RESEARCH ARTICLE

What did *Hadropithecus* Eat, and Why Should Paleoanthropologists Care?

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Over 40 years ago, Clifford Jolly noted different ways in which *Hadropithecus stenognathus* converged in its craniodental anatomy with basal hominins and with geladas. The Malagasy subfossil lemur *Hadropithecus* departs from its sister taxon, *Archaeolemur*, in that it displays comparatively large molars, reduced incisors and canines, a shortened rostrum, and thickened mandibular corpus. Its molars, however, look nothing like those of basal hominins; rather, they much more closely resemble molars of grazers such as *Theropithecus*. A number of tools have been used to interpret these traits, including dental microwear and texture analysis, molar internal and external morphology, and finite element analysis of crania. These tools, however, have failed to provide support for a simple dietary interpretation; whereas there is some consistency in the inferences they support, dietary inferences (e.g., that it was graminivorous, or that it specialized on hard objects) have been downright contradictory. Cranial shape may correlate poorly with diet. But a fundamental question remains unresolved: why do the various cranial and dental convergences exemplified by *Hadropithecus*, basal hominins, and *Theropithecus* exist? In this paper we review prior hypotheses regarding the diet of *Hadropithecus*. We then use stable carbon and nitrogen isotope data to elucidate this species' diet, summarizing earlier stable isotope analyses and presenting new data for lemurs from the central highlands of Madagascar, where *Hadropithecus* exhibits an isotopic signature strikingly different from that seen in other parts of the island. We offer a dietary explanation for these differences. *Hadropithecus* likely specialized neither on grasses nor hard objects; its staples were probably the succulent leaves of CAM plants. Nevertheless, aspects of prior hypotheses regarding the ecological significance of its morphology can be supported. Am. J. Primatol. 9999:1–15, 2015.   © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

Hadropithecus stenognathus, a recently extinct giant lemur (Primates, Archaeolemuridae) from Madagascar, bears remarkable resemblance in its cranial morphology and dental proportions to basal hominins (especially robust australopiths such as *Paranthropus boisei* and *P. robustus*) [Ryan et al., 2008] and in its molar occlusal morphology to grazing mammals such as geladas (*Theropithecus*), capybaras (*Hydrochoerus*), hippopotamuses (*Hippopotamus*), and kangaroos (*Macropus*) (Fig. 1). Like basal hominins, *Hadropithecus* has a short face, small and orthally implanted upper and lower incisors, small canines, early fusion of the mandibular symphysis, thick mandibular corpus, flaring zygoma, molariform posterior premolars and large and bucco-lingually expanded molars. Its mandibular ascending ramus is tall so that the temporomandibular joint is raised high above the mandibular occlusal plane. In contrast, its molar occlusal morphology looks nothing like that of a basal hominin. Its relatively tall cusps and crests form complex flat ribbons of enamel that retain sharp edges as they wear. Its enamel is only moderately thick (as in *Theropithecus*) and its enamel
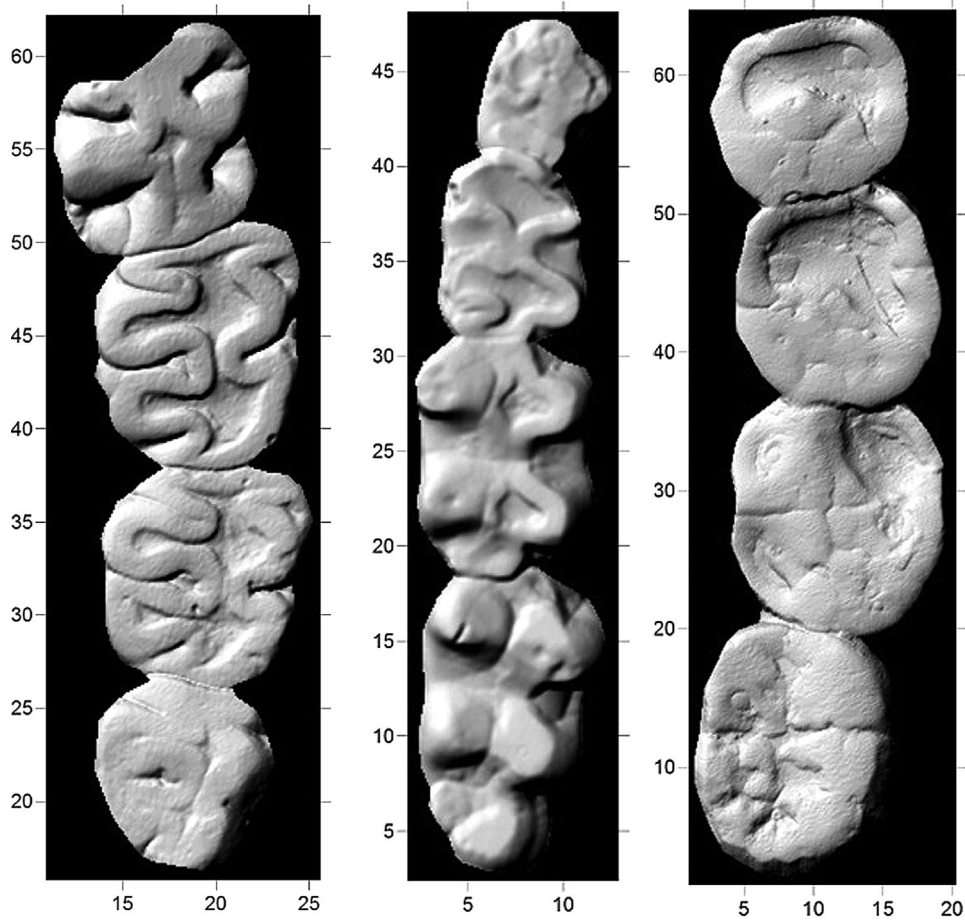
Fig. 1. Casts of mandibular cheek teeth (p4-m3) of (left to right) *Hadropithecus stenognathus* (left hemi-mandible mirror-imaged to look right, MNHN 1925-13, from Ambovombe, southern Madagascar), *Theropithecus gelada* (right hemi-mandible, AMNH 80126), and *Paranthropus boisei* (Peninj mandible). Note complex unguliform enamel folds in *Hadropithecus* and *Theropithecus*.

prisms are only weakly decussated [Godfrey et al., 2005]. Understanding how an animal with molars so similar to those of geladas and other grazers might also converge so strongly in cranial architecture, incisor and canine reduction, P4 molarization, and molar hypertrophication with basal hominins is clearly of paleoanthropological significance.

At least four hypotheses have been proposed to account for the morphological convergences of *Hadropithecus* with hominins, geladas, or both. Most have focused on diet, some more on the metric properties of food items, and others more on their material properties.

While not entirely mutually exclusive, these hypotheses do differ considerably.

H1 : *Hadropithecus* was graminivorous. Shortly after *Hadropithecus* was first described [Lorenz von Liburnau, 1899], Forsyth-Major [1900] concluded on the basis of its molar morphology that it was a grazer. In his monograph of this extinct lemur, Lamberton [1938] drew the same conclusion, citing similarities in molar morphology to the molars of hippos, while also describing postcranial similarities to monkeys, and cranial similarities to fossil and living humans.

H2 : *Hadropithecus* was a small-object feeder. Jolly [1970] embraced the notion that *Hadropithecus* ate grasses, but he proposed a somewhat broader concept to simultaneously explain this animal's dental convergence with grazers such as *Theropithecus gelada* and cranial convergences with basal hominins [see also Tattersall, 1973]. In effect, Jolly identified an adaptive complex involving extreme terrestrialism and a diet of small, tough food objects, which, he argued, could account for the dental and cranial differences between *Hadropithecus* and its sister taxon, *Archaeolemur*, just as it could account for parallel differences between *Theropithecus* and *Papio* or *Mandrillus*, and between *Australopithecus* and *Pan*. Small food items, he argued, do not require heavy incisal preparation but may require heavy repetitive mastication.

Specifically for *Hadropithecus*, Jolly [1970] argued, "By analogy with living forms, it seems likely that *Archaeolemur* fed mainly upon relatively large food-items, probably mostly fruit, requiring incisal preparation, while the diet of *Hadropithecus* was centred upon the stems, rhizomes, and probably also seeds of grasses, which, being a primate and lacking front teeth adapted for grazing, it presumably picked up by hand" (p. 622).

H3 : *Hadropithecus* was a hard-object feeder. Studies of dental microwear using scanning electron microscopy [Rafferty et al., 2002] and low magnification [Godfrey et al., 2004], as well as studies of microwear "texture" using confocal microscopy [Scott et al., 2009], all supported hard-object feeding for *Hadropithecus*. Stress-limited (hard) foods (such as nuts or certain seeds) can be large or small; they are simply foods that fail under the high loads required to fracture them. While the enamel of *Hadropithecus* was quite a bit thinner than that of its sister taxon, *Archaeolemur* (and thinner than fossil hominins) [Godfrey et al., 2005], its relative enamel thickness overlapped that of orangutans; thus, hard-object feeding could not be ruled out on this basis. Baab et al. [2014] found weak support for the hypothesis that diet accounts for variation in skull form in subfossil and living lemurs; however, they found that diet does a better job of accounting for such variation when *Hadropithecus* is scored as a hard object feeder than when this species is scored as a consumer of small, tough objects.

H4 : *Hadropithecus* was a bulk-food feeder, consuming large quantities of foods high in structural carbohydrates and poor in nutrients, requiring heavy repetitive trituration. In some ways, this hypothesis is similar to Jolly's [1970] except that it does not specify a preference for grass leaves, rhizomes, or seeds of grasses. The notion that *Hadropithecus* was, after all, a consumer of small, tough foods (that are displacement-limited rather than stress-limited) was championed by Dumont et al. [2011] on the basis of a finite element analysis (FEA) of the skulls of *Hadropithecus* and *Archaeolemur*, and by Godfrey et al. [2012] on the basis of *Hadropithecus*' dental "complexity" (orientation patch count rotated, OPCR) and Dirichlet Normal Energy (DNE, a measure similar to occlusal relief). The only other lemur with similar values for OPCR and DNE is *Prolemur simus*, the greater bamboo lemur. By manipulating the scanned models of the skulls and jaws of *Hadropithecus* and *Archaeolemur*, Dumont et al. [2011] demonstrated that the former had a significantly smaller maximum gape. FEA demonstrated less structural strength in the skull of *Hadropithecus* than in *Archaeolemur* under specified loading conditions (P4 biting at maximum gape, M2 biting at maximum gape), whether or not scaled to equal body size. On the other hand, *Hadropithecus* had greater mechanical advantage in converting muscle force to bite force (especially for its molars). Dumont et al. [2011] therefore interpreted the craniofacial and dental features of *Hadropithecus* as adaptations for withstanding repetitive loads. They also interpreted the "hard-object" signal found in microwear and enamel surface texture analysis as possibly related instead to high grit in open environments. Constantino et al. [2012] effectively supported this idea. They estimated the maximum bite forces (critical failure loads) of *Hadropithecus*, *Archaeolemur* and other subfossil lemurs using dental fracture mechanics (taking into consideration tooth size and absolute enamel thickness). They found maximum bite force in *Hadropithecus* to be comparable to that of modern *Homo sapiens*, slightly lower than that of the largest-bodied *Archaeolemur* (*A. edwardsi*), and considerably lower than those of basal hominins (especially *Paranthropus*). They concluded on this basis that *Hadropithecus* was not a hard-object processor.

Testing the above hypotheses requires understanding more precisely what *Hadropithecus* ate. Stable isotope analysis can help us do exactly this. On the basis of its high stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values, Crowley & Godfrey [2013] posited a diet for *Hadropithecus stenognathus* rich in Didiereoideae (a subfamily of spiny succulent plants that is endemic to Madagascar). In southwestern Madagascar, these succulent plants, which rely on Crassulacean Acid Metabolism (CAM), have high $\delta^{13}C$ values [Crowley & Godfrey, 2013; Kluge et al., 1991; 1995]. Additionally, Didiereoideae consumption fits the isotopic signal of *Hadropithecus* better than C_4 plants in southern Madagascar. Whereas *Hadropithecus* and *Alluaudia* (a genus of Didiereoideae) both have high $\delta^{15}N$ values, grasses have low $\delta^{15}N$ values [Crowley & Godfrey, 2013]. However, in the Central Highlands of Madagascar (hereafter CH) where Didiereoideae do not exist, isotope values for *Hadropithecus* are strikingly different from those from sites in the dry south—the Spiny Thicket (ST) and Succulent Woodland (SW) ecoregions.

Here we expand our sample of isotope data for giant lemurs and other subfossil species from the CH, and we present new comparative analyses. We do so with two primary objectives. First, we seek to better understand how *Hadropithecus* differs from other species in its stable isotope values within and across ecoregions. We focus particularly on how individuals from the CH differ from individuals in the ST and

SW. We then pool our samples for each genus across ecoregions, and compare *Hadropithecus* to (1) other extinct lemurs, and (2) extinct hippopotamuses and elephant birds. To better understand isotopic variability, we also compare *Hadropithecus* to *Microcebus* (mouse lemurs), which is a well-studied extant lemur genus with a large available stable isotope database [Crowley et al., 2011b, 2013, 2014]. Our second primary objective is to explain geographic variation in the $\delta^{13}C$ values of *Hadropithecus*. We expect $\delta^{13}C$ values in bone to be influenced by diet, and thus to be strongly correlated with the isotope values of consumed plants; if this is the case, we can use the pattern of correlation between plant and *Hadropithecus* $\delta^{13}C$ values to develop a list of candidate plants for consumption by this species. We also expect plant carbon isotope values to be influenced by soil salinity, light, moisture, and temperature [Amundson et al., 2003; Crowley et al., 2011b; van der Merwe & Medina, 1991], all of which may be correlated with elevation and latitude. Our goal is to determine which environmental variables best explain geographical variation in the carbon isotope values for *Hadropithecus*, and to identify candidate food plants that are (1) eaten by living lemurs, and (2) have $\delta^{13}C$ values that vary in a manner that is consistent with geographic isotopic variation for *Hadropithecus*.

METHODS

We compiled previously published collagen $\delta^{13}C$ and $\delta^{15}N$ isotope data for bones from giant lemurs and hippopotamuses, and collagen $\delta^{13}C$ values for bones and eggshells from elephant birds from the ST and SW ecoregions [Berger et al., 1975; Burney, 1999; Burney et al., 2004; Clarke et al., 2006; Crowley et al., 2012; Crowley & Godfrey, 2013; MacPhee, 1986]. To these data we added new isotope data from subfossil lemurs, hippopotamuses (Hippopotamidae), and elephant birds (Aepyornithidae), concentrating on specimens from the CH (Table I). We also assembled published stable isotope data for extant *Microcebus* fur from the ST, SW, and CH [Crowley et al., 2011b, 2013, 2014].

We included in our study all extinct lemur genera represented by 10 or more individuals as well as other extinct Madagascan megafauna with comparable samples. Our final dataset comprises $\delta^{13}C$ and associated $\delta^{15}N$ values (when available) for *Hadropithecus* ($n = 11$), *Archaeolemur* ($n = 31$), *Megaladapis* ($n = 25$), *Pachylemur* ($n = 27$), *Palaeopropithecus* ($n = 35$), hippopotamuses ($n = 20$), elephant birds ($n = 10$), and *Microcebus* ($n = 463$). We excluded *Mesopropithecus* spp., *Daubentonia robusta*, and *Archaeoindris fontoynontii* because of small sample sizes. Our *Hadropithecus* sample comes from five subfossil sites: Ampasambazimba (CH), Ankilibehandry (SW), Tsirave (SW), Anavoha (ST), and Andrahomana (ST) (see Fig. 2). Because the isotope data for *Microcebus* were collected from fur samples, we converted the fur values to look like subfossil collagen before comparing them to values of subfossil lemurs by (1) adding +0.9‰ to carbon and +0.8‰ to nitrogen isotope values (to allow for the average apparent enrichment between these two tissues in primates [Crowley et al., 2010]); and then (2) adding an additional +1.2‰ to fur carbon isotope values (to allow for the isotopic changes in atmospheric CO_2 resulting from the burning of fossil fuels in the Southern Hemisphere [Keeling et al., 2010]).

New subfossil isotope data (Table I) were generated following Crowley et al. [2011a]. We isolated collagen from the subfossil bone samples by decalcifying approximately 200 mg of each fragmented sample in 0.5 M EDTA for 10 days at 4 °C. We replaced the EDTA, sonicated the samples, and allowed them to sit an additional 10+ days at room temperature. We then rinsed the samples ten times using ultrapure water. We gelatinized the samples in 0.01 N HCl at 70 °C for 15 hr, filtered them using Whatman 1.5 μm glass fiber filters, and dried them under vacuum. Following sample treatment, we weighed 0.7 mg of collagenous residue into tin boats, combusted them, and analyzed their $\delta^{13}C$ and $\delta^{15}N$ values on a ThermoElectron (Finnigan) Delta-XP continuous flow system connected to an Elemental Analyzer at the University of California, Santa Cruz Stable Isotope Laboratory. Collagen preservation was evaluated using sample yield, isotope values, and elemental ratios [Ambrose, 1990].

We had previously compiled from the literature and from Google Earth a database that included latitude, longitude, and elevation for subfossil sites in Madagascar [Muldoon & Godfrey, 2013]. Using these data, we were able to extract estimated monthly site-specific rainfall and temperature data for the past 100 years from the online WorldClim database [Hijmans et al., 2005]. We selected January and July values for temperature and rainfall to represent austral summer and winter extremes, respectively. We also coded each site for soil salinity on the basis of its proximity to the coast (coastal sites are more saline than inland sites) using a simple binary code (coastal vs. inland). Finally, we compiled $\delta^{13}C$ values from the literature for both C_3 and CAM plants from localities in the vicinity of *Hadropithecus* subfossil sites (Table II).

Plant isotope data were derived from multiple plant parts (leaves, fruits, and seeds). All plant $\delta^{13}C$ values were adjusted for fractionation between herbivore collagen and diet (+5‰) [Ambrose and Norr, 1993; Crowley et al., 2011b; Kellner & Schoeninger, 2007; Koch et al., 1991; Sullivan & Krueger, 1981; van der Merwe, 1989; Vogel, 1978] and for changes in atmospheric CO_2 (+1.2‰) [Keeling et al., 2010]. Geographic distributions of candidate plants that may have been consumed by

TABLE I. New Collagen Isotope Data for This Study

Ecoregion	Site name	Type	Genus and species	Specimen ID	Element	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Atomic C:N
CH	Ampasambazimba	Lemur	*Archaeolemur edwardsi*	UA 1177	Ulna	−22.4	8.2	3.3
CH	Ampasambazimba	Lemur	*Archaeolemur edwardsi*	UA 1203	Radius	−22.8	6.8	3.3
CH	Ampasambazimba	Lemur	*Archaeolemur edwardsi*	UA 1153	Femur	−22.9	6.2	3.4
CH	Ampasambazimba	Lemur	*Archaeolemur edwardsi*	UA 1204	Ulna	−15.5	6.2	3.5
CH	Ampasambazimba	Lemur	*Archaeolemur edwardsi*	UA 1159	Humerus	−21.5	7.2	3.3
CH	Ampasambazimba	Lemur	*Archaeolemur edwardsi*	UA 1158	Humerus	−20.8	7.5	3.3
CH	Ampasambazimba	Lemur	*Hadropithecus stenognathus*	UA Uncat.	Tibia	−27.1	2.7	4.6
CH	Ampasambazimba	Lemur	*Hadropithecus stenognathus*	UA 5164	Femur	−21.3	7.8	3.4
CH	Ampasambazimba	Lemur	*Megaladapis grandidieri*	UA 3984	Ulna	−22.7	8.3	3.3
CH	Ampasambazimba	Lemur	*Megaladapis grandidieri*	UA 8688	femur	−21.7	8.0	3.2
CH	Ampasambazimba	Lemur	*Megaladapis grandidieri*	UA7914	Humerus	−21.8	8.7	3.3
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 1667	Humerus	−22.8	8.4	3.3
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 1708	Humerus	−22.6	4.9	3.2
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 2933	Femur	−21.7	9.2	3.2
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 1733	Humerus	−23.0	7.3	3.2
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 1709	Humerus	−22.8	9.0	3.3
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 1772	Femur	−22.1	9.3	3.3
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 1780	Femur	−23.7	9.4	3.4
CH	Ampasambazimba	Lemur	*Pachylemur jullyi*	UA 1675	Femur	−22.0	6.1	3.4
CH	Ampasambazimba	Lemur	*Palaeopropithecus maximus*	UA 3833	Tibia	−22.3	9.3	4.2
CH	Ampasambazimba	Lemur	*Palaeopropithecus maximus*	UA 3823	Femur	−21.6	8.6	3.7
CH	Ampasambazimba	Lemur	*Palaeopropithecus maximus*	UA 4444	Mandible	−21.9	9.2	3.4
CH	Ampasambazimba	Lemur	*Palaeopropithecus maximus*	UA 3825	Femur	−22.1	9.4	3.3
CH	Christmas river (Ilakaka)	Lemur	*Archaeolemur majori*	DPC 24153a	Humerus	−20.2	11.4	3.2
CH	Christmas river (Ilakaka)	Lemur	*Pachylemur insignis*	DPC 24156	Femur	−21.2	12.5	3.2
CH	Antsirabe	Hippopotamus	*Hexaprotodon guldbergi*	NHMW Uncat.	Rib	−25.0	3.0	3.3
CH	Antsirabe	Hippopotamus	*Hexaprotodon guldbergi*	NHMW Uncat.	Rib	−24.9	1.9	3.5
CH	Antsirabe	Hippopotamus	*Hexaprotodon guldbergi*	NHMW Uncat.	Rib	−25.9	6.5	3.2
CH	Antsirabe	Hippopotamus	*Hexaprotodon guldbergi*	NHMW Uncat.	Rib	−23.7	1.3	4.2
CH	Antsirabe	Hippopotamus	*Hexaprotodon guldbergi*	NHMW Uncat.	Rib	−25.5	2.9	3.5
CH	Masinandraina	Elephant bird	*Aepyornis* sp.	UUE–MAS-5	Tibiotarsus	−14.0[a]	6.7	3.4
ST	Ankililelo	Lemur	*Archaeolemur majori*	DPC 22008	Innominate	−22.2	6.1	4.3
ST	Ampehabe cave #12, West Mikoboka plateau	Lemur	*Palaeopropithecus ingens*	DPC 24136	Femur	−20.8	10.7	3.2
ST	Taolambiby	Hippopotamus	*Hippopotamus lemerlei*	UMASS Uncat.	Phalanx	−22.7		

CH, Central highlands, ST, Spiny thicket.
Museum codes for specimen numbers: UA, University of Antananarivo; UMASS, University of Massachusetts, Amherst; DPC, Duke Primate Center (Division of Fossil Primates), NHMW, Naturhistoriches Museum Wien; UUE, Uppsala University Evolutionsmuseet.
[a]Carbon isotope value for this specimen was previously published [Burney, 1999]. Nitrogen isotope data are new.

Fig. 2. Map of Madagascar indicating subfossil localities that have yielded *Hadropithecus* (red dots) and carbon isotope values for *Kalanchoë* species from various localities across the island [Kluge et al., 1991]. Summary isotope data are provided for *Hadropithecus* at each site. Isotope data for *Kalanchoë* (from et al. [1991]) have been converted into subfossil collagen space by adding +6.2‰.

Hadropithecus were assessed for overlap with *Hadropithecus* sites using specimen geographic searches in www.tropicos.org.

To analyze data, we applied standard statistical tests (*t*-tests and ANOVAs with post hoc tests of honestly significant differences) using SPSS 22. We used correlation and regression analysis to examine the relationships between *Hadropithecus* bone $\delta^{13}C$ values and the following characteristics of the specimen's geographic location: latitude, longitude, elevation, proximity to the coast, mean January and mean July rainfall and temperature, and regional $\delta^{13}C$ values for C_3 and CAM plants.

This research adhered to the American Society of Primatologists' principles for the ethical treatment of primates.

RESULTS

Table III compares $\delta^{13}C$ and $\delta^{15}N$ values among giant lemur taxa living in different ecoregions. We pooled isotope values for the SW and the ST because they are not significantly different; thus, we compare values for the CH to a larger sample from arid and semi-arid habitats. Both $\delta^{13}C$ and $\delta^{15}N$ values are lower in the CH than in the SW/ST, almost always significantly so. This applies to individual genera, taken alone, and to a pooled sample of all giant lemurs.

Looking only at extinct lemurs from the CH, neither average $\delta^{13}C$ values nor average $\delta^{15}N$ values differ significantly among genera (Table III). *Hadropithecus* lies at the low end of the spectra for both $\delta^{13}C$ and $\delta^{15}N$. In contrast, in the SW/ST, there are strongly significant differences in both $\delta^{13}C$ values and $\delta^{15}N$ values among lemur genera, and *Hadropithecus* has the highest values for both isotopes. Its $\delta^{13}C$ values differ significantly from those of each of the other giant lemurs, and its $\delta^{15}N$ values differ significantly from all other lemurs except *Palaeopropithecus* (Table III). The variance for $\delta^{13}C$ values for *Hadropithecus* is high in the CH (standard

TABLE II. Summary Statistics for Modern Vegetation From Five Localities

Site	Type	n	Mean Plant $\delta^{13}C \pm 1\,SD$ (Min, Max) (‰)	Mean $\delta^{13}C$ in subfossil lemur space (‰)[a]	Source
Tsinjoarivo continuous forest (Vatateza)	C$_3$	61	-29.1 ± 1.8 $(-33.0, -24.2)$	-22.9	Crowley et al. [2013]
Central highlands	CAM[b]	27	-19.1 ± 5.4 $(-11.4, -27.3)$	-12.9	Kluge et al. [1991]
Kirindy forest	C$_3$	–	-29.1 ± 1.4[c]	-22.9	Dammhahn [2008]
Dry deciduous forest and succulent woodland	CAM[b]	7	-14.5 ± 4.8 $(-11.2, -25.0)$	-8.3	Kluge et al. [1991]
Tsimanampetsotsa	C$_3$	33	-28.1[d]	-21.9	Loudon et al. [2008]
Tsimanampetsotsa	CAM	4	-14.9[d]	-8.7	Loudon et al. [2008]
Beza Mahafaly (Parcel 2)	C$_3$	54	-26.5 ± 2.0 $(-30.8, -22.8)$	-20.3	Crowley et al. [2011b]
Beza Mahafaly (Parcel 2)	CAM	50	-14.9 ± 1.3 $(-18.3, -11.3)$	-8.7	Crowley et al. [2011b]
Cap Sainte-Marie	C$_3$	55	-27.4 ± 1.5 $(-31.0, -24.9)$	-21.2	Previously unpublished
Cap Sainte-Marie	CAM	9	-13.4 ± 0.5 $(-14.2, -12.5)$	-7.2	Previously unpublished

[a]Mean $\delta^{13}C$ values for plants have been corrected by $+6.2$‰ to account for fractionation between collagen and plants (5‰) and changes in atmospheric CO_2.
[b]CAM data from Kluge et al. [1991] are derived entirely from *Kalanchoë* spp.
[c]Only summary data presented in graphical form. Values estimated.
[d]Only mean isotope values provided.

deviation, or $SD = 4.1$‰) but unexceptional in the SW/ST ($SD = 1.5$‰).

Table IV compares carbon and nitrogen isotope values for lemur genera without regard to ecoregion. ANOVAs demonstrate significant differences among genera for both $\delta^{13}C$ and $\delta^{15}N$ values. Once again, *Hadropithecus* is unusual not merely for its high mean $\delta^{13}C$ value, but also for its strikingly high $\delta^{13}C$ variance ($SD = 6.2$‰). This exceptionally high variance is a consequence of dramatic inter-regional differences, coupled with high variance within the CH itself. Variance for $\delta^{15}N$ is also high for *Hadropithecus* ($SD = 4.8$‰), though to a lesser degree.

Isotopic variance is exceptional in *Hadropithecus* despite the fact that our samples for each of the other giant lemur genera comprise multiple recognized species, while only one species is recognized for *Hadropithecus*. Data derived from a well-studied extant lemur genus, *Microcebus*, underscore the unusual nature of isotopic variation in *Hadropithecus*. In contrast to *Hadropithecus*, standard deviations of mouse lemur $\delta^{13}C$ and $\delta^{15}N$ from the CH, ST, and SW are much closer to those of other extinct lemurs (1.5‰ and 2.3‰ respectively).

Table V compares *Hadropithecus* to hippopotamuses and elephant birds from the ST, SW and CH. Mean $\delta^{13}C$ and $\delta^{15}N$ values for *Hadropithecus* are significantly higher than for either of the other two taxa. Elevated $\delta^{13}C$ values for *Hadropithecus* suggest that this species' diet differed not merely from those of other giant lemurs but also from those of hippopotamuses and elephant birds. Higher $\delta^{15}N$ values for *Hadropithecus* suggest that this lemur tended to occupy drier habitats than hippopotamuses (i.e., feeding further from bodies of water); nitrogen isotope data for elephant birds are insufficient to allow any conclusions about the habitats they occupied.

Combined, our results suggest that *Hadropithecus* had a highly unusual diet, and that in the CH it consumed plants that differed dramatically in their isotopic composition from those eaten in the ST or SW. Its isotopic signal can be summarized simply: *Hadropithecus* displays elevated $\delta^{13}C$ and $\delta^{15}N$ in arid areas (but not in the much wetter CH) and highly variable isotope values in the CH.

Several (but not all) of the environmental variables that we compiled to explore factors

TABLE III. Summary Isotope Data for Each Extinct Lemur Genus in the Central Highlands and the Succulent Woodland/Spiny Thicket

Ecoregion	Isotope	n	Hadropithecus	Archaeolemur	Megaladapis	Pachylemur	Palaeopropithecus
Central highlands	$\delta^{13}C$	25	-24.2 ± 4.1	-20.9 ± 2.6	-22.1 ± 0.6	-22.4 ± 0.8	-22.0 ± 0.3
SW/ST	$\delta^{13}C$	104	-9.6 ± 1.5	-19.8 ± 1.4	-20.6 ± 1.0	-21.0 ± 1.4	-20.5 ± 0.7
t-tests comparing $\delta^{13}C$ values in CH vs. SW/ST for each genus			$t = -9.6$, df $= 9$, $P < 0.001$	$t = -1.5$, df $= 29$, NS	$t = -2.4$, df $= 23$, $P = 0.023$	$t = -2.9$, df $= 25$, $P = 0.008$	$t = -4.0$, df $= 33$, $P < 0.001$
Central highlands	$\delta^{15}N$	25	5.3 ± 3.6	7.6 ± 1.8	8.3 ± 0.4	8.5 ± 2.2	9.1 ± 0.4
SW/ST	$\delta^{15}N$	89	13.8 ± 3.2	11.1 ± 2.2	11.4 ± 1.7	11.5 ± 1.9	13.4 ± 2.0
t-tests comparing $\delta^{15}N$ values in CH vs. SW/ST for each genus			$t = -3.2$, df $= 7$, $P = 0.01$	$t = -3.7$, df $= 25$, $P = 0.001$	$t = -3.0$, df $= 18$, $P = 0.008$	$t = -3.6$, df $= 23$, $P = 0.001$	$t = -4.2$, df $= 31$, $P < 0.001$
Summary data and t-test comparing $\delta^{13}C$ values in CH vs. SW/ST for all genera		Mean for CH $= -22.0‰$, mean for SW/ST $= -19.5‰$, $t = -3.7$, df $= 127$, $P < 0.001$				
Summary data and t-test comparing $\delta^{15}N$ values in CH vs. SW/ST for all genera		Mean for CH $= 8.1‰$, mean for SW/ST $= 12.2‰$, $t = -8.1$, df $= 112$, $P < 0.001$				
ANOVA comparing $\delta^{13}C$ values among genera within the CH		$F = 1.584$, df $= 4.20$, NS				
ANOVA comparing $\delta^{15}N$ values among genera within the CH		$F = 1.575$, df $= 4.20$, NS				
ANOVA comparing $\delta^{13}C$ values among genera within the SW/ST		$F = 179.607$, df $= 4.99$, $P < 0.001$[a]				
ANOVA comparing $\delta^{15}N$ values among genera within the SW/ST		$F = 6.040$, df $= 4.84$, $P < 0.001$[b]				

t-tests compare isotope data (Means $\pm$ SD) between ecoregions and ANOVAs compare isotope data among groups within each ecoregion.
[a]*Hadropithecus* is significantly different from all other genera.
[b]*Hadropithecus* is significantly different from all other genera except *Palaeopropithecus*.

TABLE IV. Comparing Collagen Isotope Values for Now-Extinct Lemur Genera

Genus	n	$\delta^{13}C$ mean $\pm$ SD (‰)[a]	n	$\delta^{15}N$ mean $\pm$ SD (‰)[b]
Hadropithecus	11	-12.3 ± 6.2	9	11.9 ± 4.8
Archaeolemur	31	-20.0 ± 1.8	27	10.2 ± 2.6
Megaladapis	25	-20.8 ± 1.1	20	10.9 ± 1.9
Pachylemur	27	-21.5 ± 1.4	25	10.4 ± 2.4
Palaeopropithecus	35	-20.7 ± 0.8	33	12.9 ± 2.4
ANOVA	128	$F = 40.13$, df $= 4, 124$, $P < 0.001$	113	$F = 5.20$, df $= 4, 109$, $P = 0.001$

Summary data for each group are derived from three ecoregions (ST, SW, and CH).
[a]*Hadropithecus* is significantly different from all other genera; there are no significant differences among other genera.
[b]*Hadropithecus* does not differ significantly from any other genus; *Palaeopropithecus* differs significantly from *Archaeolemur* and *Pachylemur*.

potentially influencing this pattern of variation (i.e., latitude, longitude, elevation, proximity to the coast, January and July mean rainfall and temperature, and regional $\delta^{13}C$ values for C$_3$ and CAM plants) are themselves strongly collinear. Across *Hadropithecus* sites, localities at higher elevation are also significantly closer to the equator. Rainfall is highest during the rainy season (in January, austral

TABLE V. Comparing Isotope Values for *Hadropithecus*, Hippopotamuses and Elephant Birds

Genus	n	$\delta^{13}C$ mean $\pm$ SD (‰)[a]	n	$\delta^{15}N$ mean $\pm$ SD (‰)[b]
Hadropithecus	11	-12.3 ± 6.2	9	11.9 ± 4.8
Hippopotami	20	-21.3 ± 2.8	19	7.5 ± 3.2
Elephant birds	10	-20.4 ± 5.0	1	6.7
ANOVA	40	$F = 15.613$, df $= 2, 38$, $P < 0.001$	28	$F = 4.275$, df $= 2. 26$, $P = 0.025$

Summary data for each group are derived from three ecoregions.
[a]*Hadropithecus* is significantly different from hippopotami and from elephant birds.
[b]*Hadropithecus* is significantly different from hippopotami (sample size is too small to compare *Hadropithecus* to elephant birds).

summer) and at high elevations. Temperature also changes with season, but is not significantly correlated with elevation, likely because *Hadropithecus* sites that are closer to the equator are also higher in elevation. Temperature is significantly correlated with longitude (warmer on the west coast than further east, in the CH), both for January and July. The $\delta^{13}C$ values of CAM plants are negatively correlated with elevation (CAM plants are more enriched in ^{13}C at low elevations); there is no relationship between $\delta^{13}C$ values of C_3 plants and elevation.

Two of our environmental variables are excellent predictors of $\delta^{13}C$ values for *Hadropithecus* bone: elevation ($r = -0.957$, $P < 0.001$, $n = 11$) and $\delta^{13}C$ values for CAM plants ($r = 0.923$, $P < 0.001$, $n = 11$). Two additional variables are significantly (but more weakly) correlated with $\delta^{13}C$ values for *Hadropithecus* bone: January rainfall ($r = -0.733$, $P = 0.01$, $n = 11$) and latitude ($r = -0.668$, $P = 0.025$, $n = 11$). No other variables, including $\delta^{13}C$ values for C_3 plants, are significantly correlated with $\delta^{13}C$ values for this extinct lemur. The regression with the highest adjusted R^2 value (0.90) uses elevation and $\delta^{13}C$ values for CAM plants to predict $\delta^{13}C$ values for *Hadropithecus* bone. Its multiple R value is 0.961.

CAM plants that were consumed by *Hadropithecus* should (1) have $\delta^{13}C$ values that vary in a manner consistent with geographic isotopic variation for *Hadropithecus*, (2) exist in the regions formerly occupied by *Hadropithecus*, and (3) be eaten, albeit perhaps in small quantities, by living lemurs. Table VI lists plant genera that appear to satisfy the first two criteria. Figure 1 demonstrates how dominant consumption of facultative CAM plants such as *Kalanchoë* spp. could account for the isotopic variation exhibited by *Hadropithecus*, even in the CH. The $\delta^{13}C$ values for *Kalanchoë* in the CH show tremendous variation. Table VII provides observations that support the third criterion. In most cases, the parts eaten are leaves.

DISCUSSION

Isotope data provide strong support for the inference that *Hadropithecus* specialized on CAM (and not C_3) plants. The difference between CAM and C_3 plants in accounting for variation in the carbon isotope signature of *Hadropithecus* is impressive, and comprises strong evidence that *Hadropithecus* preferred CAM plants, even in the CH. CAM plants typically have elevated $\delta^{13}C$ values in arid regions and can exhibit highly variable $\delta^{13}C$ values in humid areas [Kluge et al., 1991, 1995]. The variability of $\delta^{13}C$ values of *Hadropithecus* is truly unusual, not merely in comparison to other fossil lemurs, but in comparison to a very well measured living lemur, *Microcebus*. No other lemur, living or extinct, shows the combination of exceptionally high $\delta^{13}C$ values in arid regions and extreme variability of $\delta^{13}C$ values in humid regions, as is consistent with dedicated CAM plant consumption.

While our stable isotope values for *Hadropithecus* do not reveal plant part or parts eaten, there is good reason to believe that the succulent leaves of CAM plants were the dietary staples for *Hadropithecus* in all ecoregions. Leaves account for the vast majority of CAM consumption by extant lemurs (Table VII). Endemic CAM plants of Madagascar tend to use wind or water to disperse their seeds. *Alluaudia* and *Kalanchoë* are prime examples of this, with very tiny seeds adapted for wind dispersal and not animal consumption. Some endemic CAM plants, including all members of the Didiereoidea, have spines to protect their leaves, which strongly suggests that these plants are (or were) subjected to significant leaf predation.

There are also reasons to exclude a predominantly C_4 diet for *Hadropithecus*. Unlike C_4 plants, succulent CAM plants are abundant in the southern parts of the island and can provide food and water during the prolonged dry season, when grass leaves become desiccated and of little nutritional value. In arid places where *Hadropithecus* was abundant, isotope values in C_4 plants are less affected by aridity than are C_3 or CAM plants. Consequently, C_4 plants typically have lower $\delta^{15}N$ values than C_3 or CAM plants in arid settings, including southern Madagascar [Crowley & Godfrey, 2013; Koch et al., 1991; Swap et al., 2004]. Therefore, grass consumption cannot explain the very high $\delta^{15}N$ values for *Hadropithecus* in the arid south.

Minimal reliance by other endemic taxa on C_4 plants in Madagascar is also supported by their $\delta^{13}C$ values. Neither Madagascan hippopotamuses nor elephant birds have isotope values indicative of a diet rich in C_4 grasses [Clarke et al., 2006; Crowley & Godfrey, 2013]. Bond & Silander [2007] note the existence (albeit scant) of enriched ^{13}C for some hippopotamuses reported by Burney et al. [2004]. However, the only hippo $\delta^{13}C$ values that match dedicated C_4 grass consumption derive from a single individual *Hippopotamus* whose skull and mandible may have been brought from continental Africa to the Académie Malgache in the 1800s for comparative analysis.

A final argument against C_4 grass consumption being critical to *Hadropithecus* is that C_4 grasses likely arrived too late to explain the derived suite of traits that distinguish *Hadropithecus* from its sister taxon, *Archaeolemur*. Recent phylogenetic research based on complete or nearly complete mitochondrial genome sequences for extinct and extant lemurs suggests that the archaeolemurids diverged from a palaeopropithecid/indriid clade roughly 24 Ma [Kistler et al., 2015]. This establishes an upper limit for the divergence timing of the two archaeolemurid

TABLE VI. Carbon Isotope Values and Geographic Distributions for Candidate CAM Plants

Genus	Family	Plant $\delta^{13}C$ values (‰)	Sources for isotope data	Distribution
Aloe	Xanthorrhoeaceae	−12.9 to −14.2 (N = 4)	Unpublished data[a], Cap Sainte-Marie, Spiny thicket	Common in the Spiny thicket and central highlands. Rarer in the succulent woodland
Alluaudia	Didiereaceae	−12.7 to −16.0(N = 9)	Kluge et al. [1995] Parc National, Berenty, spiny thicket	Common in the spiny thicket. Rarer in the succulent woodland. Only present in an isolated portion of southern central highlands
		−12.0 to −15.3 (N = 10)	Winter [1979] Near Fort Dauphin	
		−13.1 to −17.1 (N = 12)	Crowley et al. [2011b] BMSR July 2007 (dry season, spiny thicket)	
		−14.0 to −15.0 (N = 5)	Crowley & Godfrey [2013] BMSR January 2009 (wet season, spiny thicket)	
Cissus	Vitaceae	−15.4 (N = 1)	Kluge et al. [1995] Parc National Berenty, spiny thicket	Present throughout spiny thicket and central highlands. Only a few localities in the succulent woodland
		−15.0 (N = 1)	Ziegler et al. [1981] Saudi Arabia	
Cynanchum	Apocynaceae	−14.5, −14.7, −26.6 (3 species, N = 1 each)	Kluge et al. [1995] Parc National Berenty, spiny thicket	Abundant throughout the spiny thicket and the central highlands. Rare in the succulent woodland
		−13.7 to −15.7 (N = 4)	Crowley et al. [2011b] BMSR July 2007	
Didierea	Didiereaceae	−20.1 (N = 1)	Kluge et al. [1995] Parc National Berenty, spiny thicket	
Euphorbia	Euphorbiaceae	−16.1 to −17.7 (N = 2)	Winter [1979] Near Fort Dauphin	Present throughout the spiny thicket, the eastern central highlands, and southern succulent woodland
		−13.0 to −17.0 (N = 7)	Kluge et al. [1995] Parc National Berenty, spiny thicket	
		−12.6 to −17.8(N = 5)	Winter [1979] Near Fort Dauphin	
		−12.3 to −17 (N = 45)	Crowley et al. [2011b] BMSR July 2007	
		−13.8 to −16.3 (N = 10)	Crowley & Godfrey [2013] BMSR January 2009	
Kalanchoë	Crassulaceae	−12.8 to −14.2 (N = 9)	Kluge et al. [1995] Parc National Berenty, spiny thicket	Present throughout the spiny thicket, central highlands, and central succulent woodland
		−20.2 to −27 (N = 2)	Kluge et al. [1995] Parc Analamazoatra, humid forest, central highlands	
		−15.9 to −22.5 (N = 2)	Kluge et al. [1995] Station forestière Manankazo, Central Highlands	
		−10.2 to −13.5 (N = 2)	Winter [1979] Near Fort Dauphin	
		−13.8 (N = 1)	Unpublished data[a], Cap Sainte-Marie, Spiny Thicket	
Seyrigia	Cucurbitaceae	−16.8 to −17.3 (N = 2)	Crowley et al. [2011b] BMSR July 2007	Present throughout the spiny thicket. Rare in the southern central highlands. Absent from the succulent woodland?
Xerosicyos	Cucurbitaceae	−13.5 to −16.0 (N = 4)	Kluge et al. [1995] Parc National Berenty, spiny thicket	Present throughout the spiny thicket in the succulent woodlands and the southern central highlands
		−15.0 (N = 1)	Winter [1979] Near Fort Dauphin	
		−11.3 to −14.2 (N = 4)	Crowley et al. [2011b] BMSR July 2007	
		−14.7 to −18.3 (N = 5)	Crowley & Godfrey [2013] BMSR January 2009	

BMSR, Beza Mahafaly Special Reserve.
[a]Previously unpublished data.

TABLE VII. Observations of Extant Lemur Species Feeding on Candidate CAM Plants

Genus	Extant lemur consumers	Sources for lemur consumer data
Aloe	*Lemur catta*	Yamashita [1996]; Goodman & Langrand [1996]; Simmen et al. [2003]; Soma [2006]; Gemmill & Gould [2008]; Gould et al. [2009]; Ellwanger & Gould [2011]; Kelley [2011]; LaFleur [2012]
Alluaudia	*Lemur catta*	Simmen et al. [2003, 2006a]; Gould et al. [2009, 2011]; Kelley [2011]; LaFleur [2012]
	Lepilemur leucopus	Charles-Dominique & Hladik [1971]; Hladik & Charles-Dominique [1974]; Russell [1977]
	Propithecus verreauxi	Richard [1977]
Didierea	*Lemur catta*	Simmen et al. [2003, 2006a]; LaFleur [2012]
Cissus	*Lemur catta*	Sussman [1977]
	Propithecus verreauxi	Simmen et al. [2003]
Cynanchum	*Lemur catta*	Sauther [1992]; Simmen et al. [2003]; Kelley [2011]
	Lepilemur leucopus	Russell [1977]
	Microcebus griseorufus	Rasoazanabary [2011]
	Propithecus verreauxi	Charrier et al. [2007]
Euphorbia	*Lemur catta*	Simmen et al. [2003, 2006b]; Ellwanger & Gould [2011]; LaFleur [2012]
	Lepilemur leucopus	Russell [1977]
	Lepilemur petteri	Nash [1998]
	Microcebus griseorufus	Rasoazanabary [2011]
	Microcebus murinus	Martin [1973]
	Propithecus verreauxi	Jolly [1966]; Richard [1974, 1977, 1978]; Yamashita [1996, 2002]; Simmen et al. [2003]
Kalanchoë	*Lemur catta*	Rakotoarisoa [1999]; Gould et al. [2003]; Simmen et al. [2003, 2006b]; Kelley [2011]
Seyrigia	*Lemur catta*	Gould et al. [2009, 2011]
	Propithecus verreauxi	Charrier et al. [2007]
Xerosicyos	*Lemur catta*	Pinkus et al. [2006]; Gould et al. [2009]; Kelley [2011]
	Lepilemur leucopus	Charles-Dominique & Hladik [1971]; Hladik & Charles-Dominique [1974]
	Microcebus griseorufus	Rasoazanabary [2011]
	Propithecus verreauxi	Yamashita [1996]; Simmen et al. [2003]

genera. Closely related lemur genera for which divergence estimates are available fall between 10 and 15 million years ($\sim$10.9 Ma for *Pachylemur* and *Varecia*, a bit more for *Eulemur-Lemur* and for *Propithecus-Avahi*) [Kistler et al., 2015]. A divergence date for *Archaeolemur* and *Hadropithecus* between 10 and 20 million years seems reasonable. This is exactly when the common ancestor of the Didiereoideae likely arrived on Madagascar. Estimates for the timing of the origin of the family to which the Didiereoideae belongs (i.e., the Didiereaceae, including the continental African Calyptrothecoideae and Portulacarioideae as well as the Madagascan Didiereoideae; see Bruyns et al., 2014) vary from 15 to $\sim$30 Ma [Arakaki et al., 2011; Ocampo & Columbus, 2010]. Arakaki et al. [2011] place the initial diversification of the Madagascan subclade at $\sim$17 Ma. Ocampo & Columbus [2010] place the divergence of African and Madagascan clades at 12.1 Ma. But even that late estimate substantially predates the global radiation of C_4 grasses [Cerling et al., 1997] and likely post-Miocene spread of C_4 grasses to Madagascar [Bond et al., 2008], which is believed to be related to a decrease in concentrations of atmospheric CO_2 below a threshold that favored C_3 photosynthesis [Cerling et al., 1997].

There is substantial evidence that C_4 grasses expanded into tropical and subtropical latitudes of continental Africa during the Late Neogene [Strömberg, 2011; Uno et al., 2011]. Furthermore, that evidence supports a latitudinal gradient, with C_4 grasses expanding 4–5 million years later in southern Africa than in eastern and central Africa [Segalen et al., 2007; Strömberg, 2011]. If the same latitudinal gradient applies beyond continental Africa, one can expect a relatively late spread of C_4 grasses to Madagascar.

The timing of the diversification of the Madagascan Didiereoideae is critical because spines protecting the leaves from predation likely evolved in the ancestral lineage soon after initial colonization. Spines occur on all extant species of Didiereoideae but not their continental African relatives. Only lemurs and elephant birds were present on Madagascar when the ancestral didiereoid arrived on the island; hippopotamuses would have arrived later. Bond & Silander [2007] ruled out elephant birds on the basis of their feeding anatomy, which makes climbing lemurs the likely candidates. Exploitation by climbing lemurs would explain the evolution of spines on the tallest branches of didiereoid trees such as *Alluaudia* [Crowley &

Godfrey, 2013], and the fact that spine length matches or slightly exceeds the leaves beneath them. Differential exploitation of this new resource might also help to explain the divergence of *Archaeolemur* and *Hadropithecus*.

Recent discoveries of some previously unknown postcranial bones of *Hadropithecus* are fascinating in this light [Godfrey et al., 1997, 2006; Lemelin et al., 2008], as they suggest that *Hadropithecus*, despite being highly terrestrial, was maladapted for speed but adept at climbing. The femur was slightly shorter than the humerus, but very robust. Its shaft was anteroposteriorly compressed as in slow climbers; its femoral condyles show an asymmetry similar to that of chimpanzees or gorillas, likely reflecting differential weight bearing during femoral rotation on the tibia under abducted femoral excursion. The patellar groove was shallow and wide. This animal was neither a leaper nor suspensory; it was also not cursorial. Polk et al. [2010] measured the density of subchrondral bone in the distal femur to reconstruct knee postures. They found a broad range, from highly flexed to highly extended. That *Hadropithecus* was slower and more deliberate than *Archaeolemur* is corroborated by data on the radius of curvature of its semicircular canals [Walker et al., 2008].

Curiously, *Hadropithecus* also had an unusual manus [Lemelin et al., 2008]. Its short digits suggest cercopithecoid-like terrestriality but differences from terrestrial cercopithecoids are also striking. Papionins in general, and *Theropithecus* in particular, have a long and mobile pollex and a very short index finger, which help them in securing small objects such as the seeds of grasses, as well as underground storage organs such as rhizomes of grasses or corms of sedges, which become essential resources when grasses are dry [Etter, 1973; Jablonski et al., 2002]. *Hadropithecus*, in contrast, had an exceptionally short thumb, which suggests poor manipulative skills. The few hand bones known for *Hadropithecus* include the fifth metacarpal and the wrist bone that articulates with it, the hamate. When fitted together, they form a peculiar angle; this carpometacarpal joint displays a hyperextended set [Lemelin et al., 2008]. This is a very odd adaptation with no known analogue in the world of primates or other mammals. One might imagine that *Hadropithecus* would have benefited from being able to remove leaves manually if it indeed specialized on the succulent leaves protected externally by long spines. At present we do not know how it would have done this. More discoveries of bones of its hand may help us to understand whether or not *Hadropithecus*' manual peculiarities relate to a unique feeding adaptation.

With our new interpretation of the diet of *Hadropithecus*, we can now better evaluate the hypotheses that have been proposed to explain this animal's dental convergences with geladas and largely cranial convergences with basal hominins. Grass blades, rhizomes, and small seeds of grasses are unlikely, despite being mechanically challenging, because the isotope signature does not fit, and because *Hadropithecus* and *Archaeolemur* likely diverged before C_4 grasses became widespread in Madagascar [H_1 and, in part, H_2]. There is no evidence that hard foods or large seeds were significant components of the diet of *Hadropithecus* [H_3]. Large seeds or fruits with hard protective coats cannot have been staples, because they derive virtually exclusively from C_3 plants. Heavy microwear pitting on the molars of *Hadropithecus* is likely to reflect high grit levels on the foods rather than the consumption of hard objects, as many endemic CAM plants of Madagascar have tiny seeds that are wind dispersed. In arid or relatively open habits, grit levels on leaves are likely to be high, whether the leaves are cropped from plants on the ground or from trees [Green & Kalthoff, 2015; Ungar et al., 1995].

Elements of Jolly's [1970] small object hypothesis [H_2] can be defended in that succulent leaves may require little incisal preparation and not more than a small gape, and may have been consumed in large quantities. Repetitive chewing may have been required. Furthermore, succulent leaves may well have been conveyed by hand to the mouth. It is not clear that the leaves of these succulents are mechanically challenging (they have yet to be systematically tested), but having molar teeth that function in the manner of a grazer is not surprising for an animal masticating large quantities of succulent leaves. High-bulk feeding [H_4] cannot be discounted; this is, in effect, a component of Jolly's small object hypothesis [H_2]. However, while some of our candidate plants do not grow tall, others are trees. *Hadropithecus* likely accessed its foods via climbing as well as on the ground. Here, Jolly's [1970] gelada analogy fails.

Finally, we stress that determining the diet of *Hadropithecus* is only the first step of several that must be taken if we are to understand its hominin and papionin likenesses. While our research here contributes importantly to this task, we recognize that more research is needed to trim our long list of candidate plants and eliminate some of them. Nitrogen isotope data, in particular, are scant.

Ultimately, we would like to be able to address the question: What ecological or dietary shift in the ancestral archaeolemurid could have produced the evolutionary shift in gnathic and dental structure that we observe in the *Hadropithecus* lineage? And why do some (but not all) of its features parallel apomorphies of basal hominins and others of *Theropithecus*? To address these questions, we must know the diets of the fossils, but that is only the beginning. We must then collect appropriate data on the mechanical properties of likely resources, the mechanical efficiency of the molars, and processes by which foods break down during mastication. In our

view, the cranial and dental convergences of *Hadropithecus* to basal hominins and to grass-eating papionins are too striking to ignore, and understanding their significance could help us to better understand the adaptive significance of the craniodental anatomy of basal hominins and of grass-eating papionins themselves.

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