | 3.8 (2.7) | 15.0 (5.0) |
| † <i>Archaeolemur edwardsi</i> | 24 | 4.2 (0.7) | 20.0 (4.6) | 45.1 (8.3) | 22.3 (3.9) | 20.4 (5.3) | 1.6 (1.5) | 3.3 (3.0) | 15.1 (3.9) |
| † PALAEOPROPITHECIDAE | | | | | | | | | |
| † <i>Babakotia radofilai</i> | 11 | 4.3 (0.8) | 13.4 (6.0) | 39.0 (4.5) | 18.8 (2.0) | 16.0 (4.0) | 0 (0) | 4.5 (2.6) | 7.5 (2.3) |
| † <i>Mesopropithecus dolichobrachion</i> | 8 | 2.8 (0.9) | 15.3 (4.1) | 34.4 (7.1) | 19.8 (4.1) | 16.4 (4.0) | 0 (0) | 1.6 (2.8) | 13.6 (4.6) |
| † <i>Mesopropithecus globiceps</i> | 9 | 2.4 (0.5) | 8.8 (3.2) | 32.4 (5.3) | 18.6 (1.9) | 11.3 (3.0) | 0 (0) | 0.8 (1.3) | 8.0 (2.8) |
| † <i>Mesopropithecus pithecoides</i> | 6 | 1.5 (0.6) | 1.7 (4.1) | 23.2 (7.7) | 13.3 (4.6) | 5.0 (5.9) | 0 (0) | 0 (0) | 1.67 (4.1) |
| † <i>Palaeopropithecus</i> sp. nov. | 2 | 2.0 (0) | 13.5 (4.9) | 31.0 (5.7) | 20.0 (2.8) | 15.0 (2.8) | 0 (0) | 0 (0) | 13.5 (5.0) |
| † <i>Palaeopropithecus ingens</i> | 7 | 2.7 (0.5) | 7.6 (6.1) | 31.9 (4.1) | 18.6 (2.5) | 10.9 (4.6) | 0 (0) | 0.4 (1.1) | 7.1 (5.1) |
| † <i>Palaeopropithecus maximus</i> | 8 | 2.0 (0.8) | 7.9 (6.4) | 27.4 (6.9) | 16.1 (5.2) | 9.3 (6.3) | 0 (0) | 1.4 (1.5) | 6.5 (5.0) |
| † <i>Archaeoindris fontoyontii</i> | 4 | 1.3 (0.5) | 5.5 (3.8) | 24.3 (8.6) | 7.5 (3.7) | 8.0 (2.2) | 0.8 (1.5) | 3.8 (2.6) | 1.0 (2.0) |
| MEGALADAPIDAE | | | | | | | | | |
| † <i>Megaladapis grandidieri</i> | 13 | 1.2 (0.4) | 0 (0) | 15.2 (6.7) | 6.6 (2.7) | 2.7 (4.2) | 0 (0) | 0 (0) | 0 (0) |
| † <i>Megaladapis madagascariensis</i> | 7 | 1.1 (0.4) | 0 (0) | 16.1 (3.4) | 8.9 (4.6) | 2.0 (3.6) | 0 (0) | 0 (0) | 0 (0) |
| † <i>Megaladapis edwardsi</i> | 14 | 1.4 (0.5) | 0 (0) | 18.9 (6.0) | 10.7 (6.2) | 3.4 (4.9) | 0 (0) | 0 (0) | 0 (0) |
| LEMURIDAE | | | | | | | | | |
| † <i>Pachylemur insignis</i> | 13 | 2.6 (0.5) | 0 (0) | 30.3 (3.6) | 18.2 (2.8) | 12.2 (2.0) | 0 (0) | 0 (0) | 0 (0) |
| † <i>Pachylemur jullyi</i> | 5 | 2.6 (0.6) | 0 (0) | 29.0 (4.7) | 19.8 (2.6) | 13.0 (2.5) | 0 (0) | 0 (0) | 0 (0) |
| ANOVA Grand mean, df (between, within) | | 2.84 (15, 140) | 10.0 (15, 140) | 33.4 (15, 140) | 16.9 (15, 140) | 13.5 (15, 140) | 0.6 (15, 140) | 1.7 (15, 140) | 7.7 (15, 140) |
| F, significance ($p <$) | | 41.76 (0.000) | 45.43 (0.000) | 40.46 (0.000) | 18.94 (0.000) | 31.12 (0.000) | 11.01 (0.000) | 7.85 (0.000) | 33.00 (0.000) |

Table 4
Selected Tukey's homogeneous subsets as derived from univariate analyses*

| Tested genus | Total pits | Total large pits | Total scratches | Scratch texture |
|----------------------|---|--|---|---|
| <i>Hadropithecus</i> | — | — | <i>Daubentonia</i> <i>Pongo</i> <i>Archaeolemur</i> | <i>Babakotia</i> <i>Archaeolemur</i> <i>Cebus apella</i> |
| <i>Archaeolemur</i> | <i>Chiropotes</i> <i>Pongo</i> <i>Cacajao</i> | <i>Cebus apella</i> <i>Daubentonia</i> <i>Chiropotes</i> | <i>Chiropotes</i> <i>Daubentonia</i> <i>Hadropithecus</i> | <i>Babakotia</i> <i>Cebus apella</i> <i>Hadropithecus</i> |
| <i>Babakotia</i> | <i>Daubentonia</i> <i>Pan</i> <i>Cebus apella</i> | <i>Ateles</i> <i>Gorilla</i> <i>Pithecia</i> | <i>Pithecia</i> <i>Pan</i> <i>Macaca</i> | <i>Archaeolemur</i> <i>Cebus apella</i> <i>Chiropotes</i> |
| <i>Megaladapis</i> | <i>Avahi</i> <i>Hylobates</i> <i>Alouatta</i> | <i>Lepilemur</i> <i>Hapalemur</i> <i>Avahi</i> | <i>Archaeoindris</i> <i>Avahi</i> <i>Lepilemur</i> | <i>Archaeoindris</i> <i>Hapalemur</i> <i>Avahi</i> |

*Because *Hadropithecus* is significantly different from all other genera in total and large pit frequencies, there are no homogeneous subsets with *Hadropithecus* for these traits.

Discriminant function analysis of phylogenetic groups

Table 6 shows the scores of extant primates on the first function of our discriminant function analysis of 36 primate genera. Seven canonical discriminant functions captured 100% of the variance in the data; chi-square tests of the significance of variance explained by each function (using Wilks' Lambda) yielded p -values < 0.001 . The first function explained 54.1% of the variance in the data, and the first three functions together explained 83.8% of the variance in the data. A strong dietary signal emerged from scores on the first function alone. This was a contrast vector separating species with relatively high pit frequencies (especially puncture pits) and coarse scratches from those with numerous, but relatively fine, scratches and few pits of any kind. Extant species with high positive scores on this function are hard-object specialists; next is a group of mixed feeders with a lot of fruit but also seeds in their diet; more folivorous species come next, along with frugivores that avoid seeds; finally, at the low end of the spectrum with high negative scores, lie *Hapalemur* and *Theropithecus*, both of which specialize on grasses of different sorts (Table 6).

Our post hoc classification success for this analysis was encouraging. The purpose of this test was to ascertain what percentage of the 595 individuals in our sample could be classified into

correct "groups" (i.e., 36 genera), on the basis of the information in the seven canonical discriminant functions. About one-third (31.6%) could be correctly classified into their proper genus. More importantly, classification mistakes tended to involve closely related taxa with similar diets, and the dietary signal in the classification tree was considerably stronger than the phylogenetic signal. Thus, for example, individuals belonging to frugivorous lemurid genera were likely to be mistaken for those belonging to other frugivorous lemurid genera, but almost never for the closely-related bamboo lemur, *Hapalemur*. On the other hand, 20% of our *Theropithecus* individuals were misclassified as belonging to *Hapalemur*, but none as belonging to any closely-related cercopithecoid genus (indeed, all of the other individuals belonging to *Theropithecus* were correctly classified). Extant taxa with similar diets did indeed cluster together in the use-wear space described by the seven axes.

Discriminant function analysis of dietary groups

Given the evident dietary signal in our data for extant primates, we felt justified in using canonical discriminant functions generated for extant species with known diets in reconstructing the diets of the giant extinct lemurs. Extant primates with a wide variety of diets are represented in our comparative database, and we feel confident that the dietary

Table 5
Dominant use-wear signal, PCA analysis*

| Genus and species | N | PCA Axis 1 scores Mean (Std. Error) |
|--|----|--|
| † <i>Hadropithecus stenognathus</i> | 9 | 2.41 (0.26) |
| † <i>Archaeolemur majori</i> | 16 | 1.65 (0.15) |
| † <i>Archaeolemur edwardsi</i> | 24 | 1.54 (0.15) |
| <i>Cebus apella</i> | 11 | 1.22 (0.13) |
| <i>Cacajao melanocephalus</i> | 5 | 1.19 (0.08) |
| <i>Daubentonia madagascariensis</i> | 4 | 1.17 (0.12) |
| <i>Chiropotes satanas</i> | 8 | 1.16 (0.15) |
| † <i>Babakotia radofilai</i> | 11 | 0.94 (0.09) |
| <i>Pongo pygmaeus</i> | 13 | 0.94 (0.15) |
| <i>Cacajao rubicunda</i> | 2 | 0.93 (0.68) |
| <i>Erythrocebus patas</i> | 5 | 0.89 (0.11) |
| <i>Pithecia pithecia</i> | 6 | 0.88 (0.13) |
| <i>Gorilla gorilla</i> | 9 | 0.86 (0.34) |
| <i>Mandrillus leucophaeus</i> | 4 | 0.80 (0.19) |
| <i>Pan paniscus</i> | 6 | 0.78 (0.14) |
| <i>Papio anubis</i> | 19 | 0.67 (0.10) |
| <i>Pithecia monachus</i> | 3 | 0.63 (0.16) |
| † <i>Mesopropithecus dolichobrachion</i> | 8 | 0.59 (0.18) |
| <i>Ateles geoffroyi</i> | 10 | 0.33 (0.12) |
| † <i>Palaeopropithecus</i> sp. nov. | 2 | 0.27 (0.22) |
| <i>Propithecus verreauxi</i> | 40 | 0.14 (0.06) |
| † <i>Mesopropithecus globiceps</i> | 9 | 0.10 (0.08) |
| † <i>Palaeopropithecus ingens</i> | 7 | 0.05 (0.18) |
| <i>Macaca fascicularis</i> | 17 | 0.04 (0.08) |
| <i>Indri indri</i> | 12 | -0.01 (0.16) |
| † <i>Pachylemur jullyi</i> | 5 | -0.02 (0.02) |
| <i>Semnopithecus entellus</i> | 44 | -0.04 (0.15) |
| † <i>Pachylemur insignis</i> | 13 | -0.09 (0.03) |
| <i>Theropithecus gelada</i> | 5 | -0.10 (0.18) |
| † <i>Palaeopropithecus maximus</i> | 8 | -0.15 (0.26) |
| <i>Eulemur rubriventer</i> | 6 | -0.19 (0.33) |
| <i>Eulemur collaris</i> | 9 | -0.25 (0.15) |
| † <i>Archaeoindris fontoynontii</i> | 4 | -0.26 (0.25) |
| <i>Varecia variegata</i> | 9 | -0.33 (0.14) |
| <i>Lemur catta</i> | 6 | -0.34 (0.06) |
| <i>Propithecus diadema</i> | 14 | -0.46 (0.18) |
| <i>Trachypithecus obscurus</i> | 26 | -0.50 (0.18) |
| <i>Eulemur fulvus</i> | 27 | -0.61 (0.10) |
| <i>Colobus polykomos</i> | 11 | -0.66 (0.22) |
| <i>Hapalemur simus</i> | 12 | -0.66 (0.11) |
| <i>Alouatta seniculus</i> | 4 | -0.69 (0.45) |
| <i>Nasalis larvatus</i> | 10 | -0.73 (0.24) |
| † <i>Mesopropithecus pithecoides</i> | 6 | -0.75 (0.22) |
| <i>Alouatta palliata</i> | 15 | -0.83 (0.12) |
| <i>Lepilemur leucopus</i> | 13 | -0.83 (0.13) |
| <i>Alouatta pigra</i> | 3 | -0.83 (0.23) |
| <i>Hylobates syndactylus</i> | 3 | -0.93 (0.23) |
| <i>Trachypithecus cristatus</i> | 11 | -0.95 (0.18) |
| <i>Hapalemur griseus</i> | 20 | -0.96 (0.06) |
| † <i>Megaladapis edwardsi</i> | 14 | -0.99 (0.13) |

Table 5 (continued)

| Genus and species | N | PCA Axis 1 scores Mean (Std. Error) |
|---------------------------------------|----|--|
| † <i>Megaladapis madagascariensis</i> | 7 | -1.15 (0.08) |
| † <i>Megaladapis grandidieri</i> | 13 | -1.17 (0.10) |
| <i>Avahi laniger</i> | 7 | -1.25 (0.13) |
| <i>Lepilemur mustelinus</i> | 6 | -1.37 (0.02) |

*Species with sample sizes of 1 are omitted. Correlations of original variables with PCA 1: number of large pits, $r = 0.95$; total pits, $r = 0.92$; scratch texture, $r = 0.88$; number of puncture pits, $r = 0.88$; percent large pits, $r = 0.81$; number of scratches, $r = 0.69$; number of medium puncture pits, $r = 0.69$; number of large puncture pits, $r = 0.59$.

categories we have sampled for extant primates are valid for the subfossil lemurs as well. We used the four dietary functions described in detail by Semprebon et al. (2004).

In brief, the first dietary diagnostic analysis we conducted (designed to discriminate the three broad dietary categories of classic folivores, mixed fruit and foliage browsers or classic frugivores, and grass consumers) generated two axes, the first separating as a remarkably discrete group grass consumers (*Hapalemur griseus*, *Hapalemur simus*, and *Theropithecus gelada*) from both folivores and frugivores, and the second polarizing folivores and frugivores with greater overlap (i.e., as a linear array with more specialized species located at either end). This analysis succeeded in classifying grouped individuals into their assigned dietary categories with 87.0% post hoc classification “success.” Our second dietary-diagnostic canonical discriminant function analysis was performed to distinguish hard-object specialists from all other primates. The single function generated by this analysis succeeded in classifying individuals into their “correct” groups with 92.4% accuracy. Our third analysis, performed to distinguish seed predators from species that either do not consume, or only incidentally consume, seeds, generated a single function with 90.1% classification “success.” [See Semprebon et al., 2004, for correlations of original variables with function scores and other, more detailed, information about these analyses.]

Table 6
Mean scores of genera on Canonical Discriminant Function 1

| | | | |
|--------------------------|------|-----------------------|------|
| <i>Hadropithecus</i> | 5.7 | <i>Indri</i> | −0.2 |
| <i>Archaeolemur</i> | 3.7 | <i>Ateles</i> | −0.4 |
| <i>Cebus</i> | 3.1 | <i>Propithecus</i> | −0.5 |
| <i>Chiropotes</i> | 2.5 | <i>Macaca</i> | −0.5 |
| <i>Daubentonia</i> | 2.4 | <i>Trachypithecus</i> | −0.6 |
| <i>Babakotia</i> | 2.1 | <i>Nasalis</i> | −0.7 |
| <i>Cacajao</i> | 2.1 | <i>Colobus</i> | −0.9 |
| <i>Pongo</i> | 2.0 | <i>Varecia</i> | −1.1 |
| <i>Mandrillus</i> | 1.9 | <i>Lemur</i> | −1.2 |
| <i>Gorilla</i> | 1.8 | <i>Eulemur</i> | −1.2 |
| <i>Pithecia</i> | 1.6 | <i>Hylobates</i> | −1.2 |
| <i>Pan</i> | 1.6 | <i>Lepilemur</i> | −1.3 |
| <i>Papio</i> | 0.9 | <i>Pachylemur</i> | −1.3 |
| <i>Erythrocebus</i> | 0.8 | <i>Megaladapis</i> | −1.4 |
| <i>Archaeoindris</i> | 0.4 | <i>Avahi</i> | −1.4 |
| <i>Mesopropithecus</i> | 0.1 | <i>Alouatta</i> | −1.5 |
| <i>Sennopithecus</i> | 0.0 | <i>Theropithecus</i> | −2.2 |
| <i>Palaeopropithecus</i> | −0.1 | <i>Hapalemur</i> | −2.8 |

The results of our discriminant function analyses for dietary groups of extant primate species are provided in Table 7. Grass consumers can be distinguished from both tree-leaf browsers and mixed fruit and foliage consumers by their relatively high scratch frequency coupled with a low pit frequency (see Semperebon et al., 2004, for further discussion). More frugivorous species can be distinguished from more folivorous species on the basis of their absolutely higher scratch and pit frequencies. Frugivores also tend to have coarser scratches than tree-foliage browsers. Puncture pits are more frequent among frugivores than among tree-foliage consumers. Hard-object specialists have coarser scratches and more pits than other primates. They have relatively higher frequencies of large pits (including large and medium *puncture* pits) than other primates. Seed predators are distinguished by the presence of puncture pits. Puncture pit frequencies appear to reflect the intensity of seed predation.

Our dietary diagnoses for the extinct lemurs (Table 8) are grounded in the above-described discriminant function analysis of use-wear traits. It is worth noting, however, that considerable dietary information can be gleaned from a graphic analysis of two simple traits—total scratch frequency and total pit frequency (Figure 1). Figure 1 displays what might be called a “Use-Wear

Trophic Triangle” for extant primates, showing the bivariate distributions of species’ centroids for specialized tree-foliage browsers (lower left), hard-object feeders (top), and grass consumers (lower right). These species comprise the extremes of the range of variation for *all* extant primate species. Most of the species in our sample are mixed fruit and foliage consumers, but not hard object specialists. These fall in a spectrum, depending on the degree to which they depend on leaves or fruit and/or seeds, spanning the region from the lower left corner to the top of the graph. Figure 2 shows a total pit versus total scratch plot for the extinct lemur species, superimposed on those extant species plotted in Figure 1. It is immediately apparent that none fall in the region occupied by extant graminivores, but that the extinct lemurs span the range from folivores to hard-object specialists.

Euclidean distance analysis

Perhaps the most informative assessment of overall similarities and differences among use-wear profiles of the extinct lemurs is provided by our Euclidean distance matrix. Table 9 reveals those taxa whose predicted dietary profiles, generated from low-magnification use-wear signals, most closely match those of the extinct lemurs. Extant species represented by a single individual were omitted from this matrix, but all 16 extinct lemur species were included. Pairwise distances between species centroids range from barely above 0 to ca. 4.4 units. Among the smallest distances are those between congeners with similar diets. For example, the distance between the centroids for *Hapalemur griseus* and *Hapalemur simus* is less than 0.1 units (more specifically, 0.06 units). However, distantly related species with similar diets are also marked by small distances between species centroids (thus, for example, the distance between *Propithecus diadema* and *Trachypithecus obscurus* is 0.09 units). Larger groups with similar diets form tight clusters; for example, all pairwise interspecific distances among *Varecia variegata*, *Eulemur rubriventer*, *Eulemur collaris*, and *Lemur catta* are under 0.1 units. The largest Euclidean distances (≥ 4.3 units) are between fine leaf or grass browsers and hard-object specialists, as, for example, the

Table 7
Discriminant function dietary predictions for extant primates

| | <i>N</i> | Probability of membership in grass-dominated dietary category | Probability of membership in leaf-dominated dietary category | Probability of membership in fruit-dominated dietary category | Probability of hard-object specialization | Predicted intensity of seed predation | Predicted main dietary staple |
|-------------------------------------|----------|---|--|---|---|---------------------------------------|-------------------------------|
| INDRIIDAE | | | | | | | |
| <i>Indri indri</i> | 12 | 0.00 | 0.20 | 0.79 | 0.02 | Moderate | Mixed fruit |
| <i>Propithecus diadema</i> | 14 | 0.00 | 0.52 | 0.47 | 0.02 | Moderate | Leaves |
| <i>Propithecus verreauxi</i> | 40 | 0.06 | 0.13 | 0.81 | 0.04 | Moderate | Mixed fruit |
| <i>Avahi laniger</i> | 7 | 0.00 | 0.88 | 0.12 | 0.00 | None | Leaves |
| MEGALADAPIDAE | | | | | | | |
| <i>Lepilemur leucopus</i> | 13 | 0.01 | 0.64 | 0.34 | 0.00 | None | Leaves |
| <i>Lepilemur mustelinus</i> | 6 | 0.00 | 0.97 | 0.03 | 0.00 | None | Leaves |
| LEMURIDAE | | | | | | | |
| <i>Varecia variegata</i> | 9 | 0.00 | 0.31 | 0.69 | 0.00 | None | Mixed fruit |
| <i>Eulemur fulvus</i> | 27 | 0.04 | 0.45 | 0.51 | 0.00 | None | Mixed fruit |
| <i>Eulemur collaris</i> | 9 | 0.03 | 0.18 | 0.78 | 0.00 | None | Mixed fruit |
| <i>Eulemur rubriventer</i> | 6 | 0.00 | 0.26 | 0.74 | 0.00 | None | Mixed fruit |
| <i>Lemur catta</i> | 6 | 0.00 | 0.23 | 0.77 | 0.00 | None | Mixed fruit |
| <i>Haplemur griseus</i> | 20 | 0.94 | 0.05 | 0.01 | 0.00 | None | Grass |
| <i>Haplemur simus</i> | 12 | 0.98 | 0.01 | 0.01 | 0.00 | None | Grass |
| DAUBENTONIIDAE | | | | | | | |
| <i>Daubentonia madagascariensis</i> | 4 | 0.00 | 0.02 | 0.98 | 0.61 | Exceptional | Mixed fruit |
| ATELIDAE | | | | | | | |
| <i>Cacajao melanocephalus</i> | 5 | 0.00 | 0.00 | 1.00 | 0.60 | Exceptional | Mixed fruit |
| <i>Chiropotes satanas</i> | 8 | 0.00 | 0.01 | 0.99 | 0.67 | Exceptional | Mixed fruit |
| <i>Pithecia pithecia</i> | 6 | 0.00 | 0.02 | 0.98 | 0.56 | Strong | Mixed fruit |
| <i>Pithecia monachus</i> | 3 | 0.00 | 0.07 | 0.93 | 0.63 | Strong | Mixed fruit |
| <i>Cacajao rubicunda</i> | 2 | 0.00 | 0.12 | 0.88 | 0.62 | Strong | Mixed fruit |
| <i>Ateles geoffroyi</i> | 10 | 0.00 | 0.10 | 0.90 | 0.36 | Moderate | Mixed fruit |
| <i>Alouatta seniculus</i> | 4 | 0.05 | 0.63 | 0.32 | 0.02 | Slight | Leaves |
| <i>Alouatta palliata</i> | 15 | 0.02 | 0.74 | 0.24 | 0.00 | None | Leaves |
| <i>Alouatta pigra</i> | 13 | 0.27 | 0.69 | 0.04 | 0.00 | None | Leaves |
| CEBIDAE | | | | | | | |
| <i>Cebus apella</i> | 11 | 0.00 | 0.03 | 0.97 | 0.80 | Exceptional | Mixed fruit |
| CERCOPITHECIDAE | | | | | | | |
| <i>Theropithecus gelada</i> | 5 | 0.97 | 0.03 | 0.01 | 0.00 | Slight | Grass |
| <i>Mandrillus leucophaeus</i> | 4 | 0.00 | 0.04 | 0.96 | 0.31 | Strong | Mixed fruit |
| <i>Papio anubis</i> | 19 | 0.08 | 0.05 | 0.87 | 0.11 | Strong | Mixed fruit |
| <i>Macaca fascicularis</i> | 17 | 0.01 | 0.17 | 0.81 | 0.00 | Moderate | Mixed fruit |
| <i>Erythrocebus patas</i> | 5 | 0.00 | 0.01 | 0.99 | 0.13 | Strong | Mixed fruit |
| <i>Trachypithecus cristatus</i> | 11 | 0.05 | 0.74 | 0.21 | 0.00 | Moderate | Leaves |
| <i>Trachypithecus obscurus</i> | 26 | 0.00 | 0.51 | 0.49 | 0.08 | Moderate | Leaves |
| <i>Semnopithecus entellus</i> | 44 | 0.02 | 0.34 | 0.64 | 0.23 | Moderate | Mixed fruit |
| <i>Nasalis larvatus</i> | 10 | 0.00 | 0.67 | 0.33 | 0.00 | Slight | Leaves |
| <i>Colobus polykomos</i> | 11 | 0.00 | 0.61 | 0.39 | 0.01 | Moderate | Leaves |
| HYLOBATIDAE | | | | | | | |
| <i>Hylobates syndactylus</i> | 7 | 0.00 | 0.71 | 0.29 | 0.00 | Slight | Leaves |
| PONGIDAE | | | | | | | |
| <i>Pongo pygmaeus</i> | 13 | 0.00 | 0.03 | 0.97 | 0.62 | Strong | Mixed fruit |
| HOMINIDAE | | | | | | | |
| <i>Pan paniscus</i> | 6 | 0.00 | 0.05 | 0.95 | 0.32 | Strong | Mixed fruit |
| <i>Gorilla gorilla</i> | 9 | 0.00 | 0.14 | 0.86 | 0.67 | Strong | Mixed fruit |

Table 8
Summary of discriminant function dietary predictions for extinct lemurs

| Taxon | N | Probability of membership in grass-dominated dietary category | Probability of membership in leaf-dominated dietary category | Probability of membership in fruit-dominated dietary category | Probability of hard-object specialization | Predicted intensity of seed predation | Predicted main dietary staple |
|--|----|---|--|---|---|---------------------------------------|-------------------------------|
| ARCHAEOLEMURIDAE | | | | | | | |
| <i>Hadropithecus stenognathus</i> | 9 | 0.00 | 0.00 | 1.00 | 0.99 | Exceptional | Mixed fruit |
| <i>Archaeolemur majori</i> | 16 | 0.00 | 0.01 | 0.99 | 0.86 | Exceptional | Mixed fruit |
| <i>Archaeolemur edwardsi</i> | 24 | 0.00 | 0.02 | 0.98 | 0.79 | Exceptional | Mixed fruit |
| PALAEOPROPITHECIDAE | | | | | | | |
| <i>Babakotia radofilai</i> | 11 | 0.00 | 0.02 | 0.98 | 0.71 | Strong | Mixed fruit |
| <i>Mesopropithecus dolichobrachion</i> | 8 | 0.00 | 0.16 | 0.84 | 0.22 | Strong | Mixed fruit |
| <i>Mesopropithecus globiceps</i> | 9 | 0.00 | 0.14 | 0.86 | 0.02 | Moderate | Mixed fruit |
| <i>Mesopropithecus pithecooides</i> | 6 | 0.02 | 0.57 | 0.41 | 0.00 | Slight | Leaves |
| <i>Palaeopropithecus</i> sp. nov. | 2 | 0.00 | 0.19 | 0.80 | 0.00 | Strong | Mixed fruit |
| <i>Palaeopropithecus ingens</i> | 7 | 0.00 | 0.12 | 0.88 | 0.02 | Moderate | Mixed fruit |
| <i>Palaeopropithecus maximus</i> | 8 | 0.01 | 0.35 | 0.64 | 0.03 | Moderate | Mixed fruit |
| <i>Archaeoindris fontoynontii</i> | 4 | 0.00 | 0.72 | 0.28 | 0.38 | Moderate | Leaves |
| MEGALADAPIDAE | | | | | | | |
| <i>Megaladapis grandidieri</i> | 13 | 0.00 | 0.93 | 0.06 | 0.00 | None | Leaves |
| <i>Megaladapis madagascariensis</i> | 7 | 0.03 | 0.92 | 0.05 | 0.00 | None | Leaves |
| <i>Megaladapis edwardsi</i> | 14 | 0.04 | 0.76 | 0.19 | 0.00 | None | Leaves |
| LEMURIDAE | | | | | | | |
| <i>Pachylemur insignis</i> | 13 | 0.02 | 0.15 | 0.84 | 0.00 | None | Mixed fruit |
| <i>Pachylemur jullyi</i> | 5 | 0.12 | 0.11 | 0.77 | 0.00 | None | Mixed fruit |

distances between *Cebus apella* and: *Alouatta palliata* (4.3 units); *Lepilemur mustelinus* (4.4 units); *Haplemur griseus* (4.4 units). The Euclidean distance matrix also reveals internally-consistent use-wear similarities and differences among extinct lemur species. Thus, for example, *Megaladapis madagascariensis* and *M. grandidieri* are separated by 0.03 units (and by ca. 0.2 units from *M. edwardsi*); *Megaladapis edwardsi* and *Alouatta palliata* by 0.06 units; *Archaeolemur majori* and *A. edwardsi* by 0.06 units. *Megaladapis madagascariensis* differs most markedly (by 4.4 units for all pairwise distances) from *Daubentonia madagascariensis*, *Chiropotes satanas*, *Cacajao melanocephalus*, *Archaeolemur majori*, *A. edwardsi*, and *Hadropithecus stenognathus*.

Extinct lemur family profiles

What follows are our dietary inferences for extinct lemur species, arranged by family. Table 10

shows the significance of use-wear differences among confamilial species.

Family Archaeolemuridae

Our data provide strong evidence that the archaeolemurids, as a group, were frugivorous seed predators that exploited hard-objects. All of the extant primate species whose dietary profiles are most similar to *Archaeolemur* or to *Hadropithecus* are hard-object feeders and seed predators (Tables 4, 8 and 9). The archaeolemurids lie at the “coarse” extreme of the use-wear spectrum produced by principal components analysis (Table 5), suggesting that their diets were coarser than those of all extant species in our primate database. The single extant primate species with the greatest similarity in use-wear pattern to both *Archaeolemur* and *Hadropithecus* is *Cebus apella*, the tufted capuchin—a hard-object feeder (Figure 3). No archaeolemurid has a use-wear signature similar to that of *Papio*, *Theropithecus*, or *Erythrocebus*—species with

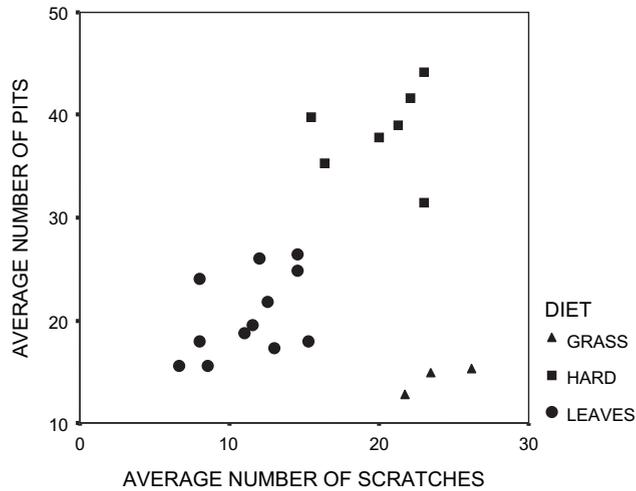


Fig. 1. Scatterplot of average number of pits (Y) on average number of scratches (X), showing selected extant primate species' centroids. The tree-foliage browsers (solid circles) comprise *Lepilemur leucopus*, *Lepilemur mustelinus*, *Avahi laniger*, *Propithecus diadema*, *Alouatta palliata*, *Alouatta pigra*, *Hylobates syndactylus*, *Trachypithecus cristatus*, *Trachypithecus obscurus*, *Nasalis larvatus*, and *Colobus polykomos*. The grass consumers (solid triangles) comprise (left to right) *Hapalemur griseus*, *Hapalemur simus*, and *Theropithecus gelada*. The hard-object specialists (solid squares) comprise *Cacajao melanocephalus*, *Chiropotes satanas*, *Cebus apella*, *Daubentonia madagascariensis*, *Pithecia pithecia*, *Pithecia monachus*, and *Cacajao rubicundus*. Mixed feeders fall in a spectrum spanning the region between folivores, grass consumers, and hard-object specialists.

which they have been repeatedly compared. Indeed, the cercopithecids with use-wear signatures closest to *Archaeolemur* and *Hadropithecus*, as assessed by Euclidean distances between species' centroids, are not savanna baboons, gelada baboons, or patas monkeys, but drills (at a distance of

ca. 1.1–1.2 units). Ironically, of all the cercopithecids in our database, the species *least* like *Hadropithecus* or *Archaeolemur* (with a distance of 3.4–3.5 units from each) is *Theropithecus gelada*. Tukey's post hoc tests of homogeneous subgroups confirm that no cercopithecid is as close to

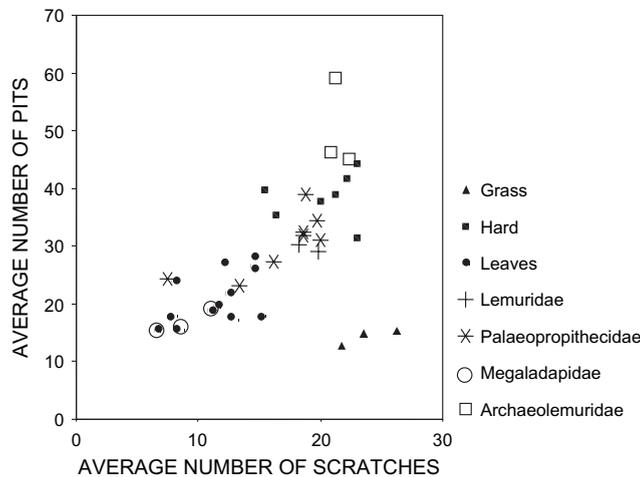


Fig. 2. Extinct lemur species centroids, coded by family, and superimposed on the extant primate Use-Wear Trophic Triangle.

Table 9
Similarity of dietary profiles as measured by the Euclidean distances between species centroids

| Extinct species | Species with similar dietary profiles (Euclidean distances under 0.3, or less than one fifteenth of the maximum Euclidean distance, 4.5, between species centroids) |
|--|---|
| <i>Hadropithecus stenognathus</i> | <i>Archaeolemur majori</i> , <i>Archaeolemur edwardsi</i> , <i>Cebus apella</i> |
| <i>Archaeolemur majori</i> | <i>Archaeolemur edwardsi</i> , <i>Hadropithecus stenognathus</i> , <i>Cebus apella</i> , <i>Chiropotes satanas</i> , <i>Cacajao melanocephalus</i> , <i>Daubentonia madagascariensis</i> |
| <i>Archaeolemur edwardsi</i> | <i>Archaeolemur majori</i> , <i>Cebus apella</i> , <i>Chiropotes satanas</i> , <i>Cacajao melanocephalus</i> , <i>Daubentonia madagascariensis</i> , <i>Hadropithecus stenognathus</i> |
| <i>Babakotia radofilai</i> | <i>Pithecia monachus</i> , <i>Pithecia pithecia</i> , <i>Cacajao rubicunda</i> , <i>Pongo pygmaeus</i> , <i>Gorilla gorilla</i> |
| <i>Mesopropithecus dolichobrachion</i> | <i>Pan paniscus</i> , <i>Mandrillus leucophaeus</i> , <i>Papio anubis</i> , <i>Palaeopropithecus</i> sp. nov. |
| <i>Mesopropithecus globiceps</i> | <i>Indri indri</i> , <i>Palaeopropithecus ingens</i> , <i>Propithecus verreauxi</i> , <i>Macaca fascicularis</i> |
| <i>Mesopropithecus pithecodes</i> | <i>Alouatta seniculus</i> , <i>Hylobates syndactylus</i> , <i>Nasalis larvatus</i> |
| <i>Palaeopropithecus</i> sp. nov. | <i>Mesopropithecus dolichobrachion</i> , <i>Papio anubis</i> , <i>Erythrocebus patas</i> |
| <i>Palaeopropithecus ingens</i> | <i>Propithecus verreauxi</i> , <i>Indri indri</i> , <i>Mesopropithecus globiceps</i> , <i>Macaca fascicularis</i> |
| <i>Palaeopropithecus maximus</i> | <i>Semnopithecus entellus</i> , <i>Indri indri</i> , <i>Trachypithecus obscurus</i> , <i>Propithecus diadema</i> , <i>Macaca fascicularis</i> |
| <i>Archaeoindris fontoynontii</i> | Nothing under 0.3. The closest species centroids, at a distance of <0.5, are <i>Colobus polykomos</i> , <i>Trachypithecus cristatus</i> , <i>Trachypithecus obscurus</i> , and <i>Propithecus diadema</i> |
| <i>Pachylemur insignis</i> | <i>Eulemur collaris</i> , <i>Lemur catta</i> , <i>Pachylemur jullyi</i> , <i>Eulemur rubriventer</i> , <i>Varecia variegata</i> |
| <i>Pachylemur jullyi</i> | <i>Eulemur collaris</i> , <i>Pachylemur insignis</i> , <i>Lemur catta</i> , <i>Eulemur rubriventer</i> , <i>Varecia variegata</i> |
| <i>Megaladapis edwardsi</i> | <i>Alouatta palliata</i> , <i>Avahi laniger</i> , <i>Lepilemur leucopus</i> , <i>Megaladapis grandidieri</i> , <i>Megaladapis madagascariensis</i> , <i>Lepilemur mustelinus</i> |
| <i>Megaladapis grandidieri</i> | <i>Megaladapis madagascariensis</i> , <i>Lepilemur mustelinus</i> , <i>Avahi laniger</i> , <i>Megaladapis edwardsi</i> , <i>Alouatta palliata</i> |
| <i>Megaladapis madagascariensis</i> | <i>Megaladapis grandidieri</i> , <i>Lepilemur mustelinus</i> , <i>Avahi laniger</i> , <i>Megaladapis edwardsi</i> , <i>Alouatta palliata</i> |

Archaeolemur or *Hadropithecus* as is *Cebus apella*, *Daubentonia*, *Chiropotes*, *Cacajao*, *Pithecia*, *Pongo*, or even lowland gorillas. Species belonging to these genera have Euclidean distances of 1.0 unit or lower to the centroids of *Archaeolemur* spp. and *Hadropithecus stenognathus*. *Archaeolemur*ids resemble extant hard-object feeders in the regular presence of coarse and hypercoarse scratches and in the abundance of large pits. Large pits are present on the teeth of all individuals. Puncture pits are always present; large puncture pits are often present, and medium puncture pits occur regularly.

Hadropithecus in particular has abundant puncture pits, including some huge craterlike features—considerably larger than typical “large” puncture pits (Figure 4). *Hadropithecus* differs markedly from *Theropithecus* (as confirmed by Tukey’s post hoc test for Honestly Significant Differences) for virtually every trait. For example, its total pit frequency is well above that of *Theropithecus* (mean difference = 44.02, $p < 0.001$), as is its frequency of puncture pits (mean difference = 22.04,

$p < 0.001$), frequency of large puncture pits (mean difference = 2.67, $p < 0.001$), etc. Scratches are considerably wider, on average, than those of *Theropithecus* (mean difference = 2.36, $p < 0.001$). Only in scratch frequency are the two taxa comparable. Indeed, *Theropithecus* has more scratches than *Hadropithecus* (scratch frequencies are high in grass consumers), but not significantly so at $\alpha = 0.05$.

Archaeolemur, like *Hadropithecus*, is very different from *Theropithecus*—with significantly higher frequencies of pits, large pits, puncture pits, and medium and large puncture pits (also including some huge, craterlike features), as well as coarser scratches. As with *Hadropithecus*, the scratch frequency does not distinguish the two. The contrast between *Archaeolemur* and savanna baboons is also striking. Pit frequencies are significantly higher in *A. majori* (mean difference = 10.9, $p < 0.05$) and *A. edwardsi* (mean difference = 9.8, $p < 0.05$) than in *Papio anubis*. Scratch width is significantly greater in both species of

Table 10

F-tests and *t*-tests of significance of use wear differences among species belonging to single families (extinct species only)

| Family | Trait | <i>F</i> (or <i>t</i>) | df | Significance (<i>p</i>) | |
|--|---|-------------------------|---------|---------------------------|--------|
| Archaeolemuridae (3 species, <i>F</i> -test) | Total pit frequency | 14.1 | (2, 46) | <0.001 | |
| | Total scratch frequency | 0.8 | (2, 46) | NS | |
| | Number of large pits | 12.2 | (2, 46) | <0.001 | |
| | Scratch texture | 1 | (2, 46) | NS | |
| | Large puncture pit frequency | 2.3 | (2, 46) | NS | |
| | Medium puncture pit frequency | 0.4 | (2, 46) | NS | |
| | Small puncture pit frequency | 4.1 | (2, 46) | <0.03 | |
| | Total puncture pit frequency | 4.5 | (2, 46) | <0.02 | |
| | PCA Axis 1 scores | 5.6 | (2, 46) | <0.01 | |
| | Palaeopropithecidae (8 species, <i>F</i> -test) | Total pit frequency | 5.6 | (7, 47) | <0.001 |
| | | Total scratch frequency | 7.2 | (7, 47) | <0.001 |
| | | Number of large pits | 5.6 | (7, 47) | <0.001 |
| | | Scratch texture | 15.4 | (7, 47) | <0.001 |
| Large puncture pit frequency | | 2.1 | (7, 47) | NS | |
| Medium puncture pit frequency | | 5.3 | (7, 47) | <0.001 | |
| Small puncture pit frequency | | 4.2 | (7, 47) | <0.002 | |
| Total puncture pit frequency | | 5.2 | (7, 47) | <0.001 | |
| PCA Axis 1 scores | | 9.6 | (7, 47) | <0.001 | |
| Megaladapidae (3 species, <i>F</i> -test) | | Total pit frequency | 1.4 | (2, 31) | NS |
| | Total scratch frequency | 2.5 | (2, 31) | NS | |
| | Number of large pits | 0.3 | (2, 31) | NS | |
| | Scratch texture | 1 | (2, 31) | NS | |
| | PCA Axis 1 scores | 0.7 | (2, 31) | NS | |
| | Lemuridae (2 species, <i>t</i> -test) | Total pit frequency | 0.6 | 16 | NS |
| Total scratch frequency | | -1.1 | 16 | NS | |
| Number of large pits | | -0.8 | 16 | NS | |
| Scratch texture | | 0.1 | 16 | NS | |
| PCA Axis 1 scores | | -1.7 | 16 | NS | |

Archaeolemur than in *Papio anubis* ($p < 0.001$). Both species of *Archaeolemur* have significantly higher numbers of large puncture pits than does *Papio* ($p < 0.001$). Baboons tend to have many small puncture pits, but, with the exception of *Mandrillus*, few large or medium ones.

Analysis of variance of single traits (Table 10) reveals significant intrafamilial differences in some use-wear signals. Invariably for the Archaeolemuridae, Tukey's post hoc tests for HSD reveal no statistically significant differences in the use-wear signatures of the two species of *Archaeolemur*, but

significant differences between *Hadropithecus* and both species of *Archaeolemur*.

Family Palaeopropithecidae

As a group, palaeopropithecids were apparently mixed fruit and foliage consumers (Table 8). The palaeopropithecids bear strong resemblances in both dental morphology and use-wear signatures to their extant relatives, the indriids. They also exhibit greater variation in their dental use-wear signatures than do modern indriids, suggesting a wider diversity of diets (Tables 5 and 9); Figure 5

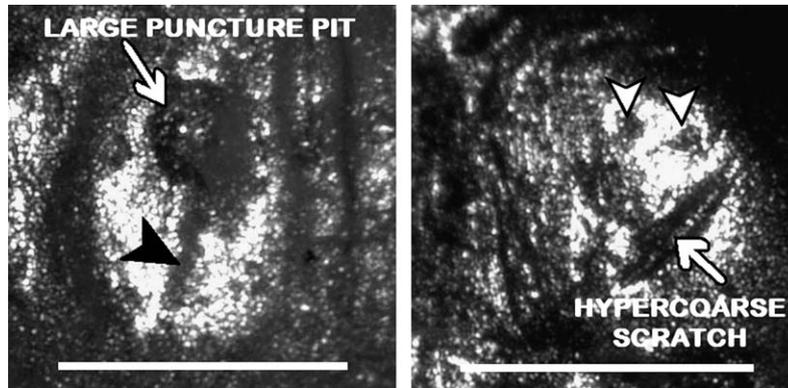


Fig. 3. Selected use-wear features, as seen under a standard stereoscopic microscope at low magnification (50X), in *Archaeolemur* and *Cebus*. Left: *Archaeolemur edwardsi* (UA 5014, M₂, from Ampasambazimba) showing a very large puncture pit and hypercoarse scratch (black arrowhead). Right: *Cebus apella* (MCZ 32173, M₂) showing medium puncture pits (white arrowheads) and a hypercoarse scratch. Scale bar = 0.4 mm.

shows the extremes. Some palaeopropithecids (especially *Babakotia radofilai*, and to a lesser extent *Mesopropithecus dolichobrachion*) exhibit coarse wear, approaching those of committed pitheciin seed predators (such as *Pithecia*, *Cacajao*; see Kinzey, 1992; Barnett and Brandon-Jones, 1997; Lambert and Garber, 1998) or large-bodied, frugivorous hominoids (*Pongo*, lowland gorillas, and *Pan*). Others (*Palaeopropithecus maximus* and other species in this genus) exhibit moderate wear, most like that of extant indriids (*Propithecus*, *Indri*), colobines (*Semnopithecus*, *Trachypithecus*),

or frugivorous cercopithecines (*Macaca fascicularis*, *Papio anubis*). Yet others (especially *Mesopropithecus pithecioides*) exhibit fine wear, suggesting high folivory, as in *Alouatta*, siamangs, or *Avahi*. Unlike the extant indriid, *Avahi*, however, no palaeopropithecid lacks puncture pits entirely; thus it is likely that all were seed predators to varying degrees.

Table 10 confirms highly significant differences among palaeopropithecid genera for almost all use-wear traits. Genus-level pairwise comparisons of members of the palaeopropithecid/indriid clade

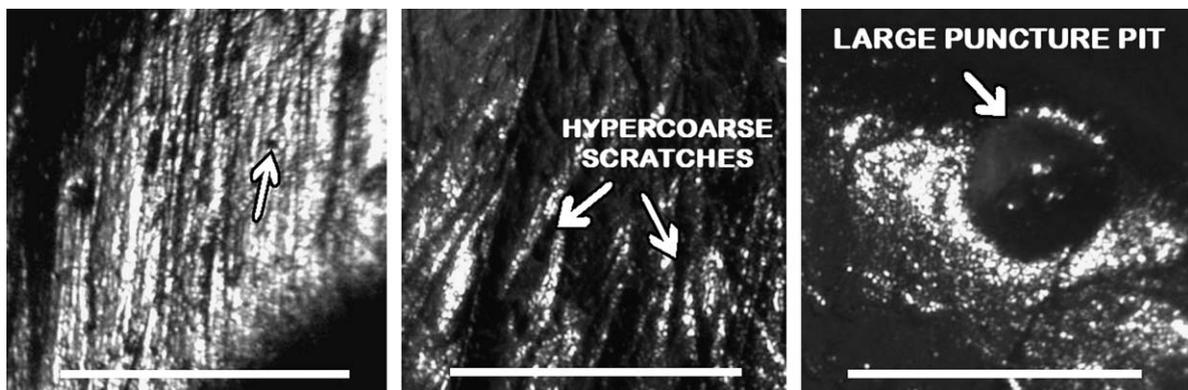


Fig. 4. Selected use-wear features, as seen under a standard stereoscopic microscope at low magnification (50X), in *Theropithecus* and *Hadropithecus*. Left: *Theropithecus gelada*, M₂ (NNM 39132), showing large pit (white arrow) and numerous fine and coarse scratches (white lines). Center: *Hadropithecus stenognathus*, M₂ (VNM 1934 IV.2) from Andrahomana, showing numerous hypercoarse scratches (dark lines). Right: *Hadropithecus stenognathus*, M₂ (UA 5124/AM 6382) from Tsirave, showing large puncture pit and numerous pits, both large (dark) and small (white). Scale bar = 0.4 mm.

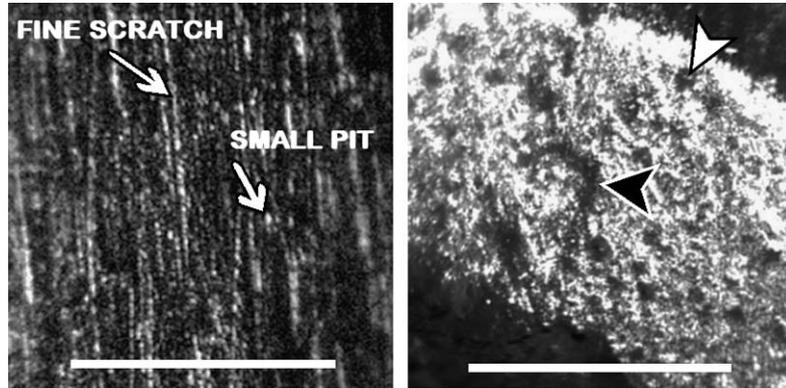


Fig. 5. Selected use-wear features, as seen under a standard stereoscopic microscope at low magnification, in two palaeopropithecoid species. Left: *Archaeoindris fontoynontii* (UA-AM 6239 M², from Ampasambazimba), showing mostly small pits (white) and fine scratches (white), as is typical of a leaf browser. Right: *Babakotia radofilai* (DPC 10994, M², from Ankarana) showing numerous puncture pits (e.g., white arrowhead), as is typical of a hard-object specialist. Note the outline of a large puncture pit near the center of the enamel band (black arrowhead). Scale bar = 0.4 mm.

demonstrate the uniqueness of *Babakotia*. All eleven *Babakotia* individuals in our database have puncture pits. *Babakotia* exhibits significantly wider scratches and more pits than each of the other genera within this clade (with Tukey's HSD post hoc probability levels ranging from < 0.05 to < 0.001). Univariate comparisons (Table 4) reveal similarities to hard-object feeders (*Daubentonia*, *Cebus apella*, *Chiropotes*, *Pithecia*), as well as to other mixed consumers of fruit and seeds (*Ateles*, *Gorilla*, *Pan*, *Macaca*). Multivariate analysis reveals its greatest overall use-wear similarity to *Pithecia*, *Cacajao*, *Pongo*, and lowland gorillas (Table 9); *Daubentonia* and *Chiropotes* also belong to the same "homogeneous subset," as revealed by Tukey's test for Honestly Significant Differences.

Of all the remaining palaeopropithecids, *Mesopropithecus dolichobrachion* exhibits the coarsest use-wear signature. It was, like *Babakotia*, most probably a mixed fruit and foliage feeder and seed cruncher, but unlike *Babakotia*, there is little evidence here of hard-object specialization (Table 8). All eight individuals in our database have puncture pits. The use-wear signature of *M. dolichobrachion* includes many large pits, but most of the puncture pits are small. Its greatest overall similarity (Table 9) is to that of a new (undescribed) species of *Palaeopropithecus*, along with some large-bodied hominoids (*Pan paniscus*) and

cercopithecoids (*Mandrillus leucophaeus* and *Papio anubis*).

Mesopropithecus globiceps was apparently a mixed fruit and foliage feeder with moderate seed predation (Table 3, Table 8). It was not a hard-object specialist. Its overall use-wear profile is most like those of *Indri*, *Palaeopropithecus* (especially *P. ingens*), *Propithecus* (especially *P. verreauxi*), and *Macaca fascicularis* (Table 9). All nine individuals in our database have puncture pits. The frequency of puncture pits on the *Mesopropithecus globiceps* molars in our sample is lower than those of *Mesopropithecus dolichobrachion*, *Babakotia radofilai*, or the new species of *Palaeopropithecus*. This may signal less seed predation and hard-object processing than in the latter group. However, these differences are not significant at $\alpha = 0.05$ (according to Tukey's post hoc test of HSD).

Palaeopropithecus ingens and *P. maximus* have similar use-wear scars (Table 3). These were apparently mixed fruit and foliage consumers and moderate seed predators; neither species appears to have been a hard-object specialist (Tables 8 and 9). Their overall use-wear profiles are most like that of other palaeopropithecids (especially *Mesopropithecus globiceps*), as well as indriids (*Indri indri*, *Propithecus verreauxi*, and *P. diadema*), colobines (*Semnopithecus entellus*, *Trachypithecus obscurus*), and macaques (*M. fascicularis*) (Table 9).

Archaeoindris has the use-wear signature of a classic folivore with fine scratches, low pit frequency, and low scratch frequency (Tables 3 and 8). However, it exhibits moderate evidence of seed predation. There are only four specimens in our sample, and two (a mandible and maxilla) may belong to a single individual (Lamberton, 1934a). Several specimens, like some large-bodied hominoids, have large and medium puncture pits. *Archaeoindris* may have normally treated seeds benignly, but occasionally processed hard foods. However, the narrow width of the scratches and relatively low number of pits suggest that *Archaeoindris* was not a hard-object specialist. Its overall use-wear profile is most similar to those of colobines (e.g., *Colobus polykomos*, *Trachypithecus cristatus*, *Trachypithecus obscurus*), as well as some of the larger-bodied extant indriids (*Propithecus diadema*) (Table 9).

Mesopropithecus pithecoides was similar to *Archaeoindris* in showing signs of leaf consumption with minimal seed predation and only slightly higher fruit consumption (Tables 3 and 6). It was apparently the most strictly folivorous member of its genus. Its scratch and pit frequencies are low; its scratches are fine (or mixed fine and coarse) in texture, and its large pit frequency is low. Only one of the six individuals in our database has any puncture pits. There is some (slight) evidence of seed predation, and no evidence of specialized hard-object exploitation (Table 8). Seed predation was probably less important here than in any other

palaeopropithecoid, as well as some indriids (*Indri* and *Propithecus*). The overall use-wear signature is quite similar to those of extant folivores (e.g., *Alouatta*, *Hylobates syndactylus*, and *Nasalis*; Table 9).

Family Megaladapidae

Our data strongly affirm that all species of *Megaladapis* were leaf-dominated browsers, with use-wear signatures most similar to those of *Avahi*, *Lepilemur*, and *Alouatta* (Tables 4, 8, 9, Figure 6). There is no evidence of seed predation; none of the species of *Megaladapis* has puncture pits. There is also no evidence of rooting behavior in *Megaladapis*. No rooting species (e.g., suids, certain rodents; Semprebon, 2002, unpublished data) exhibits the fine wear seen in the Megaladapidae, and no megaladapid has the heavy gouging and uneven surface topography often seen in rooting species.

Within the Megaladapidae, there is great uniformity of use-wear signatures (Table 10). Those of *Megaladapis madagascariensis* and *M. grandidieri* are virtually identical, and only slightly different from that of *M. edwardsi*. The latter has more pits, large pits, and scratches than does either of its congeners; the scratches are slightly wider. (None of these differences are significant at the 0.05 level.) Qualitatively, then, the overall signature of *M. edwardsi* is more similar to that of the southern sportive lemur, *Lepilemur leucopus*, than to *L. mustelinus* and other sportive lemur species

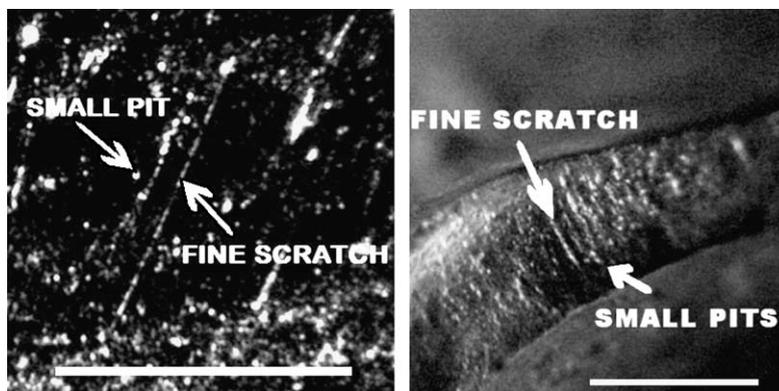


Fig. 6. Selected use-wear features, as seen under a standard stereoscopic microscope at low magnification, in *Megaladapis* and *Lepilemur*. Left: *Megaladapis madagascariensis* (UA 5493, M², from Tsiandroina) showing small pits (white) and fine scratches (white). Right: *Lepilemur mustelinus*, M² (MCZ 16352), showing small pits (white) and fine scratches (white). Scale bar = 0.4 mm.

living in more mesic environments, whereas the opposite is true for *M. madagascariensis* and *M. grandidieri*. *Lepilemur leucopus* displays the same geographic distribution today as *M. edwardsi* did in the recent past. *Megaladapis edwardsi* may have been ecologically dependent on the foods of the spiny and dry scrub forests of southern and southwestern Madagascar.

The virtual identity in use-wear signals of *M. grandidieri* and *M. madagascariensis* is intriguing given the strong evidence for their close relationship; these species are allopatric variants of the same subgenus (Vuillaume-Randriamanantena et al., 1992). The differences between the use-wear signatures of *M. edwardsi* and its congeners, albeit slight and statistically insignificant, suggest possible niche differentiation of *M. madagascariensis* and *M. edwardsi* in the south and southwest, where they were sympatric.

Family Lemuridae

Our data suggest that, like extant lemurids (see, for example, Overdorff, 1993; Freed, 1999; Vasey, 2000), the members of the extinct genus *Pachylemur* were mixed fruit and foliage consumers and not seed predators (Tables 7–9; Figure 7). As in all other lemurids, none of our molar specimens of *Pachylemur* has puncture pits. Of all extant primates sampled here, the closest living analogs to both species of *Pachylemur*, as measured by Euclidean distances between predicted-diet cent-

roids, are other lemurids—*Lemur catta*, *Eulemur collaris*, *Eulemur rubriventer*, *Varecia variegata* (but not *Hapalemur*). Thus, with the exception of the adaptively divergent bamboo lemurids, there is strong phylogenetic commonality in the use-wear signatures of extinct and extant lemurids.

The combination in *Pachylemur* of relatively high frequencies of scratches and large pits may signal a diet that was coarser (perhaps more obdurate) than is typical for other lemurids (cf., Tables 2, 3, and 5). However, there is no use-wear evidence that *Pachylemur* was a hard-object specialist (Table 8). Furthermore, Tukey's post hoc tests for HSD fail to confirm significant differences between *Pachylemur* and other lemurids (except *Hapalemur*) for most use-wear traits. The few significant differences revealed by these tests at the genus level are: (1) more scratches than in *Eulemur* ($p < 0.05$) and *Varecia* ($p < 0.01$), and (2) more large pits than in *Eulemur* ($p = 0.01$). No significant differences between the use-wear signatures of the two species of *Pachylemur* can be discerned on the basis of the samples analyzed here (Table 10). They are virtually identical.

Family Daubentoniidae

No skull of the giant extinct aye-aye has ever been discovered, and there are no known molars. However, there is strong evidence that the extinct *Daubentonia robusta* had adaptations for extractive foraging similar to those of extant aye-eyes

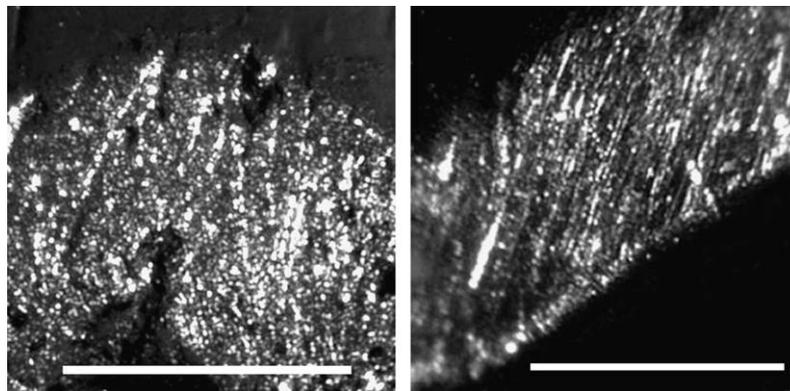


Fig. 7. Selected use-wear features, as seen under a standard stereoscopic microscope at low magnification, in two lemurids. Left: *Pachylemur jullyi* (UA 5287, M², from Ampasambazimba) showing pits and scratches of various sizes, but no puncture pits. Right: *Lemur catta*, M² (AMNH 170743), showing a wear pattern similar to that of *Pachylemur jullyi*. Scale bar = 0.4 mm.

(*D. madagascariensis*) (Lamberton, 1934b; Simons, 1994; Godfrey and Jungers, 2002). The preferred resources of extant aye-eyes are well known from field observations (Iwano and Iwakawa, 1988; Iwano et al., 1991; Sterling, 1994); they include ramy nuts and other hard foods, as well as soft insect larvae. Whereas much of the literature on the diet of aye-eyes has focused on the insect component of the diet, long-term field work has emphasized the importance of hard-object processing, and the latter is clearly registered in the use-wear signature of molars of *D. madagascariensis* (see Tables 2 and 7, Figure 8). These molars are heavily pitted, with many large pits (including puncture pits) and a mixture of coarse and hypercoarse scratches. *Daubentonia robusta* was probably three to five times heavier than *D. madagascariensis* (Godfrey et al., 1995). Given the large size of the extinct species, it is likely that fruit and seeds were important components of the diet of the giant aye-aye as well.

Discussion and conclusions

Our data corroborate some previous reconstructions of the diets of the giant extinct lemurs of Madagascar, but not others. For example, it appears that Godfrey et al. (1997a) were correct in reconstructing the Archaeolemuridae as seed

predators, but incorrect in considering grass a significant component of the diet of *Hadropithecus*. If grass was a major component of the diet of *Hadropithecus*, then its signal was masked by other foods. Our data support the conclusions recently drawn by Rafferty et al. (2002), on the basis of their SEM analysis, that *Hadropithecus* was a hard-object specialist with a diet entirely unlike that of *Theropithecus*. In fact, the pit counts of *Hadropithecus* fall entirely outside the range of variation seen in other primates.

In any case, it is clear that the diet of *Hadropithecus* has been misconstrued for more than three decades. The notion that *Hadropithecus* was graminivorous persists in the literature (Mittermeier et al., 1994; Godfrey et al., 1997a; Nowak, 1999; Garbutt, 1999; Jungers et al., 2002). Jolly (1970, p. 622) was likely correct in characterizing *Hadropithecus* as a “probable” seed predator, but he envisioned a diet similar to that of *Theropithecus gelada*, wherein the seeds being consumed were the small grains of grasses (see Iwamoto, 1993, on *Theropithecus*). Puncture pits do sometimes occur on the molars of gelada baboons, but they are quite small. There is no use-wear evidence that *Hadropithecus* was graminivorous nor that it favored the seeds of grasses.

With regard to *Archaeolemur*, our results differ markedly from those of Rafferty et al. (2002). The latter authors failed to find microwear evidence of

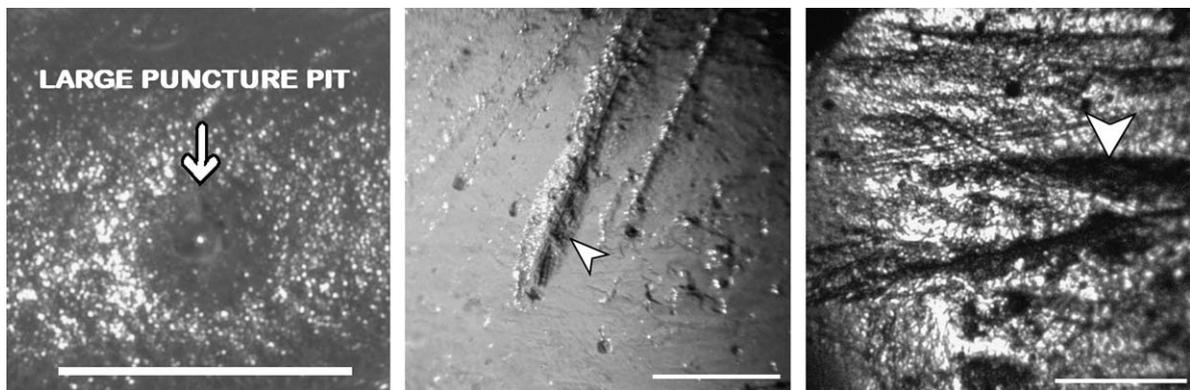


Fig. 8. Selected use-wear features, as seen under a standard stereoscopic microscope at low magnification, in *Daubentonia*. Left: *Daubentonia madagascariensis* (MCZ 16351, M²) showing large puncture pit and numerous other pits. Center and right: (NNM 2386, M²) different regions of the same tooth, showing hypercoarse scratches (white arrowheads). Note polished surface seen in center photo, presumably caused by tooth on tooth attrition when feeding on soft larvae. Scale bar = 0.4 mm.

hard-object specialization in *A. edwardsi*, and they reported some overlap in scratch width and the incidence of pitting in *Archaeolemur* and *Megaladapis madagascariensis*. We find strong evidence of hard-object specialization for all species of *Archaeolemur*, and no evidence of overlap in the use-wear signatures of *Archaeolemur* and *Megaladapis*. Indeed, these genera fall at opposite extremes of the use-wear ecospace summarized by our Euclidean distance matrix (Table 9) and by our principal components analysis of use-wear traits (Table 5).

Our data support the notion that the Palaeopropithecidae were mixed fruit, seed, and foliage consumers (Godfrey et al., 1997a), as are most indriids. However, although Godfrey et al. (1997a) reconstructed *Babakotia* as consuming more seeds than any other palaeopropithecid, and *Archaeoindris* as consuming more leaves, they did not anticipate the hard-object signal we observed in *Babakotia*, nor the intrageneric dietary variation we observed in *Mesopropithecus*. Godfrey et al.'s (1997a) assumption of greater seed predation in *Mesopropithecus* than in *Palaeopropithecus* seems only to hold for *M. dolichobrachion*.

One outcome of our use-wear analysis is the evidence for hard-object processing in species whose teeth have high shearing ratios, and therefore resemble those of classic folivores (see also Yamashita, 1998). Significant foliage consumption has been inferred for the Palaeopropithecidae (including *Babakotia*) on the basis of their sharp shearing crests and high shearing quotients (Jungers et al., 2002). Nevertheless, and in agreement with Rafferty et al. (2002), we find strong evidence for hard-object feeding in *Babakotia*. This suggests that gross external dental morphology may be a poor indicator of hard-object specialization, as this can occur in species with low cusps (*Daubentonia*, *Archaeolemur*, etc.), as well as in species whose molars have pointed cusps and long shearing crests (*Babakotia*).

Our data argue strongly against Mahé's (1976) reconstruction of *Megaladapis* as a piglike rooter (i.e., feeding on roots and tubers). Instead, they lend strong support to reconstructions of *Megaladapis*, based on dental morphology and SEM analysis (Tattersall, 1982; Godfrey et al., 1997a;

Rafferty et al., 2002), as folivorous. They do not, however, support Rafferty et al.'s claim that *M. edwardsi* had the most strictly folivorous diet of any primate species, living or extinct, or that other species of the same genus were seed predators. Godfrey et al.'s (1997a) hypothesis that the Megaladapidae specialized on leaves and avoided seeds is supported by the data collected here.

Our data support Godfrey et al.'s (1997a) interpretation of *Pachylemur* as a highly frugivorous mixed feeder, but not a seed predator. They provide weak support for Seligsohn and Szalay's (1974) inference that *Pachylemur* consumed fewer leaves and more hard stems and fruit than most *Eulemur*, as well as Ravosa's (1992) conclusion that *Pachylemur* may have had a more obdurate diet than does *Varecia*. They do not support Ravosa's (1992) hypothesis that *Pachylemur* consumed a higher percentage of leaves than does *Varecia*.

Our data speak only indirectly to the diet of the extinct aye-aye, *Daubentonia robusta*. Its congener, *D. madagascariensis*, has the use-wear signature of a classic hard-object processor. The surprisingly thick molar enamel of extant aye-ayes (Shellis et al., 1998) is easily understood in this context. We think it likely that the much-larger-bodied extinct form was yet more specialized for hard-object processing than is *D. madagascariensis*. Termite feeding alone cannot explain the peculiar feeding adaptations of *D. robusta* (see Simons, 1994). Iwano et al. (1991) hypothesized, on the basis of ramy species distributions (family Burseraceae), that the extinct species consumed *Canarium pulchrebracteatum*, while the smaller-bodied extant species specializes on *C. boivini* and *C. madagascariensis*.

A final bone of contention is the degree to which extinct lemurs exploited terrestrial food resources in savanna environments (Dewar, 1984; Burney, 1999). We found no use-wear evidence in support of a dominance of terrestrial food resources (C4 grasses, tubers, and roots) in any extinct lemur. There is no evidence in subfossil lemurs of *graminivory* or of *heavy grit* in their diets. None has the heavy gouging often seen in rooting species (such as pigs or certain rodents) outside the order Primates. Rooting does not produce the fine scratches and small pits seen in

the Megaladapidae, nor does it produce the hypercoarse scratches and large, deep, symmetrical “puncture” pits seen in extant hard-object feeders and in the Archaeolemuridae.

It is noteworthy that most of the extinct lemurs exhibit skeletal adaptations for arboreality (see review by Jungers et al., 2002). This suggests a commitment to wooded (though not necessarily closed-forest) habitats. Among the extinct lemurs, the most celebrated candidates for terrestriality (and, therefore, open-habitat exploitation) are *Archaeolemur* and *Hadropithecus* (Walker, 1974; Tattersall, 1982; Godfrey, 1988, Godfrey et al., 1997b, Godfrey and Jungers, 2002). However, strong terrestriality does not preclude a dietary dependence on tree-food resources; indeed, the most terrestrial of living lemurs (*Lemur catta*) is an excellent case in point. The use-wear evidence presented here supports the view that even the most terrestrial of extinct lemurs consumed significant amounts of hard fruit and seeds. Not considered here is the possibility that animal foods, such as gastropods or other molluscs, contributed to the hard-object signal. There is some evidence for omnivory in the Archaeolemuridae (see Burney et al., 1997; Godfrey et al., in press). It is also noteworthy that other extant primate hard-object specialists (such as *Daubentonia madagascariensis* and *Cebus apella*) are fundamentally omnivorous, and that the pit count of *Hadropithecus* falls outside the range of sampled extant primates, suggesting the consumption of something unusual.

Most of Madagascar’s extinct lemurs can be characterized as tree-foliage or mixed fruit and tree-foliage browsers. Whereas it is true that modification of the wooded habitats of Madagascar cannot explain the disappearance of those non-primate megafauna (i.e., giant tortoises, hippopotamuses, and elephant birds) that once dominated Madagascar’s open grasslands (see Dewar, 1984; Burney, 1997, 1999; Burney et al., 2003), it is also obvious that the same does not hold for the large-bodied primates. If the extinct lemurs were primarily tree-foliage or mixed fruit and tree-foliage browsers, then a reduction, invasion, or modification of woodland, thorn scrub, and forest habitats is directly implicated in their extinctions.

Our research leads us to a number of conclusions:

1. There was a significant hard-object-specialist guild among the lemurs of Madagascar. Three families of Malagasy lemurs had at least *some* members that were hard-object specialists. These were the Archaeolemuridae, Palaeopropithecidae, and Daubentoniidae.
2. Distinct families of Malagasy lemurs have characteristic use-wear signatures. The Archaeolemuridae were the most specialized of hard-object feeders. The Palaeopropithecidae, like their extant relatives (the Indriidae), were seed predators (and consumers of foliage and fruit to varying degrees). Extinct lemurids (*Pachylemur* spp.), like their extant relatives, were mixed feeders, but not seed predators. Extinct megaladapids (*Megaladapis* spp.), again like their extant relatives (*Lepilemur* spp.), were leaf browsers.
3. There is no evidence in use-wear signals observed under low magnification that any of the extinct lemurs relied on grasses, roots, and tubers. Like extant lemurs, these species appear to have depended on foods found in wooded environments. The reduction, invasion, or modification of Madagascar’s wooded habitats is implicated in the extinction of the large-bodied lemurs.

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