Evidence for Dietary Niche Separation Based on Infraorbital Foramen Size Variation among Subfossil Lemurs

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Key Words

Infraorbital foramen area • Subfossil lemurs • Paleoecology • Madagascar • Diet

Abstract

The size of the infraorbital foramen (IOF) has been used in drawing both phylogenetic and ecological inferences regarding fossil taxa. Within the order Primates, frugivores have relatively larger IOFs than folivores or insectivores. This study uses relative IOF size in lemurs to test prior trophic inferences for subfossil lemurs and to explore the pattern of variation within and across lemur families. The IOFs of individuals belonging to 12 extinct lemur species were measured and compared to those of extant Malagasy strepsirhines. Observations matched expectations drawn from more traditional approaches (e.g. dental morphology and microwear, stable isotope analysis) remarkably well. We confirm that extinct lemurs belonging to the families Megaladapidae and Palaeopropithecidae were predominantly folivorous and that species belonging to the genus *Pachylemur* (Lemuridae) were frugivores. Very high values for relative IOF area in *Archaeolemur* support frugivory but are also consistent with omnivory, as certain omnivores use facial touch cues while feeding. These results provide additional evidence that the IOF can be used as an informative osteological feature in both phylogenetic and paleoecological interpretations of the fossil record.

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Introduction

The infraorbital foramen (IOF) is located below the inferior margin of the orbit, and transmits the infraorbital nerve (ION) to specialized mechanoreceptors (Pacinian corpuscles, Merkel's disks, and Ruffini corpuscles) associated with the rhinarium, vibrissae (whiskers), and upper lip [Ebara et al., 2002]. The IOF transmits the afferent sensory ION to specialized mechanoreceptors that respond to mechanical stimuli such as tension, pressure, vibration, and displacement [Brecht et al., 1997; Marshall et al., 2006]. Some of these receptors can be found around the vibrissa shaft [Ebara et al., 2002], but others can be found in the upper lip and surrounding maxillary region. The sensory acuity of an anatomical region (e.g. finger tips, palm of hand, lips) correlates with the number of receptors located within a specific region [Kandel et al., 2000; Oelschlager and Oelschlager, 2002; Marino, 2007]. Generally, as the number of receptors associated with a particular anatomical region increases, more nerve innervation (and thus a thicker nerve) is required to transmit the sensory information detected by receptors to the brain [Jonas et al., 1992; Mackinnon and Dellon, 1995; Cull et al., 2003]. Furthermore, nerve area is a reliable estimate of total nerve axon count, as examples from total optic [Jonas et al., 1992; Cull et al., 2003] and hypoglossal [Mackinnon and Dellon, 1995] nerve area show. Mackinnon and Dellon [1995] documented variation in axon densities across an individual nerve, but when total axon count across nerve samples was calculated within a single taxon, they noted that axon count correlated with nerve area. Thus, the relative size of the ION should reflect mechanoreceptive sensory acuity (or touch sensitivity) of the maxillary region. Muchlinski [2008] showed that ION cross-sectional area accounts for 85–90% of the variance in IOF cross-sectional area across a broad selection of mammals. In terms of vascular structures, there is only a relatively small artery that passes through the IOF and no vein is present [Muchlinski, 2008]. Furthermore, IOF and ION cross-sectional area scale isometrically ($\ln \text{ION} = -0.2 + 1.0 \times \ln \text{IOF}$), thus IOF area can be used as a proxy for maxillary mechanoreception in fossils for which nerve size cannot be measured directly.

However, a more refined interpretation of IOF size variation must take into account that mammals use their snouts to explore their environment in different ways. Primates, unlike most other mammals, have relatively small IOFs [Muchlinski, 2010b], which indicates that primates depend less on 'face touch' (maxillary mechanoreception) than most other mammals – most likely a correlate of transferring touch discrimination to the fingers. Nevertheless, facial tactile exploration is important in some primate species. An animal's reliance on maxillary mechanoreception can be affected by its activity pattern (e.g. nocturnality or use of low light conditions [Klages et al., 2002]) or by its preferred substrate (arboreality [Ahl, 1986, 1987]; aquatic/subterranean [Baron et al., 1990]). Among primates, Muchlinski [2010a] established diet as the best predictor of variation in relative IOF size. In particular, relative IOF area distinguishes primate species feeding primarily on leaves or insects (with relatively small IOF areas) from those feeding primarily on fruit (with relatively large IOF areas). Interestingly, Baron et al. [1990] found a similar pattern between the volume of the trigeminal brainstem complex (both sensory and motor) and diet among both primates and soricids. They found that the trigeminal brainstem in folivorous species was smaller than in more frugivorous and insectivorous species. One implication of these findings is that folivores may depend less on max-

illary mechanoreception in food acquisition and processing than do insectivores and frugivores [Baron et al., 1990; Muchlinski, 2010a].

Food selection among primates involves, first, searching out and identifying food, and then contacting and evaluating the food [Dominy, 2004]. Primates locate foods using visual, auditory, and olfactory cues [Dominy et al., 2001]. Insect and leaf evaluation do involve some degree of maxillary mechanoreception [Lucas, 1994; Dominy et al., 2001], but most evaluation occurs in the postcanine oral cavity [Ungar, 2002]. Fruit selection and evaluation are distinct from insect and leaf assessment; in the former, fruit testing depends more heavily on rostral sensory cues [Lucas, 1994; Ungar, 1998; Dominy et al., 2001; Dominy, 2004]. Hands play an important role in evaluating fruit texture, but the premaxillary region is also critical for fruit inspection [Dominy, 2004]. Once a fruit is identified, primates are reported to inspect it haptically with their digits, lips, and incisors, which are all mechanically sensitive [Peleg, 1980]. For example, *Eulemur rubriventer* uses its hands to pull terminal branches with fruit clusters toward its face, whereupon it uses its mouth and lip to evaluate the fruit before selecting and ingesting certain ones [Tecot, 2008]. Many primates bite and taste fruit to determine the stage of maturity of a fruit, because color does not provide a clear indication of fruit edibility [Dominy et al., 2001]. Among anthropoid primates, frugivores have broader and more spatulate incisors than either insectivores or folivores, apparently because husking fruit requires more incisal preparation than either leaf or insect consumption [Ungar, 1998]. High maxillary mechanoreception (and, consequently, larger IOFs) may be an adaptation for fruit selection and evaluation [Muchlinski, 2010a]. Nobody has evaluated how maxillary mechanoreception of omnivorous primates compares with that of primate frugivores, folivores, and insectivores. Although most primates can be described as omnivorous, few are omnivores par excellence, and many of these (e.g. *Daubentonia madagascariensis*, *Cheirogaleus* spp.) can be found on the island of Madagascar.

In this study, we examined, first, whether extant and extinct lemurs show similar distributions in relative IOF area, and whether the relative IOF area differences observed in frugivorous and folivorous extant primates as documented by Muchlinski [2010a] hold for extant lemurs. We then examined variation in relative IOF area within frugivorous lemurs to see whether finer dietary groups could be distinguished, and to verify the utility of our metric in post hoc dietary predictions. Finally, we applied our metric to extinct lemurs to assess the probabilities of dietary group membership, and to determine whether dietary inferences drawn for extinct lemurs on the basis of relative IOF area match prior trophic assessments. If agreement can be demonstrated, results of this study would not merely bolster prior trophic assessments of subfossil lemur species, but they would support the broad utility of IOF area as a tool for dietary inference in extinct primates [Muchlinski, 2010a].

Materials and Methods

We measured the IOFs on 101 skulls belonging to 16 extant Malagasy strepsirhine species in 5 families (table 1). In addition, we measured the IOFs of 30 skulls of individuals belonging to 12 extinct lemur species in the following 4 families: Megaladapidae (2 species), Lemuridae (2 species), Archaeolemuridae (3 species), and Palaeopropithecidae (5 species) (table 1).

Table 1. Species sample sizes, means, and standard deviations for IOF and molar areas

	n	IOF area mm ²	SD	Molar area mm ²	SD
Cheirogaleidae					
<i>Cheirogaleus major</i>	2	1.49	0.31	11.08	0.32
<i>Cheirogaleus medius</i>	4	1.01	0.08	8.16	0.61
<i>Microcebus murinus</i>	8	0.57	0.14	4.53	0.96
<i>Mirza coquereli</i>	1	1.15	–	6.52	–
Daubentoniidae					
<i>Daubentonia madagascariensis</i>	4	2.58	0.43	16.39	0.30
Indriidae					
<i>Avahi laniger</i>	6	0.54	0.24	19.20	0.10
<i>Indri indri</i>	5	1.06	0.31	42.73	1.10
<i>Propithecus edwardsi</i>	4	1.00	0.39	34.26	1.31
<i>Propithecus verreauxi</i>	10	1.83	0.70	41.50	2.52
Archaeolemuridae					
<i>Archaeolemur edwardsi</i> [†]	3	12.16	2.08	74.94	12.97
<i>Archaeolemur majori</i> [†]	8	8.78	2.00	65.02	6.90
<i>Archaeolemur</i> sp. cf. <i>A. edwardsi</i> [†]	3	13.41	1.43	78.68	0.89
Palaeopropithecidae					
<i>Archaeoindris fontoynontii</i> [†]	1	8.56	–	366.86	–
<i>Mesopropithecus globiceps</i> [†]	2	2.38	1.66	50.72	8.60
<i>Babakotia radofilai</i> [†]	1	2.21	–	68.40	–
<i>Palaeopropithecus kelyus</i> [†]	1	4.69	–	194.18	–
<i>Palaeopropithecus maximus</i> [†]	1	8.45	–	232.40	–
Lemuridae					
<i>Eulemur fulvus</i>	10	1.68	0.65	44.49	2.61
<i>Eulemur macaco</i>	10	2.27	0.70	37.76	3.01
<i>Eulemur rubriventer</i>	5	1.54	0.56	43.55	1.75
<i>Hapalemur griseus</i>	7	0.83	0.13	25.02	1.18
<i>Lemur catta</i>	9	1.32	0.48	38.01	2.17
<i>Varecia variegata</i>	10	2.76	0.90	52.95	4.19
<i>Pachylemur insignis</i> [†]	4	5.74	2.16	72.98	8.99
<i>Pachylemur jullyi</i> [†]	1	5.99	–	75.33	–
Megaladapidae					
<i>Megaladapis edwardsi</i> [†]	1	12.49	–	490.00	–
<i>Megaladapis madagascariensis</i> [†]	4	5.18	2.11	267.86	42.90
Lepilemuridae					
<i>Lepilemur mustelinus</i>	6	0.52	0.04	14.71	0.21
[†] Extinct.					

Molds were created of the IOF outlet using a flexible and injectable molding material. These molds were sectioned and photographed under a stereomicroscope. From these images, IOF area (in mm²) was calculated using Scion Image® software (for details see Muchlinski [2010a]).

Among larger more diverse samples, IOF area is positively correlated with body mass ($p < 0.001$) [Muchlinski, 2010a, b], and thus IOF area must be size adjusted before comparisons of

species varying greatly in body size can be made. IOF area does correlate, albeit weakly, with body mass ($p = 0.05$) among the living strepsirhines in our sample. In our living strepsirhine sample, body mass ranges between 0.09 and 6.5 kg. This narrow body mass distribution can partially account for the poor correlation between body mass and IOF area. When the larger subfossil taxa were included in our analysis, we found that IOF area is significantly correlated with body mass ($p < 0.0001$). Based on these findings, IOF area must be size adjusted because larger animals have larger foramina than smaller animals.

To make such an adjustment, we used upper second molar area ('molar area' – i.e., the product of the tooth's maximum mesiodistal and buccolingual diameters) as a measure of size, and calculated the ratio of IOF to molar area for each individual. Size-adjusted IOFs for any given animal is then $\ln(\text{IOF area/molar area})$. Although molar area is often a poor indicator of body mass [Hylander, 1985; Jungers, 1990], it was selected for use here for several reasons. First, molar area measurements were available for each specimen for which IOF area was measured. Secondly, molar area is generally better correlated with body mass than are other cranial measurements, such as skull length [Muchlinski, 2002]. For our sample of 16 extant lemur species, the correlation (Pearson's r) for species means for $\ln$ molar area and $\ln$ body mass is 0.89 ($p < 0.001$). A reduced major axis regression of $\ln$ molar area on $\ln$ body mass for our extant lemur species indicates that molar area scales with slightly negative allometry, but the confidence intervals include isometry ($\ln$ molar area = $2.94 + 0.61 \ln$ body mass; CI = 0.45–0.81). A least-squares regression yields similar results ($\ln$ molar area = $2.95 + 0.58 \ln$ body mass; CI = 0.50–0.67). Ideally, in order to use molar area measurements to correct for variation in body size in extinct lemurs, we should be able to demonstrate isometric scaling for the relationship between molar area and body size across all lemurs. Of course, we cannot measure body mass in extinct lemurs; however, we can estimate their body masses using postcranial measurements, which correlate better than cranial measurements with body mass in extant mammals and indeed in lemurs [Jungers et al., 2008]. A reduced major axis regression of $\ln$ molar area on $\ln$ body mass for our 28 extinct and extant lemur species indicates that molar area scales with slightly negative allometry, but the confidence intervals include isometry ($\ln$ molar area = $3.05 + 0.57 \ln$ body mass; CI = 0.43–0.73). A least-squares regression yields similar results ($\ln$ molar area = $3.12 + 0.54 \ln$ body mass; CI = 0.39–0.67). Within our sample, we find that molar area is within the confidence limits for geometric similarity or isometric scaling (slope = 0.67), which suggests it is an appropriate surrogate for body mass for this sample.

For each extant lemur sampled, we assessed diet using the relevant literature. Each species was first placed in 1 of 2 categories, predominantly folivorous or predominantly frugivorous, on the basis of the percentage of fruit eaten (with fruit defined as any reproductive part of plants, following Muchlinski [2010a]). Kay [1973] suggests that primates with 45% fruit in their diet should be classified as frugivores. We used a more conservative value of $\geq 60\%$. We grouped taxa as frugivores if $\geq 60\%$ of their diet is fruit; if not, taxa were grouped as either folivores or omnivores based on whether the non-fruit portion of the diet was primarily leaves or a combination of food items. Because in Madagascar the protein content of fruit is low [Ganzhorn et al., 2009], Malagasy frugivores must derive their protein from foliage, animals or exudates. Those species for which animal matter is a significant proportion of the diet tend to consume little or no foliage, but exudates may be important dietary components. We therefore subdivided lemur 'frugivores' into 2 groups depending on the degree to which they supplement fruit with foliage versus some combination of animals and exudates (table 2). Our dietary groups effectively reflect variation in the relative amount of foliage in diets, from significant (folivorous) to moderate (frugivorous-folivorous) to little (frugivorous-omnivorous).

Because closely related species are more likely to share ecological and anatomical characteristics than distantly related species, we incorporated phylogenetic information into our analyses. Phylogenetically independent contrasts were calculated using the PDAP:PD-TREE module [Midford et al., 2005] of Mesquite version 2.72 [Maddison and Maddison, 2009]. The phylogenetic branching sequence used here is provided in figure 1. The phylogeny we used reflects the topology for the major clades of extant strepsirhines generated by Horvath et al. [2008] as well as information on sister taxon relationships drawn from the most comprehensive molecular analysis of extinct lemurs [Orlando et al., 2008]. All branch lengths were set to

Table 2. Dietary assessment of extant lemurs, with sources

Family and species	Diet	Notes and sources
Cheirogaleidae		
<i>Cheirogaleus major</i>	OM	Fruit, flowers, nectar, animals [Wright and Martin, 1995; Lahann, 2007; Muldoon and Goodman, 2010]
<i>Cheirogaleus medius</i>	OM	Fruit, nectar, flowers, animals [Hladik et al., 1980; Fietz and Ganzhorn, 1999; Lahann, 2007]
<i>Microcebus murinus</i>	OM	Fruit, arthropods, gums, insect secretions, small vertebrates [Radespiel et al., 2006; Lahann, 2007; Dammhahn and Kappeler, 2008]
<i>Mirza coquereli</i>	OM	Fruit, flowers, gums, insect secretions, insects [Hladik et al., 1980; Pages, 1980; Muldoon and Goodman, 2010]
Daubentoniidae		
<i>Daubentonia madagascariensis</i>	OM	Fruit, nut kernels, nectar, ants, beetle larvae, termites, earwigs [Sterling, 1994; Lhota et al., 2008]
Indriidae		
<i>Avahi laniger</i>	FL	Leaves, buds, twigs [Ganzhorn et al., 1985; Harcourt, 1991; Faulkner and Lehman, 2006]
<i>Indri indri</i>	FL	Young leaves, fruit, flowers and seeds [Powzyck, 1998]
<i>Propithecus edwardsi</i>	FL	Leaves, seeds, fruit [Hemingway, 1998; Powzyck, 1998]
<i>Propithecus verreauxi</i>	FL	Leaves, wood, bark stems, fruit, flowers [Richard, 1974; Richard, 1978; Sailer et al., 1985; Yamashita, 2002; Simmen et al., 2003]
Lemuridae		
<i>Eulemur fulvus</i>	FL	Leaves, wood, bark, stems, fruit, some insects [Sussman, 1974; Gerson, 2000; Vasey, 2000]
<i>Eulemur macaco</i>	FR	Fruit, leaves, some insects, flowers, nectar [Colquhoun, 1997; Andrews and Birkinshaw, 1998; Birkinshaw and Colquhoun, 1998]
<i>Eulemur rubriventer</i>	FR	Fruit, some leaves, insects, flowers [Overdorff, 1996; Tecot, 2008]
<i>Hapalemur griseus</i>	FL	Bamboo, leaves, fruit [Grassi, 2006]
<i>Lemur catta</i>	FL	Leaves, wood, bark, stems, fruit, some insects [Sussman, 1974; Sailer et al., 1985; Sauther, 1991; Yamashita, 2002; Simmen et al., 2003]
<i>Varecia variegata</i>	FR	Mainly fruit [Morland, 1992; Balko, 1998; Ratsimbazafy, 2002]
Lepilemuridae		
<i>Lepilemur mustelinus</i>	FL	Mainly leaves, some wood, bark, stems, fruit and flowers [Richard, 1987; Lehman, 2007]
OM = Omnivorous; FL = folivorous; FR = frugivorous.		

1 for this analysis. Contrasts were uncorrelated with contrast standard deviations [Garland et al., 1999].

Our first task was to compare relative IOF area in extinct and extant Malagasy lemurs using *t* tests, with and without incorporating phylogenetic information. We did this to check the utility of extant lemurs as a comparative database; if the values for extinct lemurs differ significantly from those for extant lemurs (particularly if they fall outside the extant lemur range), then we would be poorly justified in using extant lemur values in diagnosing diets of extinct lemurs. Next, to verify that relative IOF area reflects diet in extant lemurs, we tested the significance of differences among our 3 dietary groups, again with and without incorporating phylogenetic information. We then examined the relative IOF area scores for extinct lemurs, using their Mahalanobis distances from the 3 extant lemur dietary group centroids to classify

Fig. 1. Phylogenetic branching sequence used for the taxa in this study.

each species. Finally, a univariate discriminant function analysis (SPSS v. 14) was used to derive posterior probabilities of membership in the closest dietary group. The mathematical justification for using DFA for this task is equivalent to that for any algorithm that maximizes one sum of squares relative to another, such as classification trees or cluster analysis using Ward's metric (see Fisher [1925, chapt 49] for the classic explication). Fisher [1925] demonstrated that the

Fig. 2. A box-and-whisker plot illustrating the distributions of relative IOF area in extant and extinct Malagasy lemurs. There is no significant difference between these 2 groups.

ANOVA/regression framework enables researchers to create or form optimal groups (maximally separated on some metric – originally Euclidean) using any number of dimensions. Finally, we compared dietary predictions derived in such a manner to prior dietary assessments made using other techniques.

Results

We found no significant difference in the means of relative IOF area for extant and extinct Malagasy lemurs ($t = -0.28$, d.f. = 26, $p = 0.78$; fig. 2). These results hold when variation in relative IOF area is corrected for phylogenetic relatedness ($t = 0.66$, d.f. = 26, $p = 0.52$), and suggest that extant lemurs yield an appropriate comparative database.

Relative IOF area differs significantly in extant Malagasy lemur frugivores and folivores ($t = 4.12$, d.f. = 5.8, $p = 0.01$), with folivores having significantly smaller IOFs. These results hold when phylogenetic information is considered in the analysis ($t = 3.52$, d.f. = 14, $p < 0.001$). Within the group initially identified as extant lemur frugivores, species supplementing fruit primarily with foliage have significantly smaller IOFs than do more omnivorous species. A 3-group ANOVA confirms a strong dietary signal ($F = 91.0$, d.f. = 2.13, $p < 0.001$). Tukey's post hoc tests of honestly significant differences reveal all pairs to differ significantly ($p = 0.03$ for folivores vs. frugivore-folivores, $p < 0.001$ for folivores vs. frugivore-omnivores, and $p < 0.001$ for frugivore-folivores vs. frugivore-omnivores). The biggest differences were between folivores and frugivore-omnivores (fig. 3a). Results do not differ for relationships between phylogenetic contrasts in relative IOF scores and diet ($p = 0.05$ for folivores vs. frugivore-folivores, $p < 0.001$ for folivores vs. frugivore-omnivores, and $p = 0.02$ for frugivore-folivores vs. frugivore-omnivores). Centroid values (with standard deviations) for extant lemur dietary groups are -3.41 ± 0.18 (folivores), -3.04 ± 0.27 (frugivore-folivores), and -1.95 ± 0.15 (frugivore-omnivores).

Table 3 presents mean Mahalanobis distances from each of the 3 group centroids for each extinct lemur species. The smallest distances (suggesting most likely diet) are given in bold; these are also the predicted groups derived by univariate discriminant function analysis (and pictorially represented in figure 3b). The extant

Fig. 3. a Box-and-whisker plot illustrating differences among extant lemur members of the 3 diet groups (* $p < 0.05$; *** $p < 0.0001$). **b** The IOF area values for subfossils.

species post hoc classification success of the discriminant function analysis was 87.5%. Errors of dietary classification were limited to 1 lemurid species (*E. rubriventer*) classified by us as a frugivore but predicted to be a folivore, and 1 indriid species (*Propithecus verreauxi*) classified by us as a folivore but predicted to be a frugivore. No omnivores were misclassified by the discriminant function.

Posterior probabilities for extinct lemur membership in their ‘most likely’ dietary groups are provided in table 4, which also compares our results to those of prior studies. The general agreement is clear. *Archaeolemur edwardsi*, *Archaeolemur major*, and *Archaeolemur sp.* cf. *A. edwardsi* fall conspicuously within the frugivore-omnivore distribution. *Pachylemur jullyi* and *Pachylemur insignis* fall in the middle of the extant lemur frugivore-folivore distribution. *Mesopropithecus globiceps* also lies within the frugivore-folivore distribution. *Palaeopropithecus maximus*, *Babakotia radofilai*, *Megaladapis edwardsi*, and *Palaeopropithecus kelyus* all have significantly lower relative IOF scores than all extant Malagasy lemur frugivores and resemble stricter extant lemur folivores. *Archaeoindris fontoynontii* and *Megaladapis madagascariensis* fall below the extant lemur folivore distribution, with very small relative IOF sizes, suggesting little reliance on facial touch sensitivity, and a high percentage of foliage in their diets.

Table 3. Mahalanobis distances to extant lemur dietary group centroids

Species	Mahalanobis distance to		
	FL centroid	FR-FL centroid	FR-OM centroid
<i>Archaeolemur edwardsi</i>	8.77	4.43	0.86
<i>Archaeolemur majori</i>	7.76	3.76	0.34
<i>Archaeolemur</i> sp. cf. <i>A. edwardsi</i>	9.04	4.61	1.18
<i>Archaeoindris fontoynontii</i>	1.89	2.63	11.79
<i>Mesopropithecus globiceps</i>	1.95	0.08	7.23
<i>Babakotia radofilai</i>	0.10	1.44	9.66
<i>Palaeopropithecus kelyus</i>	1.70	2.50	11.56
<i>Palaeopropithecus maximus</i>	0.55	1.01	8.89
<i>Pachylemur insignis</i>	4.79	1.80	3.86
<i>Pachylemur jullyi</i>	4.85	1.84	3.79
<i>Megaladapis edwardsi</i>	1.41	2.31	11.21
<i>Megaladapis madagascariensis</i>	2.93	3.31	13.01

The smallest distances (suggesting most likely diet) are given in bold. FL = Folivorous; FR = frugivorous; OM = omnivorous.

Discussion

This study confirms significant differences in the relative IOF sizes of folivorous and frugivorous lemurs, and further demonstrates a highly significant difference in the relative IOF sizes of frugivorous lemurs supplementing fruit with leaves and those depending more on animals and/or exudates as sources of protein, with the latter group (our ‘frugivore-omnivores’) exhibiting relatively larger foramina. Malagasy omnivores differ markedly from insectivorous primates outside Madagascar, which tend to have relatively small IOFs [Muchlinski, 2008, 2010a, b]. The critical factor may be the manner in which food is procured, and the importance of facial tactile exploration of foods. Whereas primates in general have relatively small IOFs due to the transfer of touch discrimination from the face to the hands, the primate species with the relatively largest IOFs are the omnivorous lemurs of Madagascar. Among non-primates, facial specializations related to food exploration, and indeed food manipulation, occur in omnivores as well as herbivores. Furthermore, the living omnivorous lemurs are really primarily frugivores that supplement fruit with insects, other arthropods, gums, vertebrates, and/or insect secretions in order to reach their protein quotient; none is a classic visually directed predator of solitary flying insects [Rasmussen and Sussman, 2007].

We hypothesize that, when animals depend on sensory signals from their vibrissae and anterior dentition to explore objects of dietary interest, they tend to have exceptionally large IOFs. Among lemurs, the cheirogaleids and *Daubentonia* may fit this description. Of particular interest are those species that regularly engage in bark gouging or extractive foraging. Unfortunately, little is known about the role that facial touch sensitivity plays in the feeding ecology of these animals, and experimental research is lacking.

Table 4. Dietary inferences for subfossil lemurs based on relative IOF size, with comparisons to inferences drawn in prior studies

Species	Prior dietary assessments	Predicted diet (this paper)	Probability of membership in assigned group, %
<i>Archaeolemur edwardsi</i>	<ul style="list-style-type: none"> – Frugivore, mainly fruit with hard pericarps [Tattersall, 1973, 1982] – Mainly fruit and seeds, some leaves and fauna [Godfrey et al., 1997] – Hard object processor, <i>Cebus apella</i> or <i>Daubentonia madagascariensis</i>-like omnivore [Godfrey et al., 2004, 2005] – Varied, only facultatively a hard-object feeder [Ravosa, 1991; Rafferty et al., 2002; Scott et al., 2009] 	FR-OM	100
<i>Archaeolemur majori</i>	<ul style="list-style-type: none"> – Frugivore, mainly fruit with hard pericarps [Tattersall, 1973, 1982] – Mainly fruit and seeds, some leaves and fauna [Godfrey et al., 1997] – Hard objects, <i>Cebus apella</i> or <i>Daubentonia madagascariensis</i>-like omnivore [Godfrey et al., 2004, 2005] – Varied, only facultatively a hard-object feeder [Ravosa, 1991; Rafferty et al., 2002; Scott et al., 2009] 	FR-OM	100
<i>Archaeolemur</i> sp. cf. <i>A. edwardsi</i>	<ul style="list-style-type: none"> – Frugivore [Tattersall, 1973] – Mainly fruit and seeds, some leaves and fauna [Godfrey et al., 1997] – Hard object processor, <i>Cebus apella</i> or <i>Daubentonia madagascariensis</i>-like omnivore [Godfrey et al., 2004, 2005] – Omnivore, generalist [Burney et al., 1997; Vasey et al., in press] 	FR-OM	100
<i>Archaeoindris fontoynontii</i>	<ul style="list-style-type: none"> – Highly folivorous [Godfrey et al., 1997, 2004] 	FL	99.6
<i>Mesopropithecus globiceps</i>	<ul style="list-style-type: none"> – Folivore, some fruit and seeds [Godfrey et al., 1997] – Mixed fruit, seeds, and foliage [Godfrey et al., 2004] 	FR-FL	84.6
<i>Babakotia radofilai</i>	<ul style="list-style-type: none"> – Folivore, some fruit and seeds [Godfrey et al., 1997] – Mixed fruit, seeds, and foliage, some hard objects [Rafferty et al., 2002; Godfrey et al., 2004] 	FL	89.5
<i>Palaeopropithecus kelyus</i>	<ul style="list-style-type: none"> – Mixed fruit, seeds, and foliage [Godfrey et al., 2004] 	FL	99.4
<i>Palaeopropithecus maximus</i>	<ul style="list-style-type: none"> – Folivore, some fruit and seeds [Ravosa, 1991; Godfrey et al., 1997; Rafferty et al., 2002] – Mixed fruit, seeds, and foliage [Godfrey et al., 2004] 	FL	71.6
<i>Pachylemur insignis</i>	<ul style="list-style-type: none"> – Frugivore, hard fruits [Seligsohn and Szalay, 1974] – Highly frugivorous [Godfrey et al., 2004] – Tougher or more obdurate than foods of closest relatives [Ravosa, 1991, 1992] 	FR-FL	81.2
<i>Pachylemur jullyi</i>	<ul style="list-style-type: none"> – Highly frugivorous [Godfrey et al., 2004] 	FR-FL	75.8
<i>Megaladapis edwardsi</i>	<ul style="list-style-type: none"> – Folivore [Tattersall, 1982; Godfrey et al., 1997; Jungers et al., 2002; Rafferty et al., 2002; Scott et al., 2009] – Highly folivorous [Godfrey et al., 2004] 	FL	99.0
<i>Megaladapis madagascariensis</i>	<ul style="list-style-type: none"> – Folivore [Tattersall, 1982; Godfrey et al., 1997; Jungers et al., 2002; Rafferty et al., 2002; Scott et al., 2009] – Highly folivorous [Godfrey et al., 2004] 	FL	99.9

FR = Frugivorous; OM = omnivorous; FL = folivorous.

Nevertheless, some supporting observations exist. Consider the case of *Daubentonia*, the aye-aye, which has been described as a consumer of ‘structurally defended’ resources. These animals have unique morphological specializations (an ever-growing anterior dentition, a filiform middle finger and elongated fourth digit used in scraping) to assist in harvesting larvae from dead wood [Sterling, 1993; Lhota et al., 2008]. They use both auditory and olfactory cues to ‘mine’ for wood-boring lepidopterans and coleopterans [Erickson, 1994; Erickson, et al., 1998], and indeed are unusual among primates in their use of self-generated acoustical cues during foraging [Erikson, 1995]. Given that their targeted foods are often hidden (or ‘structurally defended’), visual cues are likely unimportant, but neither can auditory or olfactory cues explain their enlarged IOFs. Indeed, only sensory cues can explain variation in the relative size of the IOF.

In *Daubentonia*, the upper lip is immobile. However, unlike many primates, including other strepsirrhines, *Daubentonia* has long vibrissae, which are organized in a fashion similar to rodents [Muchlinski, 2010b; S. Lhota, pers. commun.]. While foraging, aye-ayes often position their faces close to the objects being explored (dead or living wood, or fruits with hard exocarps), at such a distance that the long vibrissae come into direct and continual contact with the surface [S. Lhota, pers. commun.]. In so doing, they may be able to use their vibrissae while tapping with their third digits [Lhota et al., 2008] to: (1) interpret reverberations of sound (or echoes) in the air-filled tunnels created by insects; (2) sense vibrations caused by movements of lepidopteran and coleopteran larvae within those tunnels, and perhaps (3) locate the best places to drill into fruits with targeted flesh or kernels. We propose that facial touch sensitivity is critically important to foraging aye-ayes, and that their enlarged IOFs reflect that importance. We further suggest that facial touch sensitivity is important to bark gougers (including exudate feeders) more generally, and to other extractive foragers that use their mouths and anterior teeth as exploratory and preparatory tools.

With regard to the subfossil lemurs, perhaps the most significant finding of our research is that all 3 species of *Archaeolemur* have relatively large IOFs, contrasting sharply with species at the opposite extreme of the spectrum (*M. madagascariensis*, *A. fontoynontii*, *P. kelyus*, and *M. edwardsi*). This constitutes independent corroboration of the hypothesis that *Archaeolemur* was omnivorous while the megaladapids and most of the palaeopropithecids were folivores (table 4). Also supported by our data is the hypothesis that both species of *Pachylemur* were frugivorous [Godfrey and Irwin, 2007; Crowley et al., 2011]. Of the palaeopropithecids, only *Mesopropithecus* falls squarely within range of extant lemur frugivores supplementing fruit with foliage. Its relative IOF value is similar to that of *P. verreauxi*, a physiological folivore [Campbell et al., 2000] that sometimes consumes considerable fruit, and that also falls in the middle of the extant lemur frugivore range. Stable carbon isotope data support niche separation for *Mesopropithecus* and *Propithecus*, with the former likely consuming more CAM or C4 plants [Crowley et al., 2011]. Nevertheless, relatively high fruit (or seed) consumption is not implausible for *Mesopropithecus*. Leaves appear to have been the resource favored by most, if not all, other palaeopropithecids and all megaladapids examined here. Interestingly, the giant lemurs found to be most extreme in terms of having the relatively smallest IOFs (*Megaladapis* and *Archaeoindris*) match perfectly those taxa found to have dental topographic features (‘complexity’ and ‘Dirichlet normal energy’, a metric being developed for dental surface

analysis by Jonathan Bunn and colleagues) most like those of extant lemurs specializing on tree foliage (*Lepilemur* and *Avahi*), while *Archaeolemur* resembles *Daubentonia* in its dental topographic complexity and Dirichlet normal energy measurements [Godfrey et al., 2010; Bunn et al., in press; see also Evans et al., 2007, for an explanation of ‘complexity’ or ‘orientation patch count’ measurements].

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