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Analysis of Dentition of a Living Wild Population of Ring-Tailed Lemurs (*Lemur catta*) From Beza Mahafaly, Madagascar

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ABSTRACT Detailed descriptions of the dentition of many strepsirhine primate taxa are rare, despite their importance in understanding primate evolutionary biology. While several researchers have provided detailed morphological descriptions of ring-tailed lemur dentition (e.g., Schwartz and Tattersall [1985] Am. Mus. Nat. Hist. Anthropol. Pap. *60:*1–100; Tattersall and Schwartz [1991] Am. Mus. Nat. Hist. Anthropol. Pap. *69:*2–18), there are few studies (e.g., Eaglen [1986] Am. J. Phys. Anthropol. *71:*185–201) that present quantitative data on the dentition of this species. Furthermore, prior analyses were based on museum specimens from various populations and locations. We present here quantitative and morphological data on the dentition of a population of wild *Lemur catta* from Beza Mahafaly Special Reserve, Madagascar. Measurements were made on dental casts (n = 39) taken from living members of this *L. catta* population. Our analysis indicates that no significant ($P > 0.05$) sexual dimorphism exists for the 30 dental measurements collected. These data support the generalizations (e.g., Plavcan and van Schaik [1994] Evol. Anthropol. *2:*208–214; Kappeler [1996] J. Evol. Biol. *9:*43–65) that little sexual dimorphism in dentition exists among Malagasy strepsirhines. In addition, the overall patterns of metric variation in this sample compare favorably with patterns seen among other primates, e.g., premolar measurements varying more than molars (e.g., Gingerich [1974] J. Paleontol. *48:*895–903). However, there is a degree of intraspecific morphological variation indicated, with one of the morphological traits discussed in other studies as being species-specific for *L. catta* (absence of P_4 metaconids) observed to vary between specimens. Because the patterns of variation seen in this sample are from a known breeding population, the data presented here provide an important reference for interpreting and understanding the fossil record.Am J Phys Anthropol 114:215–223, 2001.

The study of extant primate dentition has long been recognized as an integral aspect of primate evolutionary biology. Nevertheless, detailed descriptions of the dentition for many extant primate taxa have been limited. This has been the case for many of the Malagasy strepsirhines (Schwartz and Tattersall, 1985). Many older studies of primate dentition and morphology (e.g., Hill, 1953; James, 1960), while providing general descriptions of lemur dentition, lack both detailed descriptions and comparative dental metrics. Although more recent studies (e.g., Swindler, 1976) provide metric data for a wide range of primates, there remains a paucity of strepsirhine information. The ring-tailed lemur (*Lemur catta*) provides such an example. This species has been intensively studied in the wild for many years (Sauther et al., 1999), and several recent studies (Schwartz and Tattersall, 1985; Groves and Eaglen, 1988; Tattersall and Schwartz, 1991; Tattersall, 1993) have provided detailed morphological data for *L. catta* dentition. However, Eaglen (1986) presents the only published data on ring-tailed lemur dental metrics, and his data were limited to the anterior dentition. Furthermore, prior analyses (Eaglen, 1986; Kappeler, 1996) were based on museum collections representing various populations and locations, and utilized relatively small samples ($n < 10$). We present here a unique data set for strepsirhine primates based on the dentition of a single living wild population of *L. catta* from Beza Mahafaly Special Reserve, Madagascar.

MATERIALS AND METHODS

Metric and morphological data were collected from a set of dental casts taken from a wild popula-

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TABLE 1. Lemur catta *dental measurements*

Upper canine length	P_2 length
Upper canine width	P_2 width
P^2 length	P_3 length
P^2 width	P_3 width
P^3 length	P_4 length
P^3 width	P_4 width
P^4 length	M_1 length
P^4 width	M_1 width
M^1 length	M_2 length
M^1 width	M_2 width
M^2 length	M_3 length
M^2 width	M_3 width
M^3 length	Length of tooth comb
M^3 width	Maxillary tooth row length
Palate breadth at M^3	Mandibular tooth row length

tion of *L. catta* at Beza Mahafaly Special Reserve, Madagascar. This population has been the focus of a long-term study of ring-tailed lemur demography and socioecology (Sussman, 1991; Sauther, 1992, 1994; Sauther et al., 1999). As a part of this study, adult members were briefly tranquilized, during which biometric data were collected, and dental impressions were made using Caulk Dentsply, type II Jeltrate, alginate impression material, and custom-built acrylic and wax impression trays. Stone dental casts were then made from the dental impressions while in the field. Results presented here are based on casts of the upper and lower dentitions of 39 ring-tailed lemurs. Four age grades were assigned in the field, based on each of the following measures: level of dental attrition, general body condition, body weight, and reproductive traits (e.g., nipple length as a measure of female parity, and presence/absence of descended testicle and testicle size as measures of male sexual maturity). Sample sizes for each grade were: subadult = 5; young adult = 3; prime = 26; old = 5. Unless otherwise noted, results presented are based on an adult sample size (young adult, prime, and old age grades) of n = 34. Measurements for each cast were made to the nearest 0.05 mm, using Helios dial calipers. A reliability analysis was conducted 6 months after taking the original measurements, using a subsample of 15 casts. This analysis revealed a mean measurement difference of only 0.07 mm for M_1 length, a value similar to previously published values (e.g., Schuman and Brace, 1954; Swindler, 1976). A total of 30 measurements was taken following standard procedures (Swindler, 1976; Eaglen 1986; Musser and Dagosto, 1987) (Table 1, Figs. 1, 2).

Because of variation in cast quality (e.g., cast defects) and various dental anomalies, we were very conservative in our measurements and morphological analyses. The general level of attrition was scored for each tooth, based on the following categories: 0 = unworn occlusal surfaces; 1 = small wear facets and no dentin or pulp exposure; 2 = large wear facets but no dentin or pulp exposure; 3 = some dentin but no pulp exposure, few cusps still present, or for toothcomb or caniniform P_2, $\frac{1}{2}$ remaining; and 4 = pulp exposure, with cusps gone, dentin or pulp exposed across most of the surface, or for toothcomb or caniniform P_2, less than $\frac{1}{4}$ left. Based on this, a specimen was rejected if the tooth were scored as 2 or above, if it were of poor quality, or if it exhibited any pathological condition. Thus, samples sizes vary for each measure. Descriptive statistics and measures of variability (i.e., mean, standard deviation, coefficient of variation, and standard error) were calculated for each measurement. Sexual dimorphism was investigated using traditional Student's *t*-tests (significance level = 0.05), and sex differences in metric variability were tested using coefficients of variation and their standard errors, corrected for sample size, and through the use of F-ratios (Sokal and Rohlf, 1995), (significance level = 0.05). In addition, we addressed metric patterns of dental growth and development by comparing the adult sample with a much smaller sample (n = 5) of subadults. Morphological analyses were conducted to investigate the degree of intraspecific variation in this population. Traits chosen for analyses were selected, based on their use as *L. catta* diagnostic traits (Schwartz and Tattersall, 1985; Tattersall and Schwartz, 1991; Tattersall, 1993) (Table 2). Traits were scored as being either absent or present in each specimen, and were summarized based on the number of specimens for which each trait is present. Several *L. catta* comparative metrics traits noted by other workers (Schwartz and Tattersall, 1985) were also investigated (Table 2).

RESULTS

Metrics

We found no significant ($P = 0.05$) sex differences among adult specimens for any of the 30 measurements collected (Tables 3 and 4). In comparing the adult and subadult samples, we found that subadult means fit within the adult ranges for all but one measurement, with the mean subadult M^1 length being greater (Tables 3 and 6).

The following patterns were seen regarding variability in *L. catta* dentition. For both male and female samples there is a greater degree of variation in the antemolar dentition than in the molar dentition, with antemolar coefficients of variation (CVs) often exceeding 10 (Tables 4 and 5). As in individual sex samples, the antemolar dentition for the pooled sex sample exhibits more variation than is present in the molars (Table 3). Tooth widths tend to be more variable than tooth lengths within each sex (Tables 4 and 5). For females, this holds true in 10 of 13 dental measurements (77%), while for males this occurs in 9 of 13 (69%) cases. The degree of metric variation between sexes was compared, using the standard error of the coefficient of variation (corrected for sample size) and F-ratios (Table 5). These analyses indicate a small number (M^1 and P_4 width, maxillary and mandibular tooth row length) of significant ($P = 0.05$) differences, based on F-ratios, between male and female variances (Table 5). How-

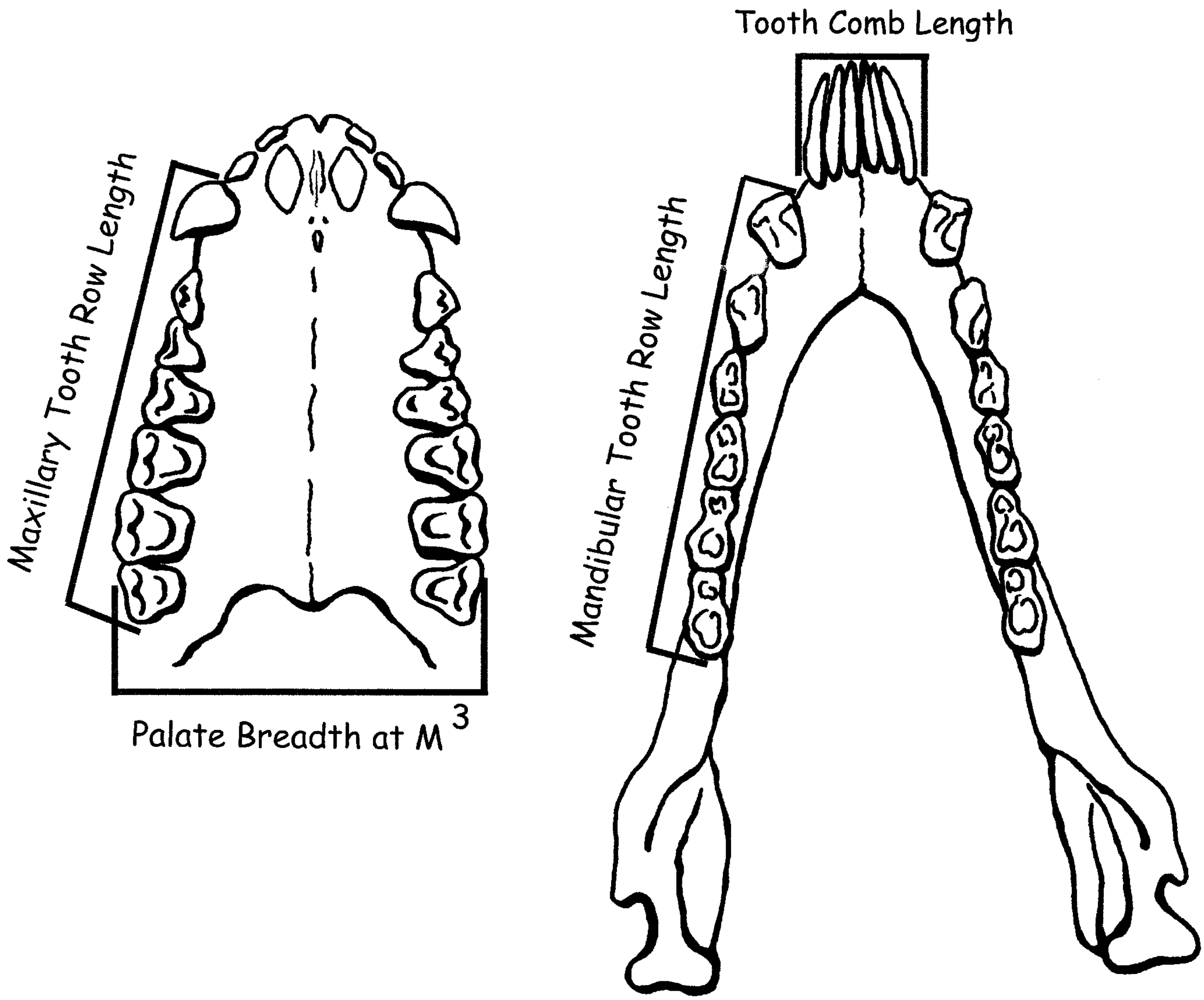

Fig. 1. *Lemur catta* maxillary and mandibular measurements.

ever, because of the small within-sex sample sizes, these apparent differences must be viewed with caution. In terms of subadults, there was less variation within the subadult sample than within the adults, with only 2 of the 16 measurements having a CV greater than 7 (Tables 3 and 6). In comparison, 11 of 30 measurements of adult samples had CVs greater than 7 (Table 3).

Comparative metrics and morphology

Focusing on comparative metric traits noted by Schwartz and Tattersall (1985) as being representative for *L. catta,* we found the following:

1. M^2 is longer and wider than M^1 (9 out of 10).
2. M^3 is longer than M^1 (3 out of 10).
3. P_3 is shorter than P_2 (7 out of 7).
4. P_4 is wider than P_2 (10 out of 10).
5. M_1 is shorter than M_2 (13 out of 15).
6. M_3 is shorter than M_1 (4 out of 8).
7. M_1 is narrower than M_2 (12 out of 13).

We examined seven morphological traits listed as species-specific for *L. catta* (Schwartz and Tattersall, 1985; Tattersall and Schwartz, 1991; Tattersall, 1993). Our results indicate the following:

1. A pinched talonid groove is present on M_1 (16 out of 16).
2. Presence of a cusp-like lower molar entoconid (14 out of 14).
3. Presence of a ledge-like cingulum on M^1 (19 out of 19).
4. No stylar development for M^2 (17 out of 17).
5. An anteriorly expanded cingulum for M^2 (29 out of 29).
6. Absence of P_4 metaconid (2 out of 21) (Fig. 3).

In terms of both comparative metric and morphological traits, our observations are for the most part consistent with the descriptions presented by Schwartz and Tattersall (1985), Tattersall and Schwartz (1991), and Tattersall (1993). However, as

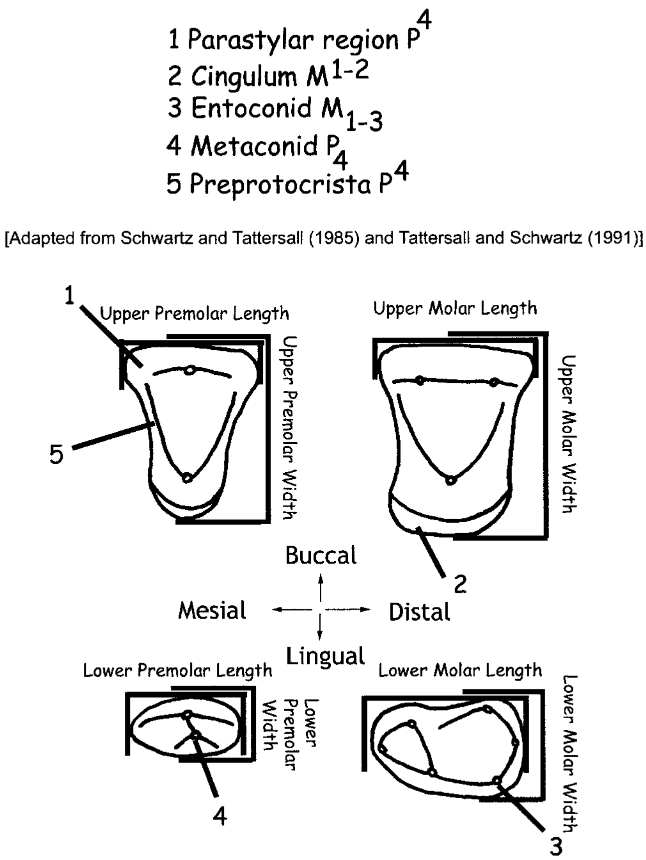

Fig. 2. Tooth measurements and tooth morphology.

discussed in greater detail below, our sample differs for one of the morphological (absence of a P_4 metaconid) and several of the comparative metric traits (M^3 being longer than M^1, and M_3 being shorter than M_1).

DISCUSSION

Metrics

Assumptions have been made about the lack of sexual dimorphism in this species. However, most measurements of sexual dimorphism have focused on absolute body size or canine size for primates in general, as well as strepsirhines in particular (Crook, 1972; Gaulin and Sailer, 1984; Kay et al., 1988). Sexual dimorphism has been noted for canine height in museum specimens of ring-tailed lemurs, but not for canine length, canine width, P2 length, or P2 width (Kappeler, 1996). We were not able to measure canine height because of canine cast imperfections in the subadult and adult mandibular casts used for this analysis. Our results, however, indicate that for all other adult dental metrics, ring-tailed lemurs lack any significant sexual dimorphism. These data support the generalizations (e.g., Plavcan and van Schaik, 1994; Kappeler, 1996) that little dental sexual dimorphism exists among the Malagasy strepsirhines.

TABLE 2. Lemur catta *morphological and comparative morphometric traits*

Lingual cingulum of M^1 and M^2 ledge-like
Distinct lingual talonid groove on M_1 pinched
Cusp-like lower molar entoconids
M^2 lacks stylar development
P_4 metaconid absent
M^2 longer and wider than M^1
M^3 longer than M^1
P_3 shorter than P_2
P_4 wider than P_2
M_1 shorter than M_2
M_3 shorter than M_1
M_1 narrower than M_2

Overall, we observed several patterns of metric variation in our sample. Our sample is weighted heavily toward animals of prime adult age grade. In addition, the majority of individual measurements do not include data from individuals of the old age grade, due to severe attrition. It is thus unlikely that the variation we see is simply the result of sampling individuals of differing ages and thus of differing levels of dental attrition. The antemolar dentition for the pooled sex sample exhibits more variation than the molars. This pattern is similar to the general pattern seen in primates, in which premolars exhibit more metric variation than molars (e.g., Gingerich, 1974; Gingerich and Schoeninger, 1979; Benefit, 1993). This primate pattern is likely the result of greater occlusal constraints on the molars vs. the premolars, which therefore allows more variation to occur in premolar size (and shape). However, this pattern of variation in our sample may also relate to the way some food is processed in ring-tailed lemurs. For example, a major food resource is the fruit of the tamarind tree (*Tamarindus indica*) (Jolly, 1966; Sussman, 1978; Sauther, 1998). This large fruit has a hard outer shell and a very fibrous matrix. When feeding, ring-tailed lemurs use only their premolars and canines to crack open the shell and chew through the tough fibrous matrix to extract individual seeds that they then swallow. This may then lead to additional pressures and/or forces operating on the antemolar dentition as compared to the molars. Therefore, habitus features may be a compounding variable in understanding patterns of primate dental variation.

Overall, premolar widths show greater variation than premolar lengths. In addition to the regular occlusal constraints, or lack thereof, this pattern of variation may also relate to interindividual variability in morphological traits, specifically the size and shape of the lingual cusps on the premolars (such as P_4 metaconid). We also observed less variation in the first and second molars as compared with the third molars. In this respect, ring-tailed lemurs again show a pattern similar to that observed in other primates (e.g., Gingerich, 1974; Gingerich and Schoeninger, 1979). The subadult population (approximately 2 years old) showed less variation when compared to the adults. This may be due to the

TABLE 3. Lemur catta *dental metrics*[1]*: pooled adult samples,* t*-test for sex differences*

	Pooled mean	Range	Standard deviation	Coefficient of variation	Mean difference	*t*-value[2]	*P* value[2]
Maxillary tooth row length	35.01	33.45–36.90	0.785	0.022	0.263	0.693	0.498
C^1 length	5.51	4.55–6.30	0.456	0.083	0.106	0.540	0.595
C^1 width	2.71	1.90–3.50	0.427	0.158	0.088	0.498	0.623
P^2 length	3.40	2.90–4.00	0.262	0.077	0.012	0.112	0.912
P^2 width	1.84	1.40–2.25	0.245	0.133	0.053	0.517	0.611
P^3 length	4.16	3.60–4.65	0.297	0.071	0.106	0.715	0.485
P^3 width	3.19	2.20–3.75	0.431	0.135	0.111	0.512	0.616
P^4 length	3.96	3.35–4.35	0.297	0.075	0.231	1.420	0.182
P^4 width	5.14	4.50–5.40	0.277	0.054	0.108	0.664	0.520
M^1 length	4.62	3.90–4.90	0.276	0.060	0.158	0.963	0.355
M^1 width	5.76	5.15–6.30	0.289	0.050	0.050	0.305	0.765
M^2 length	5.00	4.55–5.40	0.248	0.050	0.067	0.388	0.706
M^2 width	6.42	5.95–6.80	0.284	0.044	0.328	1.950	0.080
M^3 length	4.94	4.10–5.60	0.500	0.101	0.017	1.780	0.102
M^3 width	5.19	4.55–5.80	0.362	0.070	0.045	0.058	0.955
Palate breadth	26.12	24.30–27.90	0.837	0.032	0.047	1.560	0.139
Mandibular tooth row length	31.00	29.40–35.50	1.350	0.044	0.802	0.693	0.266
P_2 length	4.59	3.85–5.10	0.310	0.068	0.045	0.258	0.800
P_2 width	2.46	1.80–2.95	0.294	0.119	0.171	1.080	0.297
P_3 length	3.60	3.10–3.95	0.231	0.064	0.023	0.164	0.873
P_3 width	2.08	1.70–2.55	0.255	0.123	0.231	1.580	0.146
P_4 length	4.48	4.05–4.75	0.216	0.048	0.042	0.320	0.755
P_4 width	2.89	2.60–3.55	0.254	0.088	0.067	0.438	0.671
M_1 length	4.71	4.40–5.25	0.231	0.049	0.056	0.386	0.707
M_1 width	3.29	2.85–3.50	0.171	0.052	0.131	1.420	0.178
M_2 length	5.10	4.60–5.75	0.305	0.060	0.188	1.250	0.230
M_2 width	3.61	3.15–3.90	0.249	0.069	0.092	0.666	0.518
M_3 length	5.14	4.45–5.40	0.307	0.060	0.303	1.610	0.151
M_3 width	3.31	2.95–3.80	0.282	0.085	0.017	0.075	0.943
Tooth comb length	7.26	6.95–7.80	0.218	0.030	0.047	0.399	0.696

[1] In mm.
[2] Significance set at $P = 0.05$.

smaller sample size, but could also relate to either the earlier-mentioned occlusal effects, or to patterns of growth and development which are currently being studied (Sauther et al., in preparation). Out of the seven comparative metric traits, five showed a high level of agreement (greater than 85%) with the results of previous work (Schwartz and Tattersall, 1985). In contrast, the two remaining traits showed far less agreement (less than or equal to 50%). Of interest, these two traits both include the third molars. This probably relates to the pattern of third molars exhibiting greater interindividual metric variation, both in our data set and among primates in general (e.g., Gingerich, 1974).

Morphology

While our analysis is consistent with most of the morphological observations noted by previous studies (Schwartz and Tattersall, 1985; Tattersall and Schwartz, 1991; Tattersall, 1993), we also document a degree of intraspecific variation for one (P_4 metaconid) of the morphological traits discussed in these studies as being species-specific for *L. catta* (Fig. 3). Because our data set is from a single breeding population, we may here be sampling the normal level of variation for this trait in an actual population. In contrast, museum samples of ring-tailed lemurs often represent specimens collected from different sites and at different times, and are usually limited in terms of sample sizes.

Paleotaxonomic implications

Extant species are often used as models for understanding the diversity and adaptations of extinct forms. Therefore, as has long been noted by other workers (e.g., Swindler, et al., 1963; Swindler and Orlosky, 1974), knowledge of the degree of dental variation in extant animals is important for understanding species diversity in the fossil record. Based on earlier work (e.g., Simpson and Roe, 1939; Simpson et al., 1960), in which a CV of greater than 10 suggested an impure sample, paleontologists have often viewed this value as the upper limit of metric variation expected for a single-species fossil assemblage. As mentioned earlier, Gingerich (1974) and Gingerich and Schoeninger (1979) refined this idea, noting that molars are less variable than other tooth locations, and that CV values may vary by tooth location. Gingerich (1995) also refined the use of CVs in terms of examining patterns of sexual dimorphism in fossil species. In recent years, the use of CVs in the analysis of extinct animals has received much attention (e.g., Cope, 1989, 1993; Cope and Lacy, 1992, 1995; Benefit, 1993; Plavcan, 1993; Gingerich, 1995), and its efficacy has been challenged by some workers (e.g., Kelly and Plavcan, 1998). However, despite the limitations inherent in its use (e.g. Carrasco, 1998; Kelly and Plavcan, 1998), the CV remains a commonly used statistical tool in paleotaxonomy (e.g., Gingerich, 1995; Carrasco, 1998). In-

TABLE 4. Lemur catta *dental metrics*[1]*: male and female descriptive statistics*

	Females				Males				Male/ female ratio	Mean difference	*t*-value	*P* value
	$\bar{\chi}$	σ	CV	N	$\bar{\chi}$	σ	CV	N				
C^1 length	5.44	0.357	6.6	9	5.55	0.514	9.3	15	1.020	0.106	0.540	0.595
C^1 width	2.70	0.407	15.1	9	2.690	0.402	14.9	15	0.999	0.088	0.498	0.623
P^2 length	3.41	0.215	6.3	11	3.392	0.305	9.0	13	0.996	0.012	0.112	0.912
P^2 width	1.87	0.228	12.2	11	1.815	0.266	14.6	13	0.972	0.053	0.517	0.611
P^3 length	4.22	0.255	6.0	7	4.115	0.329	8.0	10	0.975	0.106	0.715	0.485
P^3 width	3.13	0.478	15.3	7	3.240	0.416	12.8	10	1.035	0.111	0.512	0.616
P^4 length	4.10	0.180	4.4	5	3.869	0.331	8.5	8	0.944	0.231	1.42	0.182
P^4 width	5.08	0.344	6.8	5	5.188	0.243	4.7	8	1.021	0.108	0.664	0.520
M^1 length	4.74	0.189	4.0	4	4.580	0.300	6.6	10	0.967	0.158	0.963	0.355
M^1 width	5.73	0.097	1.6	5	5.780	0.354	6.1	10	1.009	0.050	0.305	0.765
M^2 length	5.05	0.087	1.7	3	4.983	0.285	5.7	9	0.987	0.067	0.388	0.706
M^2 width	6.17	0.208	3.4	3	6.495	0.265	4.1	10	1.053	0.328	1.95	0.080
M^3 length	5.48	0.035	0.6	2	4.845	0.482	9.9	11	0.885	0.017	1.78	0.102
M^3 width	5.18	0.177	3.4	2	5.192	0.390	7.5	12	1.003	0.045	0.058	0.955
P_2 length	4.57	0.227	5.0	6	4.605	0.343	7.5	6	1.008	0.045	0.258	0.800
P_2 width	2.40	0.316	12.7	6	2.409	0.313	13.0	6	0.970	0.171	1.08	0.297
P_3 length	3.59	0.156	4.3	6	3.587	0.275	7.7	8	0.999	0.023	0.164	0.873
P_3 width	2.22	0.325	14.6	5	2.006	0.150	7.5	8	0.904	0.231	1.58	0.146
P_4 length	4.45	0.218	4.9	7	4.500	0.212	4.7	6	1.011	0.042	0.320	0.755
P_4 width	2.93	0.118	4.0	7	2.858	0.351	12.3	6	0.973	0.067	0.438	0.671
M_1 length	4.79	0.143	3.0	5	4.694	0.270	5.7	9	0.980	0.056	0.386	0.707
M_1 width	3.37	0.093	2.8	6	3.239	0.188	5.8	9	0.962	0.131	1.42	0.178
M_2 length	5.26	0.343	6.5	7	5.038	0.266	5.3	5	0.958	0.188	1.25	0.230
M_2 width	3.65	0.245	6.7	7	3.575	0.248	6.9	9	0.979	0.092	0.666	0.518
M_3 length	5.30	0.128	2.4	5	5.010	0.349	7.0	12	0.945	0.303	1.61	0.151
M_3 width	3.29	0.175	5.3	4	3.300	0.345	10.4	12	1.004	0.017	0.075	0.943
Maxillary tooth row length	34.90	0.355	1.0	8	35.113	0.956	2.7	12	1.006	0.263	0.693	0.498
Mandibular tooth row length	31.49	1.861	5.9	7	30.690	0.694	2.3	10	0.975	0.802	0.693	0.266
Palate breadth at M^3	25.73	0.778	3.0	8	26.427	0.772	2.9	11	1.027	0.047	1.56	0.139
Tooth comb length	7.33	0.277	3.8	7	7.244	0.178	2.5	9	0.988	0.047	0.399	0.696

[1] In mm.

deed, Carrasco (1999) recently suggested, based on experimental data, that of all measures of variation used in paleontology, the CV is the most reliable in assessing taxonomic diversity in a fossil assemblage.

As addressed earlier, most studies of extant primate variation have been based on mixed museum samples (for an early exception, see Schuman and Brace, 1954; for a more recent example, see Benefit, 1993). Therefore, documenting metric and morphological variation within a known breeding population has important implications for assessing species diversity in the fossil record. Our sample exhibits both pooled-sex and single-sex CVs of greater than 10 in 6 out of 26 measurements (Tables 3 and 4). Five of these six were antemolar measurements, with the sixth being M^3 length. As noted earlier, this pattern reflects the general primate pattern of antemolar teeth being more variable than molars. This overall primate pattern, however, was largely based on anthropoid primates (e.g., Gingerich, 1974; Swindler, 1976), with limited data included for prosimian taxa (e.g., Gingerich and Ryan, 1979). Although more recent discussions (e.g., Kieser and Groeneveld, 1989; Schwartz and Beutel, 1995) have presented data on prosimian dental variability, the lemurs remain underrepresented in the overall discussion of primate dental variability. Therefore, our data provide further support for this apparent general primate pattern. Our results also indicate that morphological variation in the dentition of lemurs may be greater than previously recognized. For example, the absence of a P_4 metaconid has been used by Tattersall and Schwartz (1991) in their phylogenetic analyses of lemurids. This trait (among others) has been used to distinguish *L. catta* from *Eulemur*. However, our results show that this trait is variable within *L. catta,* and in our sample, a P_4 is absent in only 2 out of 22 specimens (Fig. 3). Therefore, this trait cannot be used to distinguish *L. catta* from *Eulemur* species. These premolar data indicate that caution must be used when assessing paleotaxonomic diversity based on either premolar metric variation, or on what are thought to be (based on data from limited or mixed samples) dichotomous premolar morphological traits. Finally, because our data suggest that the differences in overall premolar vs. molar patterns may be related, at least in part, to resource utilization, we must recognize that ecological features, in addition to phylogenetic relationships, may influence the degrees of variation seen in fossil assemblages.

CONCLUSIONS

Our results confirm the existence of little or no dental sexual dimorphism in a living population of ring-tailed lemurs. The patterns of dental variation in this population are also consistent with the overall patterns seen among other primates. Because of the detailed ecological data available for this sample, we also suggest a potential role for ecology (e.g.,

TABLE 5. Dental metric variability compared between sexes[1]

Variable	Female			Male			F-ratio[2]
	CV	SE±	n	CV	SE±	n	
C^1 length	6.79	1.60	9	9.46	1.23	15	2.06
C^1 width	15.52	3.66	9	15.15	2.77	15	1.03
P^2 length	6.45	1.37	11	9.17	1.80	13	2.02
P^2 width	12.48	2.66	11	14.88	2.92	13	1.37
P^3 length	6.21	1.66	7	8.20	1.83	10	1.66
P^3 width	15.83	4.23	7	13.12	2.94	10	1.32
P^4 length	4.62	1.46	5	8.77	2.19	8	3.44
P^4 width	7.14	2.26	5	4.85	1.21	8	2.00
M^1 length	4.25	1.50	4	6.77	1.51	10	2.50
M^1 width	1.68	0.53	5	6.25	1.40	10	13.89*
M^2 length	1.84	0.75	3	5.86	1.38	9	10.13
M^2 width	3.68	1.50	3	4.20	0.94	10	1.63
M^3 length	0.68	0.34	2	10.13	2.16	11	232.00
M^3 width	3.83	1.91	2	7.66	1.56	12	4.90
P_2 length	5.21	1.51	6	7.82	2.26	6	2.27
P_2 width	13.23	3.83	6	13.55	3.92	6	1.00
P_3 length	4.48	1.30	6	7.94	1.99	8	3.17
P_3 width	15.33	4.85	5	7.73	1.93	8	4.61
P_4 length	5.08	1.36	7	4.90	1.42	6	1.07
P_4 width	4.14	1.11	7	12.82	3.70	6	8.79*
M_1 length	3.15	0.99	5	5.86	1.38	9	3.48
M_1 width	2.92	0.84	6	5.96	1.41	9	1.56
M_2 length	6.73	1.80	7	5.57	1.76	5	1.66
M_2 width	6.94	1.86	7	7.09	1.67	9	1.03
M_3 length	2.52	0.80	5	7.15	1.46	12	7.63
M_3 width	5.63	1.99	4	10.62	2.17	12	3.84
Maxillary tooth row length	1.03	0.26	8	2.76	0.56	12	7.25*
Mandibular tooth row length	6.11	1.64	7	2.36	0.53	10	7.18*
Palate breadth	3.09	0.77	8	2.97	0.61	11	1.02
Toothcomb length	3.94	1.05	7	2.57	0.61	9	2.41

[1] CVs and standard errors corrected for sample size following Sokal and Rohlf (1995). Measurements in mm.
[2] F-ratios based on standard deviations from Table 4.
* $P = 0.05$ (significant).

TABLE 6. Lemur catta *dental metrics: subadult descriptive statistics*[1]

	$\bar{\chi}$	σ	CV	N
P^2 length[2]	3.52	0.06	0.02	3
P^2 width	1.77	0.40	0.23	3
P^3 length	4.38	0.20	0.05	3
P^3 width	2.85	0.30	0.11	3
P^4 length	4.03	0.09	0.02	4
P^4 width	5.24	0.39	0.07	4
M^1 length	4.98	0.19	0.04	4*
M^1 width	5.94	0.41	0.07	4
M^2 length	5.33	0.23	0.04	3
M^2 width	6.50	0.45	0.07	4
P_4 length	4.61	0.08	0.02	4
P_4 width	2.90	0.10	0.04	3
M_1 length	5.05	0.24	0.05	4
M_1 width	3.40	0.11	0.03	4
M_2 length	5.28	0.29	0.06	3
M_2 width	3.78	0.13	0.03	3

[1] In mm.
[2] Due to cast quality, not all measurements were available.
* Significantly different from adults.

diet) as a compounding variable in understanding patterns of metric dental variation. Our results also indicate a greater amount of morphological variation in the dentition of ring-tailed lemurs than has been recognized by previous workers. As these data are from a known breeding population, they provide a confident measure of the degree of morphological variation that can be expected in a single-species primate sample. This in turn has important implications for understanding the fossil record. As the current data set also includes detailed life history and ecological data for each individual (e.g., Sussman, 1991; Sauther and Sussman, in preparation), the results of this study provide basal data for further analyses.

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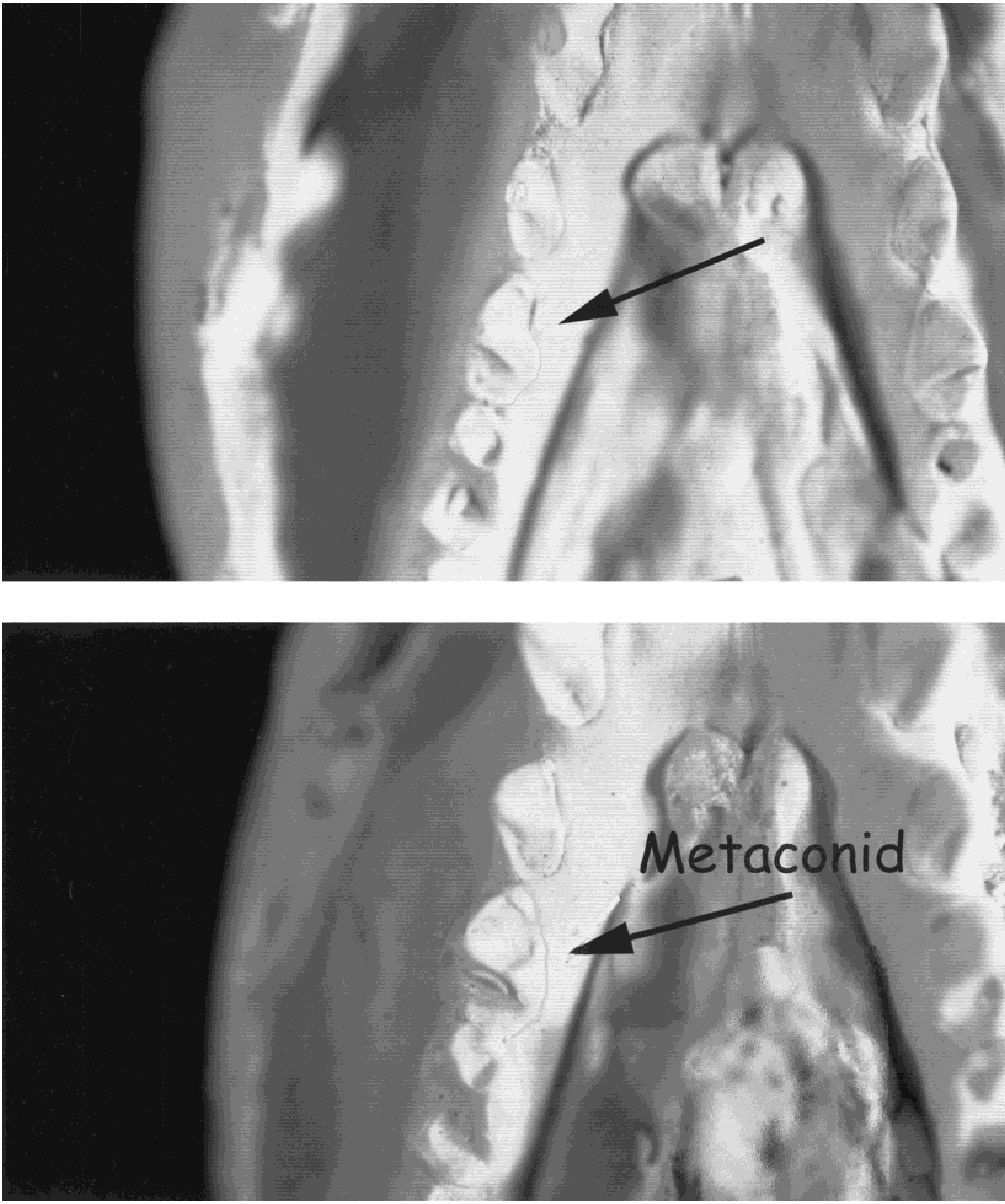

Fig. 3. Comparison of P_4 metaconid variation.

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