

## THE DIET OF WORMS: AN ANALYSIS OF MOLE DENTAL MICROWEAR

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We compared microwear from shearing facets of lower molars from *Parascalops breweri* (the hairy-tailed mole) and *Scapanus orarius* (the coast mole) with that from other small mammal species including a tenrec, a hedgehog, 3 primates, and 2 bats. The 2 mole species exhibit a distinct microwear pattern that is characterized by many short, narrow scratches, and relatively few pits. Although the molars of the streaked tenrec (*Hemicentetes nigriceps*) differ profoundly in morphology from those of moles, they show a very similar pattern of microwear on their shearing facets. This common pattern (missing in the rest of the comparison sample) is likely a product of the importance of earthworms in the diets of both *H. nigriceps* and the moles and is plausibly explained by the interaction between teeth and soil from the inside and outside of earthworms. These results may be useful in interpreting microwear patterns in fossil mammals.

Key words: dental microwear, *Hemicentetes*, moles, *Parascalops*, *Scapanus*, tenrecs

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The use of dental-microwear analysis as a tool for dietary reconstruction of extinct organisms relies on possession of a database of modern analogs. It is particularly necessary to look at microwear in a sampling of modern taxa that includes all likely or plausible dietary components or that comprises the conceivable range of physical properties of food items. Much of the work done on modern small-mammal microwear has focused on attempts to reconstruct dietary behavior in primates (Crompton et al. 1998; Jablonski and Crompton 1994; Strait 1991, 1993, 1997; Teaford et al. 1996). For that reason, most modern taxa selected as analogs are either primates or species whose diets are similar to those of extant primates. Modern primates can be placed in many different dietary categories, including

primarily insectivorous or faunivorous forms such as galagos and tarsiers, folivores such as colobine monkeys, frugivores including orangutans, and more generalized omnivores like chimpanzees and modern humans (Fleagle 1999). Nonprimate taxa considered useful analogs include bats and marsupials of insectivorous or frugivorous habits (Strait 1991), which generally occupy a niche space similar to that of extant primates.

It may be a mistake, however, to limit the study of modern analogs to primates or to animals whose dietary range includes a similar cross section of foods. This is true even if one's primary interest is in reconstructing ancient primate behavior and particularly if one wishes to reconstruct diets in nonprimate fossil taxa, because there are dietary categories that are missing from the typical repertoire of modern primates. Also,

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primate diets tend to be rather complex. Howler monkeys, for example, are primarily folivorous, including not only a wide range of different leaves in their diets, but also flowers and fruits when these foods are available (Milton 1980; Teaford and Glander 1996). This range of variation can make microwear patterns complicated to analyze. For this reason, modern primates do not provide a full range of possible comparisons for microwear analyses in fossil mammals in general.

One example of a food item that is underrepresented in primate diets is earthworms. The analysis of dental microwear in animals such as moles, that include a high proportion of earthworms in their diet, is certainly a necessary 1st step to identifying such a dietary emphasis in fossil mammals. However, effects of earthworm-eating may also be more broadly interesting. Earthworms present some generally interesting challenges from the point of view of physical properties. Oral processing of earthworms will inevitably require the teeth to come into contact with small particles of soil. As evidence of this, earth was found in stomach contents of the earthworm-eating streaked tenrec, *Hemicentetes nigriceps* (Eisenberg and Gould 1970).

Annelids are not the only food source that is likely to incorporate soil. Any kind of root, tuber, or grub will be soil-covered if eaten without washing. Among modern primates, for example, the baboon *Papio* is known to ingest tubers and corms when available (Altmann 1998; Altmann and Altmann 1970; DeVore and Hall 1965; Post 1982). Modern humans also include tubers and roots as part of their diet, and it has been hypothesized that the ingestion of these foods in the dirty state could have left its mark on prehistoric hominoid teeth (De Bonis and Koufos 1994; Pastor and Johnston 1992; Ungar 1996). Earthworms, however, are distinct from most other soil-covered food sources in that they lack other elements that are likely to produce microwear features. In addition, they contain a par-

ticularly large concentration of soil because it is found both inside the gut and outside the body. For these reasons, animals that eat a high proportion of earthworms give us a natural experimental model for effects of soil on teeth.

This study aims to test the hypothesis that molar dental microwear in mammals that eat earthworms will be distinct from that observed in mammals whose diets do not generally include foods that contain or are covered in soil. Toward this end, we analyzed microwear on the shearing facets of lower molars from 2 mole species (the hairy-tailed mole, *Parascalops breweri*, and the coast mole, *Scapanus orarius*) to provide insights into the microwear signature from earthworm-eating, in an attempt to shed light on more general effects of soil mastication. An additional earthworm-eating taxon, the tenrec (*H. nigriceps*), was also analyzed as a control for differences in tooth shape. Tooth shape is a variable that is not generally controlled for in microwear studies (Gordon 1988), but it might be predicted that differences such as inclination of tooth facets and degree to which a tooth is high-crowned may affect the pattern observed. If, however, taxa with very different tooth shapes share a microwear pattern, it follows that this is more likely to represent a general pattern that can be tied to properties of the common food items.

Animals that include a significant proportion of earthworms in their diets are generally of small body size, so the most appropriate taxa for comparison with these taxa are other small mammals. Small body size limits an animal's ability to ingest leaves and other foods that require extensive postoral processing (Cork 1994; Kay and Hylander 1978; McNab 1986; Nagy 1987). Apart from this constraint, however, small mammals include in their diets virtually everything imaginable, from insects, lizards, and fish, to fruit, flowers, and gums. Taxa having a variety of different diets were included in this study, in an attempt

TABLE 1.—Taxa examined for dental microwear in this study. Basis = type of data used to infer dietary information (S = stomach contents, F = fecal analysis, O = observations of feeding).

Species	Diet	Basis	Reference
<b>Chiroptera</b>			
<i>Noctilio leporinus</i>	47% insect, 53% fish	S	Flemming et al. (1972)
<i>Myotis blythii</i>	100% insects (65.1% Tettigoniidae, 18.7% Lepidoptera larvae, 7.7% cockchafers)	F	Arlettaz and Perrin (1995)
<b>Primates</b>			
<i>Galago alleni</i>	73% fruit, 25% insects	S	Charles-Dominique (1977)
<i>Tarsius bancanus</i>	89% insects, 11% vertebrate prey	O	Niemitz (1984)
<i>Galago demidovii</i>	70% animal matter, 19% fruit, 10% gums	S	Charles-Dominique (1977)
<b>Insectivora</b>			
<i>Hemiechinus auritus</i>	99% invertebrates (87% insects)	O?	Zherebtzova (1982)
	Insects, bacrachians, lizards, snakes, small birds, and mammals	O?	Roberts (1977)
<i>Scapanus orarius</i>	69.9% earthworms, 25.1% Diptera, 1.6% Lepidoptera, 0.9% Coleoptera, 0.6% Chilopoda, 0.3% Orthoptera, 0.2% Hymenoptera, 1.2% vegetable matter	S	Moore (1933)
	93% earthworms, 2% slugs, 2% larval insects, 1% adult insects,	S	Glendenning (1959)
	56.2% earthworms, 8.7% adult insects, 7.4% insect larvae, 6.7% centipedes & millipedes, 6% mouse/shrew remains, 5.2% insect pupae, 7.8% fungi	S	Whitaker et al. (1979)
<i>Parascalops breweri</i>	34% earthworms, 29% insect larvae and pupae, 18% adult insects, 2% millipedes and centipedes, 1% snails and slugs, 1% sowbugs, 2% sand and rootlets, 14% detritus	S	Eadie (1939)
<i>Hemicentetes nigriceps</i>	~100% earthworms (with ingested earth, arachnoid abdomen)	S	Eisenberg and Gould (1970)

to represent a cross section of dietary categories (Table 1).

One problem inherent to studying small mammals is that direct observation of their behavior is difficult. In most cases, therefore, dietary information is acquired indirectly, by examining either stomach contents or fecal remains (Table 1). Clearly, neither of these methods is ideal because foods that are easily broken down or are difficult to identify will be underrepresented. Also, the limited information available for most taxa means that temporal and geographic variations are rarely studied. These factors can profoundly affect what is known

of a taxon's diet and of the resulting microwear signature (Teaford and Glander 1996). Thus, data in Table 1 for fine-scale quantitative differences in diets should be interpreted with caution.

#### MATERIALS AND METHODS

Species studied included 2 chiropterans (*Noctilio leporinus*, the fisherman bat, and *Myotis blythii*, the lesser mouse-eared bat); 3 primates (the dwarf galagos, *Galago alleni*, *G. demidovii*, and the Bornean tarsier, *Tarsius bancanus*); and 4 insectivores (*S. orarius*, *P. breweri*, *H. nigriceps*, and the long-eared desert hedgehog, *Hemiechinus auritus*). All these species eat animal

matter, with 3 of the insectivores having a large component of earthworms in their diet (Table 1). Only taxa with mean body weights between 30 and 300 g were included (Nowak 1991). These particular species were selected because quantitative information on their diets was available (Table 1). Only wild-caught specimens were used (all from the collection of the National Museum of Natural History, Washington D.C.). Ages of individuals were unknown, but micrographs were only taken from fully erupted adult teeth. Individuals with very heavily worn teeth were excluded for 2 reasons. First, this method controls for possible ontogenetic changes in diet, although previous studies have found no significant ontogenetic changes in microwear signature (King et al. 1999). Second, as a tooth becomes worn down, its shearing facets may occupy less area. When working with small mammals, even micrographs taken at a magnification of 500 $\times$  will encompass much of the area of the facets under study. As animals age and the area available for sampling decreases, it becomes very difficult to obtain a useable micrograph.

Lower 1st and 2nd molars were carefully cleaned with acetone and sterile laboratory swabs (VWR, New Milford, Connecticut) under a dissecting binocular microscope. Impressions were taken with President Jet Regular Body polysiloxane (Coltene/Whaledent Inc., Mahwah, New Jersey) delivered by a fine-caliber intraoral tip. Araldite GY 506 Epoxy resin mixed with HY956 hardener (Ciba-Geigy, Bridgeport, Connecticut) was poured into the molds using a plastic transfer pipette and a micropipette when necessary, and the impressions were centrifuged for 2 min at 1,000 rpm. The casts were affixed to stubs for scanning electron microscopes (Structure Probe Inc., West Chester, Pennsylvania) using Duco Cement (DuPont, Wilmington, Delaware), and their bases were painted with silver paint (Structure Probe Inc.) to ensure good conduction. Casts were then sputter-coated before being placed in an AMRAY 1810 scanning electron microscope (Amray Inc., Bedford, Massachusetts). All pictures were taken from shearing facets. Crushing facets were not studied because they were very difficult to clean in these small mammals. By contrast, position of shearing facets made them relatively easy to clean. When possible, the facet on the talonid side of the hypoflexid of m1 was used. When the talonid facet of m1 was obscured, the facet on the buccal side

of the trigonid of m1 or either facet on m2 was used. Only a single facet was sampled from each individual. The combined use of different shearing facets is justified by findings that interspecific variability is generally greater than interfacet variability within a species (Teaford and Walker 1984).

All scanning electron micrographs were taken in secondary emissions mode at a magnification of 500 $\times$  and a working distance of 12 mm. In taking micrographs, specimens were oriented as perpendicular as possible to the electron beam. Precise methods of standardizing orientation were rendered impossible by differences in tooth shape between various taxa. Thus, only a measure of the homogeneity of feature orientation (R; as described by Ungar 1994) was analyzed. For this measurement, differences in orientation between micrographs (such as those in Fig. 1) are irrelevant.

An area of standardized size, corresponding to a field of view of 0.02 mm<sup>2</sup> on the original teeth, was digitized from each micrograph using Microwear 3.0 $\beta$  (Ungar 1997). In some micrographs, the number of features observed exceeded the maximum allowed in this program (999), and in others, part of the image was obscured. In these cases, the grid option in Microwear 3.0 $\beta$  was used to section off a portion of the micrograph to be digitized. Feature totals were then adjusted to be comparable with other images (Strait 1991). A total of more than 1,000 features for any micrograph may seem high to workers in microwear. These high counts are probably a product of a size-scaling effect with very small mammals (i.e., there are more, smaller features in a given area) and the fact that all the specimens used in this analysis were exceptionally clean so that even very tiny pits and scratches could be counted. Features that extended outside the field of view were measured to the edge of the image. Because this was done consistently for all specimens, this practice should not introduce any systematic bias to the results.

All statistical tests were performed using SYSTAT 8.0. The variables recorded for each individual were number of features (R; number of scratches + number of pits), number of scratches, number of pits, scratch length, scratch width, homogeneity of scratch orientation (R; the degree to which scratches are oriented in the same way—Ungar 1994), and pit width. Percentage of pits relative to total number

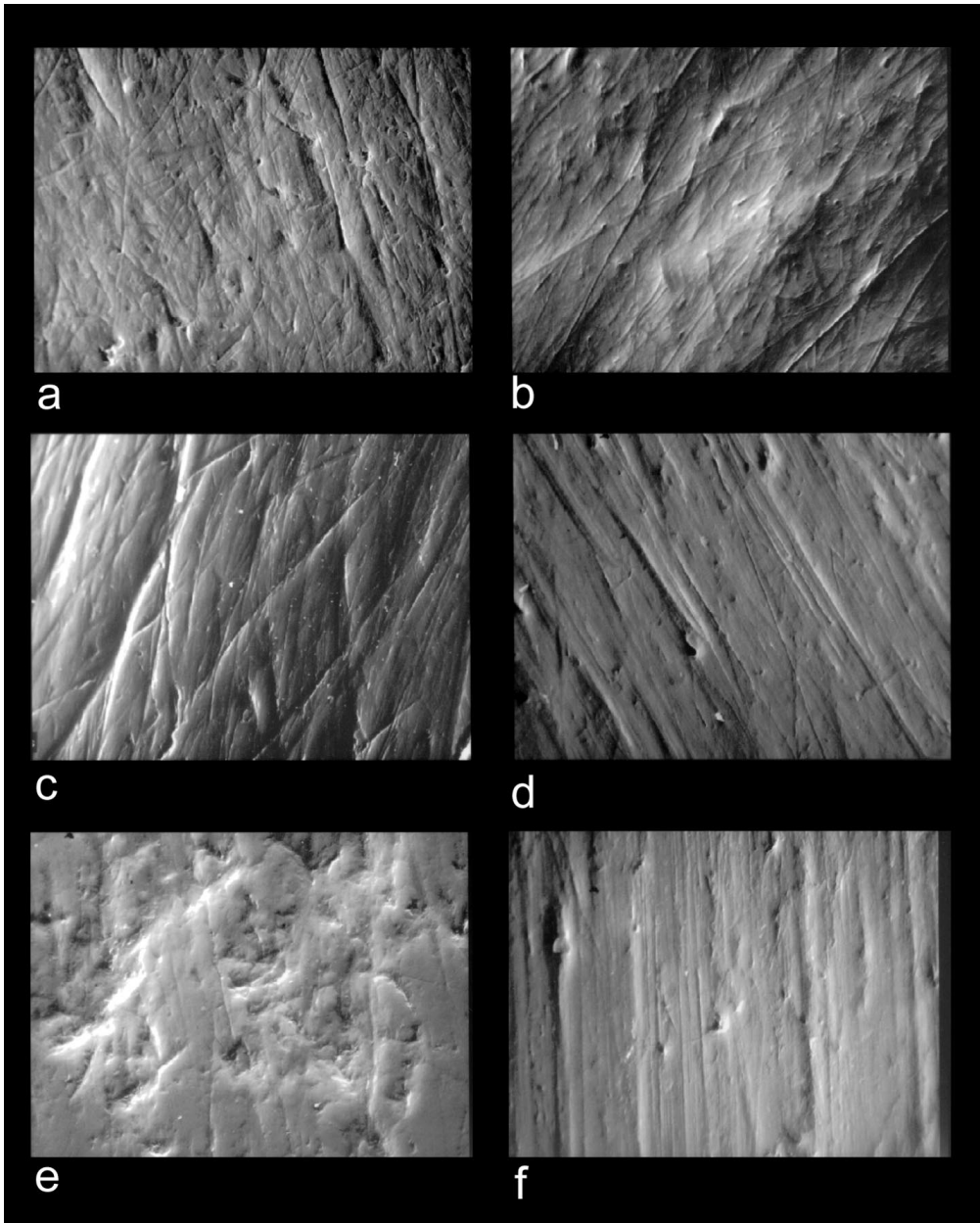


FIG. 1.—Microwear from shearing facets of the lower molars of a) *Scapanus orarius* (coast mole), b) *Parascalops breweri* (hairy-tailed mole), c) *Hemicentetes nigriceps* (streaked tenrec), d) *Myotis blythii* (lesser mouse-eared bat), and e and f) *Galago alleni* (dwarf galago).

of features (calculated as the number of pits divided by the total number of features) was also computed and used in these analyses.

For each variable, the overall analysis of variance (omnibus ANOVA) indicated whether there were any significant differences between

means. When the omnibus ANOVA was significant at the  $\alpha = 0.05$  level, Tukey post hoc tests were used to locate differences between mean values for different species. Log or rank transformations were performed, when necessary, to make data conform better to assumptions of nor-

malinity and equality of variances. It proved unnecessary to transform the variables number of features and number of scratches. Pit number and percentage of pits were log transformed, whereas the remaining variables (scratch length, scratch width, homogeneity of scratch orientation, and pit width) were rank transformed. With these transformations, all variables successfully passed Lilliefors test for normality. Variables were not excluded if they failed Bartlett's test for equality of variance (even after transformation) because of the susceptibility of this test to small sample sizes and nonnormal distribution and because of the robustness of single-factor ANOVA (Zar 1984). Although this may be seen as a reason not to perform transformations, using transformed data that conform better to the assumptions of ANOVA whenever possible increases confidence in the validity of our results.

Principal components analysis (PCA) was also performed to highlight patterns in the data (Dunteman 1989). This method assigns similar values to taxa that vary in similar ways, allowing a clearer separation of groups, in some cases, than afforded by analysis of variables in isolation. In this way, PCA can make a valuable addition to microwear studies, particularly when only small sample sizes are available (as is often the case when working with fossil taxa). This could allow an appreciation of a coordinated pattern of distinctive characteristics that could be related to physical properties of food, tooth shape, etc.

## RESULTS

*Analyses of variance.*—For most of the variables, there were significant differences between species at the  $\alpha = 0.05$  level, with the only exception being the variable total feature number ( $P = 0.061$ ; Table 2). In general, the 2 moles (*P. breweri* and *S. orarius*) and the 1 tenrec (*H. nigriceps*) had many scratches and relatively few pits on their shearing facets (Table 2; Figs. 1a–c). The latter is particularly evident for *P. breweri* and *H. nigriceps*, which have a significantly lower percentage of pits than the other taxa, including the other mole. In addition, scratches on teeth of the tenrec and the moles are relatively short and narrow. This is especially clear in comparison with

the lesser mouse-eared bat, *M. blythii*. Although this chiropteran has relatively few scratches, it also has relatively few pits and, overall, the lowest total feature counts (although this difference is not statistically significant). The scratches largely cover the sampled surface (Fig. 1d). Although this is similar to the situation in the tenrec and the moles, for *M. blythii* scratches are less numerous but significantly longer and wider than scratches for most of the other taxa, including *H. nigriceps*, *S. orarius*, and *P. breweri* (Table 2).

*Principal components analysis.*—Among all 62 individuals in this study, the 1st principal component accounted for 51.2% and the 2nd for 33.0% of total variance (Fig. 2). The 1st principal component has high negative loadings on feature count variables (particularly number of features) and high positive loadings on variables representing feature characteristics (particularly pit width and scratch length). Thus, taxa with low values on the 1st component have numerous features and generally short scratches and narrow pits. The 2nd component has high positive loadings on pit characteristics (particularly percentage pits and number of pits) and high negative loadings on scratch characteristics (number of scratches and homogeneity of scratch orientation). Individuals with low scores on the 2nd component have relatively few pits and many regularly oriented scratches.

The PCA plot (Fig. 2) shows a fairly distinct cluster for the moles and the tenrec, which generally have low scores on both 1st and 2nd principal components. *M. blythii* specimens also cluster fairly well together, with high values on the 1st component and values around 0 on the 2nd. *N. leporinus* specimens form an even more distinct cluster between  $-1.3$  and  $0.3$  on the 1st component, and between  $-0.2$  and  $1.3$  on the 2nd. The other taxa cluster less well.

## DISCUSSION

Moles (at least the 2 species sampled here) show a pattern of molar microwear

TABLE 2.—Variables quantifying dental microwear. Sample size,  $n$  = number of individuals sampled. Statistics for omnibus ANOVA shown at bottom of table ( $d.f. = 8, 53$ ). Superscript values indicate results of the post hoc Tukey tests; each superscript refers to the species differing significantly at the  $\alpha = 0.05$  level. Species 7, 8, and 9 have diets abundant in earthworms (diet described in Table 1).

Taxon	$n$	Number of features		Number of scratches		Number of pits	
		$\bar{X}$	$SE$	$\bar{X}$	$SE$	$\bar{X}$	$SE$
1. <i>Hemiechinus auritus</i>	6	772.83	105.26	295.83 <sup>7-9</sup>	44.67	479.83 <sup>7</sup>	97.51
2. <i>Tarsius bancanus</i>	8	699.63	81.24	277.63 <sup>7-9</sup>	33.40	422.00 <sup>7</sup>	54.46
3. <i>Galago alleni</i>	5	869.80	89.29	394.40 <sup>7,9</sup>	50.19	475.40 <sup>7</sup>	101.66
4. <i>Galago demidovii</i>	4	908.75	162.27	434.50 <sup>9</sup>	45.70	474.25	124.85
5. <i>Noctilio leporinus</i>	8	894.75	45.46	394.00 <sup>7,9</sup>	26.97	500.88 <sup>7,9</sup>	34.88
6. <i>Myotis blythii</i>	11	641.73	61.29	277.91 <sup>7-9</sup>	21.18	363.82	152.89
7. <i>Parascalops breweri</i>	10	762.50	22.89	559.20 <sup>1-3,5,6</sup>	23.73	203.30 <sup>1-3,5,8</sup>	11.02
8. <i>Scapanus orarius</i>	7	929.43	90.06	503.14 <sup>1,2,6</sup>	42.51	426.14 <sup>7</sup>	52.45
9. <i>Hemicentetes nigriceps</i>	3	874.08	74.51	662.85 <sup>1-6</sup>	26.27	211.23 <sup>5</sup>	48.26
Statistical values							
$P$ , ANOVA		0.061		<0.001		<0.001	
$F$ , ANOVA		2.02		14.06		4.55	

distinct from microwear in a range of small mammals that do not eat earthworms. Specifically, shearing facets of moles are marked by very numerous, short, narrow scratches and relatively few pits. This pattern seems consistent with a diet that forces teeth to shear against soil while processing food.

It is possible that this distinctive pattern reflects some element of phylogeny, tooth size or shape, or method of mastication, rather than diet. However, studying facets that play the same functional role in chewing (i.e., shearing) acts as a control for differences in method of mastication. Limiting the size range of taxa somewhat controls for tooth size.

Inclusion of the earthworm-eating tenrec *H. nigriceps* serves as a crucial test of the dietary basis for the microwear signature documented in the moles. The tenrec is significantly larger than either mole (with a maximum weight of 280 g for *H. nigriceps*, compared with only 170 g for *S. orarius*, the larger of the 2 moles—Nowak 1991) and has teeth that are markedly different morphologically. *H. nigriceps* has zalambodont molars, with very tall trigonids and

extremely reduced talonids. Moles show a dilambodont pattern, with trigonids and talonids that are nearly equal in height. These profound differences in tooth shape also suggest differences in method of mastication. Therefore, *H. nigriceps* is comparable to moles only in being an insectivore that eats a diet rich in earthworms. The fact that *H. nigriceps* generally covaries in number of scratches and percentage of pits with *P. breweri*, the more extreme of the 2 moles in demonstrating the pattern described previously, provides strong support for the interpretation that this pattern is diet related. This is clearly demonstrated by the PCA. As is evident in Fig. 2, *H. nigriceps* clusters with the moles, particularly with *P. breweri*. The moles and *H. nigriceps* do not cluster with the other insectivore, *H. auritus* (a hedgehog), which suggests that this pattern is related to diet rather than phylogeny.

Two other taxa emerged from this study as having particularly interesting microwear patterns. *M. blythii* has distinctive teeth, with unusually wide and long scratches that are regularly oriented (Table 2). This bat consumes a diet of 100% insects. It is possible that this pattern is related to this spe-

TABLE 2.—Extended.

Scratch length ( $\mu\text{m}$ )		Scratch orientation		Scratch width ( $\mu\text{m}$ )		Pit width ( $\mu\text{m}$ )		% pits ( $\mu\text{m}$ )	
$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
10.49	1.03	0.597	0.093	1.03 <sup>3,4,7-9</sup>	0.071	1.26	0.086	59.76 <sup>7,9</sup>	6.09
11.19	1.04	0.638	0.056	0.98 <sup>4,7-9</sup>	0.044	1.26 <sup>5</sup>	0.039	59.79 <sup>7,9</sup>	2.61
9.70	1.03	0.697	0.087	0.84 <sup>1,6</sup>	0.011	1.13 <sup>6</sup>	0.027	52.41 <sup>7,9</sup>	7.99
8.66 <sup>6</sup>	1.36	0.737	0.027	0.79 <sup>1,2,6</sup>	0.031	1.23	0.064	49.27 <sup>7,9</sup>	5.88
9.92 <sup>6</sup>	0.41	0.631 <sup>6</sup>	0.031	0.86 <sup>6,7,9</sup>	0.014	1.09 <sup>2,6,7</sup>	0.017	55.83 <sup>7,9</sup>	2.37
15.48 <sup>4,5,7-9</sup>	1.50	0.800 <sup>5</sup>	0.037	1.11 <sup>3-5,7-9</sup>	0.038	1.38 <sup>3,5,8,9</sup>	0.040	55.27 <sup>7,9</sup>	2.39
10.08 <sup>6</sup>	0.20	0.708	0.018	0.75 <sup>1,2,5,6</sup>	0.017	1.22 <sup>5</sup>	0.028	26.78 <sup>1-6,8</sup>	1.44
9.56 <sup>6</sup>	0.36	0.726	0.031	0.81 <sup>1,2,6</sup>	0.020	1.14 <sup>6</sup>	0.026	45.42 <sup>7,9</sup>	1.75
8.85 <sup>6</sup>	0.47	0.761	0.042	0.70 <sup>1,2,5,6</sup>	0.042	1.10 <sup>6</sup>	0.058	23.57 <sup>1-6,8</sup>	3.51
0.002		0.050		<0.001		<0.001		<0.001	
3.76		2.12		21.80		6.70		19.89	

cialized diet, not found in any of the other species in this study. This taxon also has very high-crowned teeth, so it seems likely that tooth shape may play a role in the distinctiveness of this pattern, particularly in

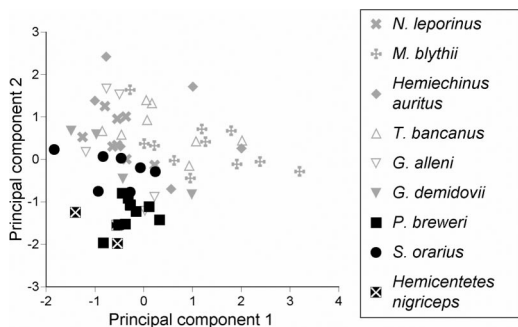


FIG. 2.—Bivariate plot of individual scores on principal components 1 and 2. Component 1 accounts for 51.2% and component 2 for 33.0% of total variation. Earthworm-eating moles and the tenrec (black symbols) cluster in the lower left-hand corner of plot. Specimens of *Noctilio leporinus* also form a fairly distinctive cluster, indicating that its members generally covary in number, morphology, and regularity of orientation of their microwear features. Diet of species shown in Table 1.

the notable length of the scratches. Further comparisons, incorporating a reference sample including more insect specialists with a range of tooth shapes, would be needed to better understand this pattern.

By contrast, the fisherman bat (*N. leporinus*) was not particularly distinctive, although specimens did form a strong cluster in the PCA (Fig. 2). As its name suggests, the diet of this bat includes high proportions of fish (Fleming et al. 1972). The distinctiveness of this form only in the context of the multivariate PCA suggests that it may be necessary to consider a variety of variables simultaneously to identify this unusual diet in a fossil taxon. In other words, no single variable appears to provide a strong signal for fish-eating, but covariance in a suite of variables may allow recognition of this diet.

The other taxa were not distinguished either in ANOVA or in the PCA, possibly because of relatively low sample size. This lack of coherence may have a more satisfying explanation, however. Marked variability among individuals was notable for several taxa and is particularly clear for *G.*

*alleni*, for which we had 2 sharply contrasting micrographs (Figs. 1e and 1f). It is clear from differences in these 2 images that individuals must have eaten rather different foods, with the large pits in Fig. 1e likely reflecting a diet richer in hard food. This suggests that the less well-clustered taxa in the PCA plot represent groups in which teeth of different individuals have encountered different ranges of physical properties relative to the diet of the taxon as a whole. This contrast reveals 1 difficulty for museum-based microwear analysis that relies on published information for dietary information. As a result of the relatively short "lifespan" of microwear, with features in some circumstances being created and obliterated within 24 h (Teaford and Oyen 1989), omnivorous taxa in which each individual eats a wide range of food on a regular basis could show very different microwear patterns from species in which individuals specialize over a short term on a particular food and then switch to another food. Yet, in the literature, both taxa may be presented as having similar omnivorous diets. Therefore, when recording and reporting dietary information on omnivores, it is important for microwear analysis to distinguish between taxa in which all members are year-round generalists and those in which members alternate between short-term (perhaps seasonal) specializations.

Results of this study have implications for future investigations of any mammal that may include soil-covered food in its diet. Specifically, an unusual preponderance of short, narrow scratches on the molar shearing facets may signal ingestion of soil on food. However, a number of other factors can influence this microwear pattern. For instance, many soil-covered foods will have physical properties different from those of earthworms. Eating tubers, for example, requires the teeth to break down plant cell walls, possibly leading to wider scratches (as seen in some leaf-eating larger mammals—King et al. 1999). Hard objects, such as shellfish, may be covered with sand,

but their consumption would likely produce more numerous, larger pits than observed here for earthworm-eating taxa (Teaford and Walker 1984). This might also be the case for acidic food (e.g., fruit), independent of how much dirt was on their exterior. Also, soil can have many different grain sizes and shapes (Ungar 1994). For example, as particle size increases, a threshold will be crossed from fine abrasives, which might scratch teeth by sliding between them, to larger or more angular abrasives (i.e., very sandy soil), which gouge or pit teeth, even on the shearing facets. Using museum samples provides no way to control for these variables because locality data available are not sufficiently precise to allow for a detailed reconstruction of soil types. These results could be augmented, therefore, by experimental tests comparing animals whose diets were specifically controlled for soil variables.

In spite of these caveats, the point remains that earthworms probably contain nothing but soil that could scratch teeth. As a result, moles that habitually eat earthworms give us a natural experimental model of effects of soil on teeth. The net effect is a distinctive, consistent pattern that could be used to help decipher the diets of fossil mammals of many different orders.

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