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Understanding Eocene primate palaeobiology using a comprehensive analysis of living primate ecology, biology and behaviour

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Abstract The comparative method is central to interpretations of Eocene primate palaeobiology. This method rests upon a thorough study of analogous living forms. With a rapidly increasing knowledge of such forms, most notably the Malagasy lemurs, our ability to advance the study of Eocene primate ecology, biology and behaviour far exceeds that of even just a few years ago. Here we present such a comparison. Based on our data collected from both living lemurs and extant lemur skeletal specimens, we are able to make a number of comparisons that provide insight into middle Eocene primate ecology and palaeobiology. At the Beza Mahafaly Special Reserve, Madagascar, omnivorous living ring-tailed lemurs that feed on large, hard and tough fruits display a pattern of frequent post-canine tooth wear laterality (62 %) when compared to sympatric, folivorous Verreaux's sifaka (4 %). Our results indicate that *Notharctus* does not display a high frequency of tooth wear laterality (7 %), indicating folivory without processing large, hard fruits with its postcanines. Our data on *Notharctus* tooth wear also indicate, similar to living ring-tailed lemurs at Beza Mahafaly, that numerous individuals (21 %) survived long enough to experience heavy tooth wear, contrary to the assumption that heavy tooth wear leads to the rapid death of the individual. Finally, our data on trauma and injury from a living lemur population suggest that the reported wrist injury in *Darwinius masillae* (i.e. "Ida") did not necessarily lead to her death, as numerous ring-tailed lemurs at Beza Mahafaly survive with similar or even more traumatic injuries and maintain the ability to climb. Thus, our data from living primates provide a broad comparative framework for interpreting the ecology, biology and behaviour of Eocene forms.

Introduction

There has been a long history of interpreting the ecology and behaviour of extinct primates through comparisons with comparable, living forms (Covert 1986, 1997), and the comparative method is central for answering many questions in primate evolutionary biology (Anthony and Kay 1993). Specifically, for Eocene primates, the extant strepsirrhine primates have provided an important template for interpreting body size, anatomy, locomotion and dietary preferences for these extinct forms (Covert 1986). These early comparisons focused primarily on large questions of overall primate adaptations (e.g. Covert 1986) and were limited in terms of interpreting their ecology. This approach was primarily due to the paucity of studies of extant strepsirrhine behavioural ecology that could provide good living models to assess comparable extinct forms. However, over the past two decades, there has been a dramatic increase in research on extant lemur ecology, biology and locomotion (e.g. Gould and Sauther 2006; Jolly et al. 2006; Kappeler

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and Ganzhorn 1993; Rakotosamimanana et al. 1999). With continued field work by workers from various institutions (e.g. University of Michigan, University of Colorado, University of California–Berkeley, the Carnegie Museum of Natural History, the Denver Museum of Nature and Science), which has produced large samples of Eocene primate materials from the intermontane basins of North America (e.g. Anemone and Covert 2000; Beard et al. 1991; Beard and MacPhee 1994; Covert and Hamrick 1993; Gunnell 1995, 1997; Murphey et al. 2001; Rose et al. 1999; Ross and Covert 2000; Williams and Covert 1994), it is now possible to provide important contextual data for expanding our understanding of the biology of extinct Eocene (and other) fossil primates.

Assessing patterns of tooth-use wear in primate fossils has a long history. However, since its development in the 1970s and 1980s (e.g. Walker et al. 1978), analyses of dental microwear have dominated dental wear assessment, with patterns of overall or gross wear receiving far less attention (e.g. Ungar 2002). Our long-term work in Madagascar combines data on feeding ecology and food properties in a single primate community to identify the proximate causes of primate tooth wear, and thus provides an interpretive framework for assessing patterns of gross tooth wear in primate fossils. Specifically, we have documented identifiable patterns of tooth wear produced by consuming specific foods with particular properties (e.g. Cuozzo and Sauther 2004, 2006; Sauther and Cuozzo 2009). In numerous descriptions of Eocene primates (and many other early Tertiary mammals), specimens are often noted as displaying varying degrees of gross tooth wear, with authors commonly lamenting that "heavy" wear obscures dental traits needed for taxonomic identification. Yet these patterns of heavy tooth wear can be quite informative in terms of assessing the behaviour and ecology of extinct forms (e.g. Jablonski et al. 2008).

In this paper we use data collected during our 25-year research on living lemur's dental ecology and biology and from our long-term work on extant lemur skeletal samples to contextualise Eocene primate ecology, biology and behaviour (Cuozzo and Sauther 2004, 2006; Sauther et al. 2002; Sauther and Cuozzo 2008). Specifically, we compare our extant dental and biological data to information derived from our analyses of 29 notharctine specimens collected from a number of museums in North America. We use these data to explore patterns of tooth wear as well as the potential of laterality in tooth wear (or lack thereof) in living and/or extant lemurs, in which tooth wear laterality corresponds to broad dietary behaviours and categories. We also use our extant primate biological information to re-visit the interpretation of the taphonomy and behaviour of one of the most important Eocene primate finds to date, Ida (*Darwinius masillae*).

Methods

Extant samples

Within the framework of our ongoing Lemur Biology Project, we have collected in-depth dental and biological data for a wild population of lemurs living within and around the Beza Mahafaly Special Reserve (BMSR), in southwestern Madagascar. As part of a project to understand and monitor the effects of habitat and climate on lemur ecology, over 300 individual ring-tailed lemurs, *Lemur catta*, have been monitored over a 25-year period at BMSR. The collected data include health and medical evaluations as well as dental assessments of these individuals in yearly captures (Cuozzo et al. 2010; Sussman et al. 2012) across a 10-year period beginning in 2003. In 2006 we also collected comparable biological and dental information from 25 living ring-tailed lemurs at Tsimanampesotse National Park, in southwestern Madagascar. In addition, skeletal remains for wild ring-tailed lemurs (*L. catta*) and sifaka (*Propithecus verreauxi*) have been collected over a 25-year period, now housed at the BMSR, and these provide patterns of dental ecology and pathology as well as skeletal injury, disease and trauma. Extant comparative lemur dental and skeletal samples also come from the American Museum of Natural History (AMNH), the United States National Museum of Natural History (USNM), The Natural History Museum, London, Harvard's Museum of Comparative Zoology and the Museum für Naturkunde, Berlin (BMNH). Quantitative data on extant ring-tailed lemur tooth wear from BMSR presented herein come from individuals captured in 2011 (*n*=51). The 2011 data set includes lemurs ranging in age from 3 years through those in their mid teens. These older lemurs were first captured in 2003 as full adults, and thus they were categorised by their minimum age when captured in 2011. All animal captures were conducted with IACUC (Institutional Animal Care and Use Committee) approval from the University of North Dakota and/or the University of Colorado–Boulder and followed protocols established over the 25-year history of this project (e.g. Sauther and Cuozzo 2009; Sussman et al. 2012).

Eocene notharctine samples

Notharctines have long been argued to share a number of morphological traits with living Malagasy indriids, especially members of the genus *Propithecus* (Covert 1986). Based on their anatomy, notharctines are believed to have been folivorous leapers similar to living indriids such as sifaka. For example, the intermembral index of *Notharctus* is 60, which is similar to the intermembral index of 59 found in the vertical clinger and leaper *P. verreauxi* (Fleagle 1998). Here we present tooth wear and wear laterality data for 29 *Notharctus* specimens (Table 1), obtained from collections

housed at the USNM, the Denver Museum of Nature and Science (DMNS) and the AMNH.

Wear scores

Each tooth position was scored for degree of overall or gross wear in both the *Notharctus* and *L. catta* samples. Wear status was scored using an ordinal wear scale (0–4), and values were assigned as 0=unworn occlusal surface; 1= small wear facets and no dentine or pulp exposure; 2=large wear facets and no dentine or pulp exposure; 3=some dentine and pulp exposure, few cusps still present and for canine and tooth comb, 50 % remaining; 4=pulp exposure, with cusps gone, dentine or pulp exposed across most of the surface, or partial crown remaining and for canine and toothcomb, less than 1/4 remaining. A post-canine "whole mouth" wear score index was calculated for each individual as: sum of scores for left and right P1–M3 and p1–m3/total

number of tooth positions scored. A first molar mean wear score was also calculated, as follows: combined M1 and m1 wear scores/total number of first molar tooth positions scored for each individual. These indices were divided into the following wear score categories: "low"=scores 0.00–1.00; "medium"=scores 1.01–2.00; "medium high"=scores 2.01–3.00 and "high"=3.01–4.00. Note that all tooth positions were not available for scoring in each individual, especially in the fossil sample.

Assessment of laterality in tooth wear

Our assessment of tooth wear laterality is based on the tooth wear methods described above. Among ring-tailed lemurs at two localities in Madagascar [BMSR (2011) and Tsimanampesotse National Park (2006)], tooth wear data were collected from captured, sedated lemurs, during our standard biological and biomedical examinations. Lemurs were

Table 1 *Notharctus* specimens sampled

Museum number	Museum[a]	Taxon	Mean wear score by individual for P1–P3 and/or p1–p3[b]	Laterality
1727.002	AMNH	*Notharctus tenebrosus*	3.00	No
5009.001	AMNH	*Notharctus rostratus*	3.00	No
18988.001	AMNH	*Notharctus tenebrosus*	3.00	No
11985	AMNH	*Notharctus robustior*	2.40	No
14568	AMNH	*Notharctus tenebrosus*	3.33	Yes
11480	AMNH	*Notharctus tenebrosus*	3.61	No
12579	AMNH	*Notharctus tenebrosus*	1.00	No
11466	AMNH	*Notharctus tenebrosus*	2.40	No
13384	DMNS	*Notharctus sp.*	2.00	No
6331	DMNS	*Notharctus sp.*	3.33	Yes
18418	DMNS	*Notharctus sp.*	2.40	No
18551	DMNS	*Notharctus sp.*	3.00	No
6791	DMNS	*Notharctus sp.*	3.00	No
54729	DMNS	*Notharctus sp.*	2.00	No
6169	DMNS	*Notharctus robustior*	3.00	No
21864	USNM	*Notharctus tenebrosus*	1.39	No
21968	USNM	*Notharctus tenebrosus*	2.00	No
13238	USNM	*Notharctus robustior*	2.00	No
22036	USNM	*Notharctus robustior*	3.00	No
22007	USNM	*Notharctus robustior*	2.00	No
21980	USNM	*Notharctus robustior*	3.50	No
21969	USNM	*Notharctus tenebrosus*	1.67	No
13234	USNM	*Notharctus tenebrosus*	3.25	No
22025	USNM	*Notharctus tenebrosus*	2.75	Yes
23278	USNM	*Notharctus robustior*	1.80	No
13230	USNM	*Notharctus tenebrosus*	4.00	No
244365	USNM	*Notharctus tenebrosus*	0.58	Yes
13-65	USNM	*Notharctus tenebrosus*	1.80	No
23277	USNM	*Notharctus tenebrosus*	2.00	No

[a]AMNH, American Museum of Natural History; DMNS, Denver Museum of Nature and Science; USNM, National Museum of Natural History

[b]Mean wear score by individual for P1–P3 and/or p1–p3

captured following our protocols established over more than a decade of annual lemur research in Madagascar, and with veterinary supervision (e.g. Larsen et al. 2011a, b; Miller et al. 2007). Tooth wear was scored for each post-canine tooth in the arcade, and laterality was determined if at least one tooth position displayed a difference in wear score between the left and right tooth. For lemur cranial/skeletal specimens (e.g. Verreaux's sifaka), tooth wear was scored for all tooth positions for which both left and right teeth were present. Due to varying degrees of preservation, not all tooth positions in the skeletal specimens possessed both left and right teeth. A similar protocol was used for the Eocene *Notharctus* specimens. Only specimens with associated left and right tooth rows were analysed, and as few complete skulls and/or maxillae are available, most specimens consisted of partial left and right mandibular specimens. Laterality was assessed if at least one tooth from a given position was present in both the left and right tooth row. As a note, our notharctine sample is quite conservative, as only specimens for which a confident association between the left and right tooth rows (or individual tooth positions) was available were studied.

Results and discussion

Notharctine dental ecology

Overall wear patterns

Worn teeth are problematic for taxonomic study, as taxonomic indicators, such as specific accessory cusps, are not visible on worn teeth (Ungar and M'Kirera 2003). As such, worn teeth have frequently received less attention in palaeontological studies. However, patterns of even extensive wear, especially when put in context with patterns found in living mammals for which good behavioural and ecological data are available, can provide insight into the biology and ecology of both living and fossil individuals (Cuozzo and Sauther 2012). A good example is found in the *Notharctus tenebrosus* specimen, AMNH 11480. Figure 1 compares this specimen with that of an extant lemurid, *Eulemur albifrons*. AMNH 11480 shows both a dramatic and uniform level of wear, with the crowns worn smooth from the incisors all the way to the molars. Importantly, even though both specimens show heavy wear, they each retain enamel-shearing crests that likely allow the continued processing of leafy foods.

Table 2 compares whole mouth wear scores for *Notharctus* compared to the extant lemur *L. catta* from our research at BMSR. Low, medium and heavy wear are all represented in the *Notharctus* samples, indicating that there does not appear to be a bias towards only individuals with limited wear being present in the fossil record. The distribution of
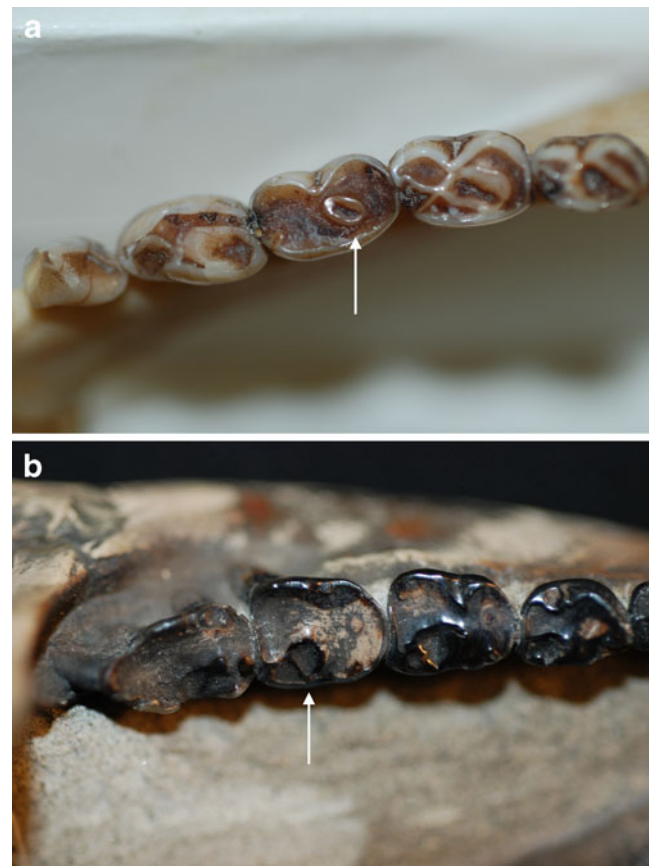

Figure 1 Extensive mandibular molar wear in an extant *Eulemur fulvus albifrons* specimen (AMNH 100560) (**a**) compared to similarly heavy mandibular molar wear in a *Notharctus tenebrosus* specimen (AMNH 11480) (**b**). Note that although both specimens are heavily worn, they each retain enamel-shearing crests (*arrow*) indicative of the continued ability to process leaves. Photo credit: Michelle L. Sauther

wear pattern is thus similar to that seen in a living lemur population in that individuals with medium through high levels of wear are frequently present. Table 3 provides a similar comparison for the first molars, which are often the only teeth represented in the fossil record. Again, individuals with all stages of wear are represented in *Notharcus*, and this distribution of M1 wear frequency is similar to that found in the living ring-tailed lemurs in that individuals with medium to heavy M1 wear are well-represented. It's important to note that the large number of older lemurs in our study population influences the frequency of heavy M1 wear in this extant sample. Nevertheless, there is a similarity between this Eocene form and a living lemur species in that living into the later stages of life (based on the display of heavy tooth wear) is not simply a characteristic of modern primates. While we recognise that our *Notharctus* specimens represent a range of strata and cross a number of temporal units, our comparison indicates that living primates do live and continue to survive with heavy dental wear (contra Lucas 2004) and that this pattern of surviving

Table 2 Distribution of whole mouth wear scores[a] for 29 *Notharctus* specimens and 51 living wild *Lemur catta* specimens

	Scores			
	Low (0.00–1.00)	Medium (1.01–2.00)	Medium high (2.01–3.00)	High (3.01–4.00)
Notharctus				
Number of Individuals	2	10	11	6
Percentage	6.8	34.5	37.9	20.6
Lemur catta				
Number of Individuals	0	14	7	30
Percentage	0	27.5	13.7	58.8

[a] Whole mouth wear score= mean wear for each individual [(sum of scores for left and right P1–M3 and p1–m3)/(total number of tooth positions scored)]. Scores are based on a minimum of four or more teeth for the fossil specimens. Not all tooth positions were available for each individual

severe wear can be seen deep into the primate fossil record and is thus not an anomaly.

Table 4 provides comparisons of mean post-canine gross tooth wear. In general, there is a pattern of more overall wear in the post-canine dentition in *L. catta* when compared to *Notharctus* (14/20 tooth positions). As we have discussed in detail elsewhere (e.g. Cuozzo and Sauther 2004, 2006; Cuozzo et al. 2008, 2010; Sauther and Cuozzo 2009), greater post-canine wear in omnivorous *L. catta* from BMSR reflects this population's use of a number of mechanically challenging food sources (e.g. hard, tough and large), particularly tamarind (*Tamarindus indica*), which is their primary fallback food at this location. Specifically, the greater degree of wear in *L. catta* compared to *Notharctus* for P4 and M1 in all four quadrants reflects the placement of this challenging fallback food during food processing, rather than being a product of eruption sequence. *L. catta* P4s and M2s display similar degrees of gross tooth wear, which contrasts with the pattern of eruption in this species, where P4s erupt much later than M2s (e.g. Eaglen 1985). In comparison, for *Notharctus* the M1s and M2s are consistently the most worn. This pattern of wear corresponds to the general pattern of dental eruption in primates in which the first and second molars are the first permanent food processing teeth to erupt. The frequency of more pronounced wear in seven of the eight premolar positions scored in *L. catta*

suggests a disproportionate amount of food processing on these tooth positions relative to that seen in *Notharctus*. In other words, it appears from these data that ring-tailed lemurs at BMSR frequently use the anterior portion of the post-canine tooth row when processing foods, in contrast to *Notharctus*, where there is a more consistent use of the entire tooth row for processing foods. This would be expected for a folivorous primate, where leaves are chewed throughout the mouth, rather than for primates who emphasise a certain portion of the tooth row for processing specific foods—in this case, *L. catta* at BMSR (e.g. Cuozzo and Sauther 2006; Sauther and Cuozzo 2009).

Eocene primate dental ecology

Figure 2 demonstrates heavy incisor and canine wear in an extant indriid, *Indri indri* (BMNH 84277) and in *Notharctus tenebrosus* specimen AMNH 11480. Unlike other lemurs, which have either absent or reduced incisors, indriid upper incisors are quadrate and well developed (Cuozzo and Yamashita 2006), which facilitates cropping of mature leaves as well as seed predation and even bark consumption, which can be an important source of water in the dry season for indriids (Powzyk and Mowry 2007; Richard 1977, 1978). In both specimens the wear has produced a flattened surface, and in both cases the pulp cavity can be clearly

Table 3 First molar mean wear scores[a] for 26 *Notharctus* specimens and 51 living wild *L. catta* specimens

Specimens	Scores			
	Low (0.00–1.00)	Medium (1.01–2.00)	Medium high (2.01–3.00)	High (3.01–4.00)
Notharctus				
Number of Individuals	1	9	8	8
Percentage	3.9	34.6	30.8	30.8
L. catta				
Number of Individuals	0	1	19	31
Percentage	0	2.0	37.3	60.8

[a] First molar mean wear score = (combined M1 and m1 wear scores)/(number of first molar tooth positions scored for each individual)

Table 4 Comparison of gross tooth wear score means between Eocene *Notharctus* sp. and extant *L. catta* from the Beza Mahafaly Special Reserve, Madagascar

Tooth position	*Notharctus* sp.			*L. catta*			p value[a]
	Mean	Standard deviation	n	Mean	Standard deviation	n	
Right P^3	1.600	0.548	5	2.902	1.118	51	0.0134*
Right P^4	1.857	0.378	7	3.100	1.093	50	0.0045*
Right M^1	2.000	0.707	9	3.627	1.131	51	0.0001*
Right M^2	2.222	0.667	9	3.176	1.228	51	0.0275*
Right M^3	1.571	0.787	7	2.549	1.137	51	0.0323*
Left P^3	1.833	0.753	6	2.902	1.153	51	0.0316*
Left P^4	2.000	0.000	5	3.078	1.036	51	0.0249*
Left M^1	2.500	0.548	6	3.608	1.041	51	0.0135*
Left M^2	2.667	0.516	6	3.078	1.146	51	0.3912
Left M^3	2.000	0.816	4	2.588	1.203	51	0.3432
Right P_3	2.000	0.707	9	2.725	0.981	51	0.0386*
Right P_4	2.200	1.082	15	3.118	1.032	51	0.0039*
Right M_1	3.000	0.918	20	3.647	0.996	51	0.0143*
Right M_2	2.810	0.928	21	3.294	1.082	51	0.0769
Right M_3	2.267	0.961	15	2.706	1.221	51	0.2056
Left P_3	2.200	0.837	5	2.765	1.050	51	0.2500
Left P_4	2.071	0.997	14	3.098	1.044	51	0.0016*
Left M_1	2.895	0.875	19	3.667	0.931	51	0.0025*
Left M_2	2.550	0.887	20	3.275	1.041	51	0.0077*
Left M3	2.143	1.099	14	2.725	1.133	51	0.0913

[a]Values followed by an asterisk indicate a significant difference between *Notharctus* sp. and *Lemur catta* mean wear scores ($p < 0.05$)

seen. Given the ubiquity of this wear pattern in living indriids, we can posit that in *Notharctus*, this is a normal wear pattern for a folivorous primate. We also argue that the indriids provide a suitable analogue for assessing wear in *Notharctus*, which, like indriids, possesses stout incisors. Although lacking the strepsirrhine tooth comb, the robust lower and upper incisors of *Notharctus* are functionally similar to the stout maxillary and toothcomb incisors in indriids (Cuozzo and Yamashita 2006), which are apparently used in processing foods, such as seeds, bark and mature leaves, that likely have challenging mechanical properties (i.e. being tough and/or abrasive). The notable incisor wear in some *Notharctus* specimens suggests the use of such foods being initially processed with the anterior teeth.

Another important pattern relevant to understanding *Notharctus* dental ecology is the relative amount of wear across the dental arcade. Figure 3 shows the dental arcade and a close-up of the worn left mandibular canine of a *N. robustior* specimen (DMNS 6169). In this specimen, the left maxillary canine demonstrates heavy wear but lp1–lp4 show only limited wear. This is followed by moderate to heavy wear for lm1–lm2, with lm3 also showing only limited wear (Fig 3a) The canine has extensive wear and the pulp cavity is exposed (Fig 3b). This pattern of wear is notable in the skeletal collection at our research site in Madagascar as well as other indriid museum samples we have analysed. For living indriids such as *P. verreauxi*, we have tied such heavy anterior wear accompanied by less wear on the posterior teeth to their feeding ecology, which includes large fruits of the tamarind tree (*Tamarindus indica*) as well as mature leaves as important food resources (Yamashita et al. 2012). This can be seen in Fig. 4 where both tamarind fruit and mature leaves are initially processed almost completely with the anterior dentition. In both cases, the canines are engaged during food processing. This brings up the interesting possibility that some Eocene primates were initially processing large fruits, bark, seeds and/or abrasive leaves utilising their canines in much the same way as living indriids.

Our results also add to the discussion regarding the ecology of other Eocene fossil primates, such as the *Ganlea megacanina* (Beard et al. 2009) and *Pondaungia cotteri* (Jaeger et al. 2004). *G. megacanina* has a massive mandibular canine showing heavy wear, suggesting that these primates were using their lower canines to pry open hard tropical fruits much like living *Chiropotes* and *Pithecia* species in South America, which initially open hard foods with their canines and subsequently process the soft inner portions with their thin enameled post-canine teeth (Martin et al. 2003). *Pondaungia cotteri* (NMMP 24) has only a moderate-sized canine with a mandibular apical canine facet, but is also argued to have focused on a hard food diet (Jaeger et al. 2004). Heavy apical canine wear in these and
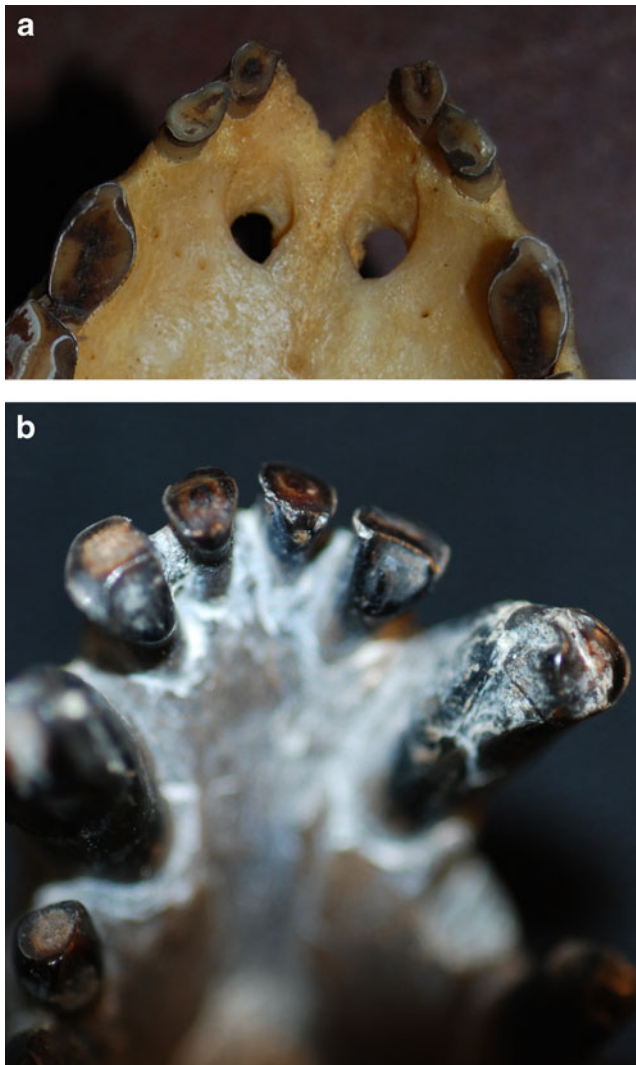
Figure 2 Extensively worn upper incisors and canines in an extant lemur, *Indri indri* (BMNH 84277) (**a**), compared to heavily worn lower incisors and canines in a *Notharctus tenebosus* specimen (AMNH 11480) (**b**). Photo credit: Michelle L. Sauther

Figure 3 The lower left dental arcade of *Notharctus robustior* (DMNS 6169) showing differential wear (**a**) and a closeup of the heavily worn canine (**b**). Photo credit: Michelle L. Sauther

other specimens has been suggested to indicate that the entire group of Burmese amphipithecids was hard object feeders (Beard et al. 2009). The indriids have a mandibular toothcomb and so do not have large lower canines. However, as can be seen in Fig. 5, heavy maxillary apical canine wear facets are commonly seen in living folivorous indriids, indicating that extensive wear can also occur through the processing of a variety of challenging foods beyond hard tropical fruits. This once again points out how comparing wear patterns in living primates can provide information on ecological interpretations in the fossil record.

Laterality in tooth wear can also be helpful for determining feeding patterns in fossil primates. Table 5 compares *Notharctus* laterality with the indriid *P. verreauxi* and the lemurid *L. catta* from two habitats, namely, a dry spiny forest and a deciduous gallery forest. In *L. catta*, large food

items, such as tamarind fruit, are held in the hand and processed on the post-canine teeth (Fig. 6), whereas as already noted, *P. verreauxi* initially process larger fruits and leaves at the front of the mouth. Due to their size, the large foods processed by the post-canine dentition in *L. catta* can only be processed on either the right or left tooth rows in a single feeding bout. As can be seen in Table 4, *Notharctus* follows the indriid pattern of exhibiting no dental laterality, indicating that even if large and/or challenging foods were initially processed with the anterior teeth, subsequent feeding did not favour one or the other side of the mouth. This is what would be expected of a folivorous primate.

Patterns of injury in living lemurs and the death of Darwinius masillae

In addition to expanding our understanding of Eocene primate dental ecology, comparisons with living populations can also contribute to our interpretation of death and injury in the fossil record. One of the most famous examples is that of *Darwinius masillae* ("Ida"), a nearly perfectly preserved middle Eocene primate specimen. Using applied micro-computed tomography analyses, researchers have been able to confirm that a callus on the right wrist indicates that sometime during her lifetime this individual broke the wrist and survived for at least 1 month (the minimal time to develop such a callus) after this trauma (Franzen et al. 2011). It has been hypothesised that such a trauma seriously

Figure 4 Examples of behavioural ecology linked to incisor and canine wear in an extant lemur, *Propithecus verreauxi*, from the Beza Mahafaly Special Reserve (BMSR), Madagascar. **a** Feeding on fruits utilising the canines, **b** feeding on large mature leaves using the canines and incisors. Photo credit: Michelle L. Sauther
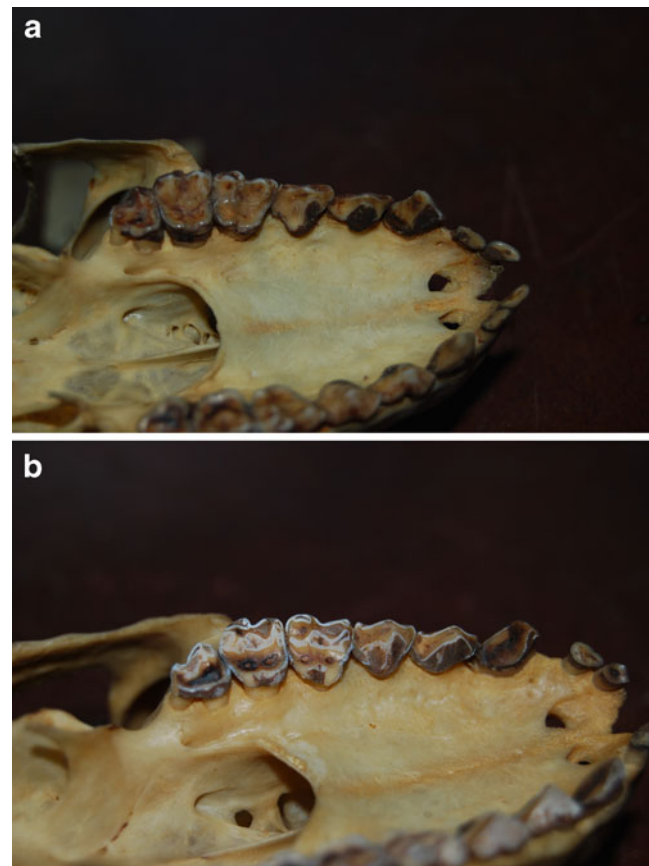
Figure 5 Comparison of canine and post-canine wear in an extant indriidae, *Indri indri*. **a** Unworn specimen (BMNH 84279), **b** worn specimen (BMNH 84283). Note the heavy incisor and canine wear compared to the post-canine teeth in **b**. Photo credit: Michelle L. Sauther

crippled this individual and that she was no longer able to climb and live in the trees, and as such, she eventually succumbed to the periodic poisonous gas characteristic of the middle Eocene Lake Messel environment, drowned in the lake and was fossilised (Franzen et al. 2011).

Our work at BMSR has documented a variety of injuries, including broken humeri, ulnae and femora. Some of these are quite dramatic injuries, following which the individuals survived long enough for extensive healing to occur (Fig. 7). In these cases, individuals were still able to climb and move within

the trees, even with limbs that no longer grasped. In 2003 we evaluated a male adult *L. catta* (lemur #115) whose right wrist was swollen with the carpal bones calcified to the point that crepitus was evident when the wrist was moved. In 2004 we recaptured this same individual as part of our annual health evaluations. At this time he was in good condition, but he had developed an infected abscess on the right wrist (Fig. 8a) which is in the same area as that seen in *Darwinius masillae* (Fig. 8b). In 2005 we captured him once again and he still exhibited the infected abscess. We did not see this individual again after 2005. During the years when he was still a part of the study population, he continued to exhibit normal behaviours, including climbing and moving within the trees. While we cannot ascertain for sure the fate of our male lemur, given that we have been carrying out yearly demographic census for nearly 10 years, if he survived he must have migrated completely out of our study area, which is common among the Beza Mahafaly ring-tailed lemurs, who may migrate as far as 10 km from the reserve. Our extensive study of wild ring-tailed lemurs documents that these primates can sustain considerable trauma, yet continue to move in the trees and recover, suggesting that *Darwinius masillae* may have been able to

Table 5 Whole mouth laterality for folivorous Northarctines, folivorous wild extant *Propithecus verreauxi* and wild extant omnivorous *L. catta*

Taxon/location	*n*	Number with laterality	% Laterality[a]
BMSR Gallery Forest *Lemur catta*	47	29	62*
TNP Spiny Forest *Lemur catta*	24	6	25*
BMSR Gallery Forest *Propithecus verreauxi*	73	3	4
Notharctus sp.	28	4	7

TNP, Tsimanampesotse National Park

[a] Values followed by an asterisk indicate a significant difference between *Notharctus* and lemur species (*p*<0.05, *df*=1)

survive her initial trauma for some time. Given the relatively frequent occurrence of severe trauma survived by Beza Mahafaly lemurs, our data bring into question the interpretation of this injury being a direct factor in her death. However, if she did develop an infected abscess this could have created a serious infection that may have impacted her ability to survive.

Conclusions

While worn teeth are often ignored in the fossil record due to the absence of diagnostic taxonomic features, they can

provide an important avenue in understanding fossil primate ecology, biology and behaviour. From the work presented here we can see that individuals with worn teeth were an important part of this record, and the pattern of wear provides insight into their ecology when compared to living primates whose ecology and behaviour are well known.

It is imperative that palaeobiologists frame their work in the context of what is known about living animals, and it is the responsibility of those workers who study living organisms to conduct and produce meaningful research that allows those who study fossil forms to access and utilise these data. One of the primary goals of our research programme is to do just that—to provide a context from extant primate ecology, biology, and behaviour to interpret the biology of extinct Eocene (and other) fossil primates. For example, the pattern of tooth-use wear described for *Ganlea megacanina* as well as *Pondaungia cotteri* is similar to that of the BMSR indriid, *Propithecus verreauxi*, in which canines show marked canine apical facets, while the

Figure 6 A ring-tailed lemur, *Lemur catta*, feeding on a large fruit of *Tamarindus indica* using its post-canine teeth. Photo credit: Michelle L. Sauther
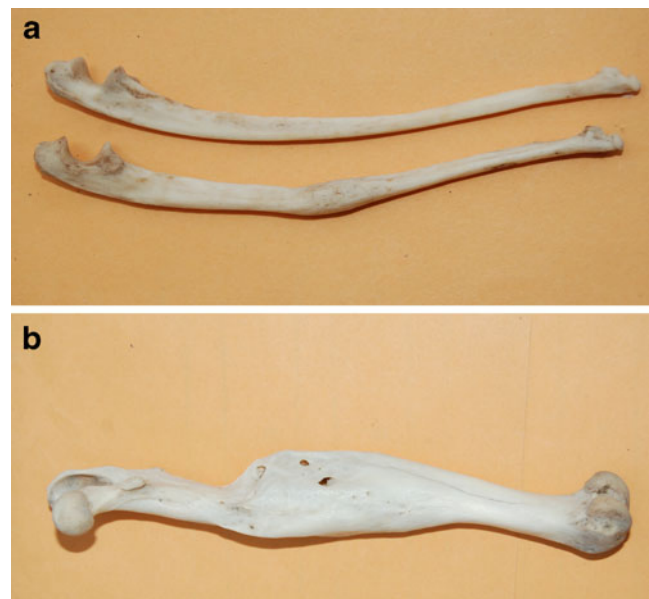

Figure 7 Examples of trauma with healing in wild ring-tailed lemurs *L. catta* from the BMSR. **a** Broken and healed ulna, **b** broken and healed femur. Photo credit: Michelle L. Sauther
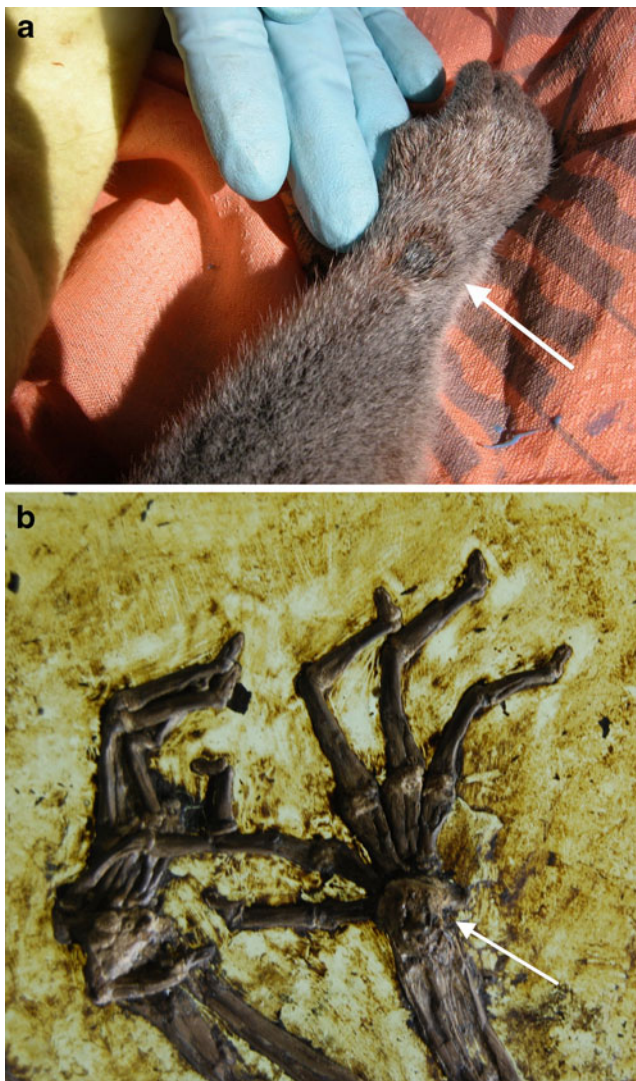
Figure 8 Wrist trauma with abscess in a male wild ring-tailed lemur *L. catta* from the BMSR (**a**) compared to callus on the right wrist of the *Darwinius masillae* specimen (**b**). Photo credit: Michelle L. Sauther

post-canine teeth display far less severe wear. As the canine wear pattern of BMSR indriids reflects the long-term use of a food that is not only hard and tough, but also contains with biogenic silica, it is also possible that *G. megacanina* and *P. cotteri* regularly used a fallback food with similar mechanical and physical properties. Detailed work on living animals can thus add important details to current discussions regarding the palaeobiology of long-extinct primates.

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