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Source: *Journal of Mammalogy*, Vol. 76, No. 4 (Nov., 1995), pp. 1127-1136
Published by: American Society of Mammalogists
Stable URL: http://www.jstor.org/stable/1382604
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ENAMEL THICKNESS AND DIETARY ADAPTATION AMONG EXTANT PRIMATES AND CHIROPTERANS

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Among fossil primates, thick enamel has been interpreted as an adaptation to hard-object feeding. However, correlations between thickness of enamel and diet have not been investigated rigorously among extant taxa. Thickness of enamel was compared within and between congeneric pairs that feed on hard and soft objects from two primate and three chiropteran families. Within each pair, the hard-object feeder exhibits relatively thicker enamel than its congener that feeds on softer items. However, there is overlap in both types of feeders, and the hypothesis that a specific value of enamel thickness be used to separate hard- and soft-object feeders is rejected. Dietary inferences based on thickness of enamel should be made only within an appropriate taxonomic context.

Key words: thickness of enamel, Primates, Chiroptera, dietary adaptation

Recent interest in tooth enamel has yielded a number of novel interpretations of growth, development, and diet for a variety of fossil primates (Beynon and Reid, 1987; Boyde and Martin, 1984; Bromage and Dean, 1985; Dean, 1987*a*, 1987*b*; Martin, 1983, 1985). Studies of enamel thickness among fossil apes and humans have been influential in providing a database for interpretations of dietary adaptations. Thick enamel commonly is associated with hard-object feeding (Andrews, 1981; Jolly, 1970; Kay, 1981; Martin, 1983; Simons, 1976). The explanation invoked in these cases is that thicker enamel resists wear longer than thinner enamel simply because more tissue must be removed before dentine is exposed. Indeed, increased thickness of enamel among cercopithecoids and cebids feeding on hard objects was reported by Kay (1981). Despite the recent attention given to identifying the taxonomic and functional components of thick enamel, some questions remain. For example, is thick enamel a response to a dietary shift toward hard-object feeding that is peculiar to primates or does it occur in other mammals? Another question of particular relevance to paleoecologists is whether an extinct species can be classified as either a hard- or soft-object feeder based upon thickness of enamel.

I address these questions by testing two specific hypotheses concerning thickness of enamel and dietary adaptation using samples of living primates and chiropterans with well-documented dietary regimes. The first hypothesis is that species consuming hard foods exhibit relatively thicker enamel than do closely related species that consume soft food items. The second hypothesis is that there is a threshold of relative thickness of enamel that separates all hard-object feeders from all soft-object feeders regardless of taxonomic affiliation, differences in body size, and variation in physical properties of specific food items.

Previous evaluations of enamel in primates have illustrated positive correlations between the absolute thickness of enamel and body mass (Kay, 1981; Molnar and Gantt, 1977). For lack of adequate sample size, however, relative thickness of enamel and dentinal area have not been subjected to statistical analysis (Martin, 1983). To as-

Journal of Mammalogy, 76(4):1127–1136, 1995

TABLE 1.—*List of sampled congeneric pairs. Within each pair, one hard-object feeding and one soft-object feeding species was sampled from a single genus. Assignments to feeding category (i.e., hard or soft) were made from assessments of dietary data found in the literature. In most instances, support for these assignments has been found in independent analyses of cranial and dental anatomy.*

Taxon	Type of feeder	References for dietary data	Supporting morphological data
Order Chiroptera			
Family Vespertilionidae			
Myotis velifer	Hard	Anthony and Kunz, 1977; Belwood and Fenton, 1976; Buchler, 1976; Kunz, 1974; Whitaker, 1972; Whitaker et al., 1977	Freeman, 1979, 1981*a*, 1981*b*
Myotis lucifugus	Soft		
Family Hipposideridae			
Hipposideros commersoni	Hard	Vaughn, 1977; Whitaker and Black, 1976	Freeman, 1979, 1981*a*, 1981*b*
Hipposideros caffer	Soft		
Family Molossidae			
Eumops underwoodi	Hard	Easterla and Whitaker, 1972; Ross, 1976	Freeman, 1979, 1981*a*, 1981*b*
Eumops perotis	Soft		
Order Primates			
Family Cebidae			
Cebus apella	Hard	Freese and Oppenheimer, 1981; Fleagle et al., Izawa, 1979; Izawa and Mizuno, 1977; Struthsaker and Leland, 1977; Terborgh, 1983	Kinzey, 1974; Rosenberger and Kinzey, 1976; Teaford, 1985; Teaford and Walker, 1984
Cebus capucinus	Soft		
Family Cercopithecidae			
Cercocebus albigena	Hard	Chalmers, 1968; Kingdon, 1974; Waser, 1977	Kingdon, 1974
Cercocebus torquatus	Soft		

sess this issue, values of relative thickness of enamel from a wide variety of mammals were collected and analyzed in the present study.

MATERIALS AND METHODS

Choice of species.—Chiropterans in this study are insectivorous microchiropterans. One species of each pair feeds primarily on hard and the other on soft insects (Table 1). Although all insects have a chitinous exoskeleton, the hardness of this layer varies such that some insects, such as beetles, crickets, and wasps, are hard, while others, such as mayflies, aphids and moths, are soft (Freeman, 1979; Strait, 1993). Experimental studies by Strait (1991) and Hepburn and Chandler (1976) have illustrated that soft-bodied insects are indeed pliant and ductile, while hard-bodied insects are tough and strong. Bats that eat hard insects have shorter, more robust skulls and mandibles and larger, but often fewer, teeth than do bats that specialize in soft prey items (Freeman, 1979, 1981*a*, 1981*b*). Taxa included in this study exemplify these dietary and morphological extremes.

Among primates, the families Cebidae and Cercopithecidae contain congeneric pairs of hard- and soft-object feeders. All of these species are generalized feeders that consume a wide variety of fruits, flowers, and leaves. However, one member of each pair also specializes in feeding on hard nuts or fruits. Within each pair the species that consumes hard foods exhibits greater robusticity in cranial or dental morphology than the species that consumes softer foods (Kingdon, 1974; Kinzey, 1974; Rosenberger and Kinzey, 1976; Teaford, 1985 Teaford and Walker, 1984).

To evaluate enamel thickness within a broader framework, 13 additional taxa including chiropterans, primates, insectivorans, microsyopids (a fossil family of unknown ordinal affinity), and a dermopteran were sampled (Table 2). These taxa are intermediate in size between the sampled primate and chiropteran pairs and permit an investigation of correlations between measures of

TABLE 2.—*Sample sizes for study of enamel thickness and estimates of body mass (in grams).*

Taxon	*n*	Body mass	Reference
Order Lipotyphla			
Atelerix albiventris	2	485	Kingdon, 1974
Erinaceus europaeus	2	912.5	Eisenberg, 1981
Order Chiroptera			
Balantiopteryx plicata	4	7.5	Walker, 1975
Eumops perotis	2	55	Vaughan, 1959
Eumops underwoodi	3	57.1	Cockrum and Gardner, 1960
Hipposideros caffer	3	9.7[a]	
Hipposideros commersoni	5	130	Kingdon, 1974
Myotis lucifugus	4	9	Eisenberg, 1981
Myotis velifer	3	13.1	Barbour and Davis, 1969
Rhinolophus simulator	1	16	Walker, 1975
Rhinopoma hardwickei	1	11	Kingdon, 1974
Rousettus amplexicaudatus	2	65[a]	
Taphozous mauritianus	3	22.5	Kingdon, 1974
Order Primates			
Cebus apella	1	2,620	Fleagle, 1988
Cebus capucinus	3	2,700	Eisenberg, 1981
Cercocebus albigena	2	7,690	Fleagle, 1988
Cercocebus torquatus	3	10,625	Fleagle, 1988
Galagoides alleni	2	295	Fleagle, 1988
Galagoides demidovii	1	60	Eisenberg, 1981
Homo sapiens	5	60,000	Eisenberg, 1981
Macaca fasicularis	1	4,030	Fleagle, 1988
Order Dermoptera			
Cynocephalus	3	1,250	Walker, 1975
Order incertae sedis			
Microsyops[b]	4		

[a] Based on data recorded for specimens housed at the Carnegie Museum of Natural History.

[b] Fossil taxa; no body-mass data.

thickness of enamel, body mass, and tooth size that are not unduly influenced by the relatively small body mass of chiropteran congeners or large mass of primate congeners.

Measurements of enamel thickness.—Thickness of enamel varies between teeth of the same individual as well as between different sections taken from the same tooth (Beynon and Wood, 1986; Martin, 1983). Therefore, to compare thickness of enamel from different individuals, measurements were collected from homologous teeth and identical planes of section. A lower first molar from each individual was embedded in polymethylmethacrylate and sectioned along a plane passing through the tips of the protoconid and metaconid downward through the cervix and often the anterior tooth root. The surface of the distal section was polished and lightly etched with 0.5% H_3PO_4 to more clearly differentiate the tooth from the embedding material. Each section was photographed using an Amray® 1810D electron microscope equipped with a solid-state backscattered electron detector (kv = 25, working distance = 24 mm, condenser lens = 3.5, emission current = 50–60, and aperture size = 200 μm). While an effort was made to sample only teeth that were not worn, dentine was slightly exposed at the tips of the cusps on several specimens. In these cases, the outlines of the enamel cap were reconstructed using the available contours of the enamel-dentine junction and outer surface of the tooth.

Area of enamel, length of the enamel-dentine junction, and area of dentine were measured on each specimen (Fig. 1) using Sigma Scan® digitizing software and a Summa Sketch® digitizing tablet. Two ratios describing thickness of enamel were calculated (Martin, 1983, 1985). Average

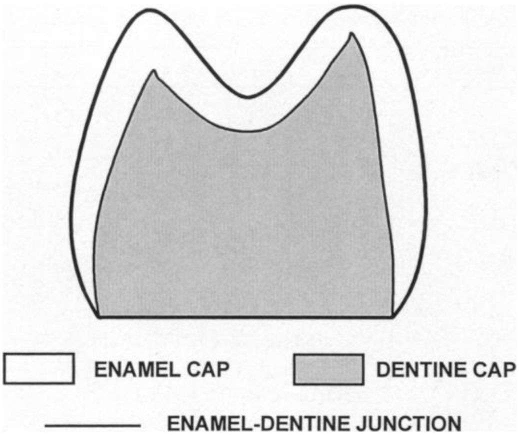

FIG. 1.—Diagram of a cross-sectioned tooth illustrating areas of enamel and dentine and length of enamel-dentine junction.

thickness of the enamel was calculated as the area of the enamel cap divided by length of the enamel-dentine junction. This average value was multiplied by 100 and divided by the square root of dentinal area to produce a value termed relative enamel thickness (Martin, 1983). Because it is adjusted for body size, relative enamel thickness is of particular interest in comparisons of taxa that span a wide range of body sizes.

These preparation techniques are destructive because relatively unworn teeth are removed from dentaries and sectioned with the result that they have little use for other analyses. Therefore, while this study encompasses a diverse sample of taxa, sample sizes for each species are necessarily limited.

Statistical analysis.—For comparisons within pairs of congeners, a specialized *t*-test for comparing a single specimen to a sample mean was used to evaluate the two species of *Cebus,* while the Wilcoxon two-sample test was used to evaluate differences between members of the other pairs (Sokal and Rohlf, 1981). A sign test was used to assess the pattern of differences between hard- and soft-object feeders across all pairs (Sokal and Rohlf, 1981). This nonparametric, paired-comparisons test assumes an equal probability of either species within each pair exhibiting the highest value of relative enamel thickness and is used to identify any nonrandom trend in differences between hard- and soft-object feeders across all sampled pairs.

Associations among enamel and dentinal measurements, body mass, and tooth size within the entire sample as well as among primates and chiropterans separately were assessed using Pearson's product-moment correlation analysis (Sokal and Rohlf, 1981). Estimates of body mass were obtained from the literature or directly from the label of the museum specimen (Table 2). To limit the effects on correlation coefficients of differences in magnitude between variables, all variables were transformed to a linear scale and submitted to a natural log transformation prior to analysis (Smith, 1984).

RESULTS

Comparisons between congeners.—Illustrated in Fig. 2 are the mean, ±1 *SE,* sample size, and probability values for comparisons of values of relative enamel thickness within the sampled pairs. In all cases, species that consume hard foods exhibit relatively thicker enamel than species of the same genus that consume soft foods. With the exception of *Myotis,* ranges of standard errors do not overlap within pairs. Although statistically significant differences are evident only between species of *Hipposideros,* results of a sign test indicate that the consistently higher values of relative enamel thickness among hard-object feeders within all five pairs of congeners is statistically significant ($P = 0.03$; Sokal and Rohlf, 1981).

Illustrated in Table 3 are sample sizes, means, and standard deviations of all enamel and dentinal measurements. Primate species that consume hard food items have shorter enamel-dentine junctions and less dentine than their congeners that feed on soft foods. Within each pair, the species with the absolutely largest teeth exhibits the absolutely largest area of enamel; this includes the hard-object feeding *Cebus apella* and the soft-object feeding *Cercocebus torquatus.* In contrast, chiropterans that consume hard foods uniformly exhibit larger areas of enamel and dentine and longer enamel-dentine junctions than their congeners that consume soft foods. This pattern exists even when the soft-object feeder has absolutely larger teeth (*Eumops*).

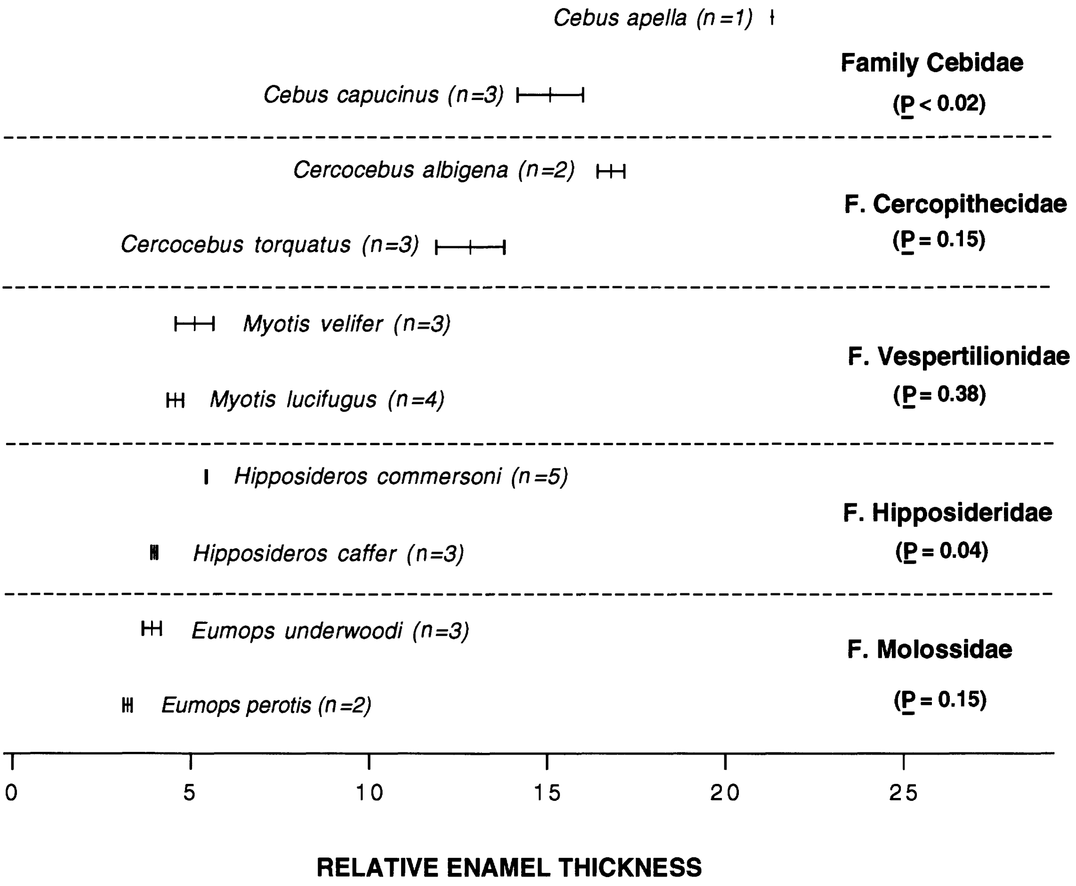

FIG. 2.—Mean and 1*SE* (vertical and horizontal bars, respectively) for relative enamel thickness among primate and chiropteran congeneric pairs of hard- and soft-object feeders. The sample size (*n*) is provided for each taxon and level of statistical difference (based on a Wilcoxon two-sample test or a specialized *t*-test comparing a single specimen to a sample mean) is given for comparisons within each pair.

Analyses of correlation.—Correlation coefficients for all possible comparisons between enamel and dentinal measurements, tooth size, and body mass based on the pooled sample of 23 taxa are presented in Table 4. As expected for variables that are components of the same structure, highly significant correlations ($P < 0.001$) characterize the relationships among virtually all pairs of enamel and dentinal measurements. The only exception is the slightly weaker ($P < 0.01$) association between relative enamel thickness and length of the enamel-dentine junction.

Results of separate correlation analyses for primate and chiropteran values of relative enamel thickness against tooth area and body mass appear in Table 5. With the exception of the weaker association between size parameters and relative enamel thickness among bats, the samples for both groups display similar patterns of association between the size variables and measurements of enamel and dentine.

DISCUSSION

The hypothesis that hard-object feeders have relatively thicker enamel than do closely related soft-object feeders is supported tentatively by the results of conge-

TABLE 3.—*Means and standard deviations (in millimeters) of enamel and dentinal values for sample congeneric pairs of hard-object and soft-object feeders.*

Taxon	Type of feeder	*n*	Area of tooth	Enamel area	Length of enamel-dentine junction	Dentine area	Enamel thickness	
							Average	Relative
Cebus apella	Hard	1	5.02	13.59	13.74	21.44	0.99	21.36
Cebus capucinus	Soft	3	4.35 ± 0.052	11.14 ± 1.256	14.81 ± 0.373	24.69 ± 0.383	0.75 ± 0.074	15.13 ± 1.587
Cercocebus albigena	Hard	2	6.89 ± 0.072	26.61 ± 0.205	21.91 ± 0.069	47.97 ± 1.925	1.17 ± 0.013	16.85 ± 0.530
Cercocebus torquatus	Soft	3	7.93 ± 0.204	38.40 ± 2.951	31.21 ± 2.572	92.71 ± 9.838	1.24 ± 0.118	12.89 ± 1.659
Eumops underwoodi	Hard	3	2.47 ± 0.196	1.43 ± 0.123	11.41 ± 1.142	10.47 ± 1.686	0.126 ± 0.009	3.91 ± 0.433
Eumops perotis	Soft	2	2.71 ± 0.098	0.998 ± 0.028	10.67 ± 0.254	8.33 ± 0.073	0.094 ± 0.005	3.24 ± 0.156
Hipposideros commersoni	Hard	5	2.48 ± 0.197	2.01 ± 0.353	11.67 ± 1.005	9.95 ± 2.378	0.171 ± 0.016	5.47 ± 0.224
Hipposideros caffer	Soft	3	1.22 ± 0.123	0.244 ± 0.014	4.95 ± 0.141	1.53 ± 0.076	0.049 ± 0.002	3.99 ± 0.130
Myotis velifer	Hard	3	1.37 ± 0.052	0.444 ± 0.090	5.81 ± 0.254	2.18 ± 0.183	0.076 ± 0.016	5.14 ± 0.919
Myotis lucifugus	Soft	4	1.01 ± 0.058	0.223 ± 0.033	4.37 ± 0.264	1.230 ± 0.101	0.051 ± 0.005	4.60 ± 0.416

neric comparisons (significant differences were found only between species of *Hipposideros*). In strong support of the first hypothesis, data presented in Fig. 2 illustrate that increased thickness of enamel is consistently associated with eating hard food items among congeneric pairs from phylogenetically disparate backgrounds. The results of a sign test, indicating a low probability ($P = 0.03$) of this pattern occurring randomly, demonstrate a strong functional association between thickness of enamel and dietary adaptation.

The hypothesis that a threshold value of enamel thickness separates hard-object feeders from soft-object regardless of taxonomic affiliation or variation in body size and the physical properties of specific food items can be rejected. Overlap in values of relative enamel thickness among hard- and soft-object feeders occur both within and between Primates and Chiroptera (Fig. 2).

In partitioning values of relative enamel thickness into the absolute value of enamel thickness, enamel-dentine junction length, and dentinal area, chiropteran and primate species that specialize on hard food items exhibit thicker enamel relative to their congeners through different patterns of proportion between enamel and dentine variables. That relatively thick enamel is achieved through different combinations of factors illustrates that thick enamel is analogous and has evolved independently on both familial and ordinal levels.

The significant association between enamel and dentine measurements, tooth size, and body mass (Table 4) is expected as all of these elements contribute to overall tooth morphology. In accord with the results of previous studies (e.g., Kay, 1981; Molnar and Gantt, 1977), relatively thick enamel is significantly associated with body mass and tooth size. However, values of relative enamel thickness exhibit the weakest associations with tooth size and body mass. This weak correlation suggests that the adjustment of size contained within the calculation of relative enamel thickness elim-

TABLE 4.—*Correlations among enamel and dentinal measurements, tooth size, and body mass. Measurements include tooth area (mesiodistal length X buccolingual breadth = AREA) and body mass (MASS). Abbreviations for enamel, dentine, and measurements of enamel-dentine junction are described in Table 3. Correlations involving body mass have a slightly lower sample size (*$n = 21$*) than do correlations that include tooth area (*$n = 22$*) or other combinations of variables (*$n = 23$*). Unless indicated, all correlation coefficients are highly significant (*$P < 0.001$*).*

	1	2	3	4	5	6	7
1. Area of tooth	0.88	0.51	0.86	0.89	0.84	0.92	1.00
2. Enamel area	0.92	0.59	0.92	0.92	0.92	1.00	
3. Length of enamel-dentine junction	0.87	0.45*	0.79	0.92	1.00		
4. Dentine area	0.90	0.50	0.84	1.00			
5. Average	0.93	0.67	1.00				
6. Relative enamel thickness	0.54	1.00					

* $P < 0.01$.

inates some, although not all, of the size component inherent in measurements of enamel volume.

Chiropterans and primates exhibit similar patterns of correlation between enamel and dentinal variables and both tooth area and body mass (Table 5). In both cases, values of relative enamel thickness lack a significant association with either tooth area or body size. Correlations involving enamel area are strong while those involving dentine area are weaker. A notable feature of these correlation results is the weaker association between relative enamel thickness and size variables among bats ($r = -0.20$ and -0.07) compared with primates ($r = 0.42$ and 0.43). There are several possible explanations for these dissimilar strengths of association.

One possibility is that the methods of measuring relative enamel thickness and dentine area developed for primates (Martin, 1983) may not be appropriate for chiropteran teeth. The dramatic differences in dental morphology between primates and chiropterans (i.e., bunodont versus high-crowned sectorial molars) supports this suggestion. Differences in ranges of body mass among primates and chiropterans constitute a second possible cause of the different strengths of correlation within these groups. Although all variables were transformed to a linear scale and logged, the larger range of primate body mass compared to chiropteran body mass may have influenced the correlation analysis (Smith, 1984).

A third explanation for different patterns of correlation between relative enamel thickness and body mass among chiropterans and primates rests on a consideration of

TABLE 5.—*Correlations between enamel and dentine variables and both tooth area and body mass among chiropterans and primates.*

	Tooth area		Body mass	
Variable	Chiroptera ($n = 10$)	Primates ($n = 8$)	Chiroptera ($n = 11$)	Primates ($n = 8$)
Relative enamel thickness	−0.20	0.42	−0.07	0.43
Enamel area	0.90***	0.93***	0.91***	0.93***
Length of enamel-dentine junction	0.87***	0.86**	0.87***	1.00***
Dentine area	0.82***	0.79**	0.87***	1.00***
Average enamel thickness	0.74**	0.86**	0.83*	0.85***

** $P < 0.01$.
*** $P < 0.001$.

the mass requirements of chiropteran flight. Among flying animals, the largest variety of wing sizes and shapes are found among taxa with body mass ranging from 10 to 100 g (Pennycuik, 1986). Within this size range, requirements for wing size and shape are more relaxed than for either larger or smaller animals. Insectivorous chiropterans are continually faced with foraging for mobile prey and require a wide repertoire of flight characteristics (Hill and Smith, 1984). For these taxa, it is possible that maintaining a body weight between 10 and 100 g permits a plastic response to changes in availability of prey items and capabilities of predator detection. Dental enamel is the densest tissue in the vertebrate body (Brand and Isselhard, 1986; Osborn, 1981). Given the possible advantage among insect-feeding bats of constraining body mass, limiting the relative amount of enamel as body size increases may be one means of minimizing weight.

SUMMARY AND CONCLUSIONS

Among living mammalian taxa with known dietary habits, relative thickness of enamel is an accurate although broad indicator of dietary habits. Increased enamel thickness is a common correlate of hard-object feeding as illustrated by its high degree of convergence over higher-level taxonomic categories.

Data presented here can be used as a base from which analogies to fossil primates and other mammals can be made. However, these data demonstrate that interpretations of dietary adaptation to feeding on hard foods cannot be made from taxonomically isolated samples. There is no threshold value of relative enamel thickness that separates hard-object feeders from soft-object feeders either within or between orders.

It is unclear whether this result should be attributed to the sensitivity of relative enamel thickness to differences in body size or to variation in the physical properties of specific food items that are obscured by the general terms hard and soft. In either case, values of enamel thickness obtained from a single species are not adequate information with which to infer an adaptation to either hard or soft foods. Even in the presence of comparative information, caution must be exercised when using relative enamel thickness to infer dietary specializations.

ACKNOWLEDGMENTS

I thank curators at the following institutions for the loan of specimens used in this study: Academy of Natural Sciences, Philadelphia; Carnegie Museum of Natural History; Department of Anatomical Sciences, State University of New York at Stony Brook; Department of Zoology, University of Michigan; Florida Museum of Natural History; Florida State Museum; Midwestern State University; Museum of Southwestern Biology, University of New Mexico; Museum of Vertebrate Zoology, University of California at Berkeley; Texas Tech University Museum. I also thank D. Krause, W. Jungers, and S. Strait for comments regarding this manuscript and L. Martin and F. Grine for access to and assistance with scanning electron microscopy. This project was supported by a National Science Foundation dissertation improvement grant (BNS 8922966).

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Submitted 9 March 1994. Accepted 19 January 1995.

Associate Editor was Patricia W. Freeman.