DENTAL MICROWEAR IN TRIASSIC AMNIOTES: IMPLICATIONS FOR PALEOECOLOGY AND MASTICATORY MECHANICS

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ABSTRACT—Features of dental microwear have been used to infer diet in fossil mammals based on comparisons with analogues or modern representatives, because material properties of the food and jaw mechanics can be inferred from microwear attributes that are easily compared across diverse groups. However, only rarely has dental microwear analysis been applied to more ancient non-mammalian taxa without modern relatives. We examine patterns of dental microwear in two distantly related groups–traversodontid cynodonts (at least two distinct taxa) and a possible 'prosauropod' dinosaur, both from the mid-late Triassic of Madagascar. Pitting was absent in most specimens examined. Scratch length and orientation heterogeneity, factors that have been suggested to reflect the hardness of the diet, differ significantly between the traversodontids and the 'prosauropod' analyzed, and may suggest some degree of resource partitioning between these two types of coexisting herbivores. The 'prosauropod' appears to have fed on softer plant material than the traversodontids did, whereas shorter scratch lengths and lower orientation consistency suggest that the traversodontids fed on more resistant vegetation. Rose diagrams of orientations of microwear features exhibit a clear bimodality of jaw motion in the traversodontid cynodonts, with a dominant postero-dorsal power stroke and significant horizontal motion in the antero-posterior direction. In contrast, the 'prosauropod' jaw motion was simple and orthal.

INTRODUCTION

Recently, terrestrial sediments of "Isalo II" (of the Isalo Group) from the southern Morondava Basin of Madagascar (Besairie, 1936) have yielded a diverse mid-late Triassic fauna, including the island's first traversodontid cynodonts (Flynn et al., 1999, 2000) and potentially the oldest known prosauropod (Flynn et al., 1999). The latter was tentatively identified based on synapomorphies of the dentary and maxillae shared with Prosauropoda (Flynn et al., 1999), although preparation of additional cranial and postcranial material likely pertaining to this taxon suggests that it may represent a more basal archosaur (thus, to reflect this uncertainty, we conservatively refer to this archosaur taxon as 'prosauropod' in quotation marks throughout this paper).

Previous studies of the dental morphology of traversodontid cynodonts (Reisz and Sues, 2000) and prosauropods (Barrett, 2000) suggest that species of both taxa were potentially herbivorous. Traversodontids are characterized by bucco-lingually expanded post-canine teeth and precise occlusion, supporting complex chewing mechanisms (Crompton, 1972). Prosauropods bear leaf-shaped cuspidate teeth, which are often associated with herbivory (Barrett, 2000).

Previous studies of masticatory mechanics in traversodontid cynodonts has relied on the well-formed wear facets on traversodontid teeth, which indicate precise occlusion and are used to reconstruct jaw motion. Crompton (1972) examined the masticatory mechanics of several traversodontid (gomphodont) cynodonts and found evidence for postero-dorsal and antero-dorsal jaw motion. He also found that the degree of antero-posterior motion varied among species of traversodontids, with *Massetognathus* displaying greater antero-posterior movement

during mastication than *Scalenodon.* In this study, we examine whether dental microwear analyses support Crompton's hypotheses for traversodontid jaw mechanics. Although the 'prosauropod' does not display wear facets, microwear analysis may be able to discern repetitive jaw motion in this taxon.

These two distantly-related taxa with herbivorous diets inferred from gross morphological evidence provide an opportunity to assess the utility of dental microwear analysis in dietary reconstruction of extinct taxa. Examination of dental microwear features has yielded insight into the diets of many extinct mammals, especially primates (e.g., Gordon, 1982; Teaford, 1985, 1988a, 1988b; Teaford and Walker, 1984; Ungar, 1996; Ungar and Spencer, 1999). Studies on extant primates have confirmed that differences in diet among populations and species are reflected in the patterns of dental microwear (see Ungar, 1996). Furthermore, similar patterns of dental microwear have been shown to more closely reflect similarity in diet than similarity in molar morphology or other potential functional influences. Most paleontological analyses of dental microwear concentrate on anthropoids (Teaford and Walker, 1984; Teaford and Lytle, 1996; Ungar and Teaford, 1996; Ungar and Spencer, 1999), although other fossil primates (Strait, 1991; Teaford, Maas, and Simons, 1996; Ungar, 1996), artiodactyls (Solounias and Hayek, 1993), rodents (Rensberger, 1982), carnivorans (Van Valkenburgh et al., 1990), and the entirely extinct groups of carpolestids (Biknevicius, 1986) and multituberculates (Krause, 1982) have also been examined. In a rare study of microwear analysis in wholly extinct taxa without modern analogues, Fiorillo (1998) examined enamel in two sympatric sauropod dinosaurs, establishing a general separation in their diets, with only minimal evidence of resource overlap. The reasons for this previous bias towards analysis of lineages with living representatives are apparent; inferring diet from microwear patterns for animals without modern representatives is necessarily more tentative. However, the underlying bases of microwear analysis are the general correlations among the material properties of food items, mas-

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ticatory mechanics, and the respective effects of each on dental microwear, and thus should be broadly applicable to extinct as well as living forms. Previously documented relationships between particular microwear features, broad dietary categories, and the material properties of food items are used to extrapolate the potential dietary significance of the examined taxa.

Dental microwear reflects a number of influences and processes, including the material properties of food, jaw mechanics, enamel microstructure, and taphonomic effects. Previous researchers have experimentally assessed the influence of these factors, allowing isolation of their effects. As the majority of studies of dental microwear have been concerned with reconstruction of diet, the influence of the material properties of food has received the greatest attention. In analyses of microwear, four variables are generally considered: (1) feature length, (2) feature breadth, (3) feature density, and (4) feature orientation.

Studies of taphonomic effects on dental microwear (Gordon, 1983; King et al., 1999) have demonstrated that the primary effect of chemical and physical weathering is obliteration of microwear features, rather than creation of pseudo-microwear features. Weathering thereby obscures, rather than alters, the inferred diet. Although researchers have suggested that dust on food items during ingestion may create microwear features, little empirical evidence exists at present to assess its potential influence on microwear (Ungar and Teaford, 1995).

Feature length and breadth are used to distinguish between pits and scratches. A scratch is defined as a feature with a length :breadth ratio greater than 4:1 and a pit as having a ratio of less than 4:1 (Ungar, 1996). Teaford and Walker (1984) demonstrated that pit-to-scratch frequencies among anthropoid primates effectively distinguished between hard-object frugivores (highest pit-to-scratch ratio), soft-object frugivores, and folivores (lowest pit-to-scratch ratios). Carnivores also tend to exhibit high degrees of pitting, due to bone processing. Scratch length is influenced by the material properties of food in a similar way to pit-to-scratch ratios. Longer scratch lengths result from shearing, rather than crushing, movements during mastication, and are typical of taxa processing softer food items (Teaford and Walker, 1984; Ungar, 1996). Scratch breadth, in contrast, is potentially influenced by a greater number of factors, including the magnitude of compressive forces during mastication and differences in enamel microstructure (Maas, 1991, 1994).

In studies of extant and recently extinct taxa, feature density (number of features per unit area) has been an effective measure of the coarseness of a diet (Ungar, 1996). Coarseness can be due to a primarily hard-object diet (seeds, bone), in which case pits would be the dominant feature, or to the phytoliths of grasses, which would produce a high incidence of scratching.

Lastly, Grine (1986) and Van Valkenburgh et al. (1990) suggested that orientation consistency may also relate to the material properties of food. They suggested that high orientation consistency (i.e., a preponderance of orientations in a single direction) on shearing surfaces indicates a diet of softer foods. Lower consistency, a wide range or distribution of orientations, would suggest a diet of harder and more brittle foods. Orientation consistency is not yet a well-established measure in dental microwear analysis. Here, we examine it in combination with scratch length and feature orientation distributions (using rose diagrams), as a potentially useful measure of the resistance of dietary items. Orientation consistency may be influenced by masticatory mechanics, with high variance in feature orientation simply reflecting high variance in jaw motion. However, differences in orientation consistency observed on the dentition of mammals with precise occlusion and regular masticatory mechanics, but different diets, support the idea that orientation consistency may also be influenced by the material properties of food items.

Although dental microwear analysis has rarely been employed for dietary reconstruction of taxa without modern representatives or analogues, it has been used to reconstruct jaw mechanics in extinct groups. Fiorillo (1998) used rose-diagram analysis of dental microwear in two sauropod dinosaurs to demonstrate the existence of jaw translation in both taxa, with a lesser degree of rostral-caudal jaw movement in *Camarasaurus* than in *Diplodocus*. Barrett (2001) and Rybczynski and Vickaryous (2001) analyzed microwear orientations to assess the complexity of jaw motion in thyreophoran dinosaurs, showing that movement was not restricted to the dorso-ventral plane, as previously thought. Thus, microwear features can be used to reconstruct jaw mechanics in extinct animals without modern analogues.

Precise dietary reconstruction may be impossible for taxa without modern analogues or close living relatives, but analysis of microwear features may permit more general inferences about diet. We use the analysis of dental microwear to confirm previous interpretations that these species were, in fact, herbivorous, and to examine whether there are systematic differences in microwear within and between the traversodontids and the 'prosauropod' in this fauna. In addition, we can use dental microwear analysis to examine jaw mechanics in these ancient taxa. Here, we use rose diagrams of microwear feature orientation to infer the masticatory mechanics of the traversodontid cynodonts and 'prosauropod' archosaur.

MATERIALS AND METHODS

Specimens

We examined postcanine teeth from nine traversodontid cynodont individuals and teeth from eight 'prosauropod' individuals from the mid-late Triassic of Madagascar (Table 1). Teeth were deemed suitable for microwear analysis according to the criteria of Teaford (1988b). Specifically, teeth with unusually large gouges, oddly shaped marks, extreme weathering, or unusually smooth surfaces were discarded. Because weathering generally erases microwear features (King et al., 1999), all microwear sites fulfilling the criteria discussed above were examined, regardless of location, though no overlapping sites from a single wear facet were used in the analyses. In the remainder of this paper, the term "specimen" refers to individuals, some of

TABLE 1. List of specimens used in analysis of dental microwear

Species	Tooth position	Specimen number
Cynodont Specimens		
Dadadon besairiei	Lower dentition	8-2-96-39
(Flynn et al., 2000)	Lower dentition	8-2-96-43
	Lower dentition	8-22-98-183
	Lower dentition	9-11-98-553
	Upper dentition	PR 2232
	Upper dentition	UA 10606
Unnamed traversodontid 1	Lower dentition	8-22-98-182
Unnamed traversodontid 2	Upper dentition	9-3-98-430
	Lower dentition	9-4-98-444
'Prosauropod' Archosaur Specimens		
Prosauropod indet.	?	8-22-97-92-1
(Flynn et al., 1999)	?	8-22-97-92-2
	?	8-22-97-92-3
	?	8-22-97-92-4
	?	8-28-97-140
	?	8-29-97-156
	?	8-30-98-352
	?	9-8-98-524

Abbreviations: PR, Field Museum fossil reptile collections; **UA**, University of Antananarivo, Madagascar fossil collections; other numbers refer to field collection numbers for specimens currently housed in the Field Museum collections, with month-day-year-sequential number (and suffix number 1 to 4 for isolated teeth from one collected sample number).

which have multiple teeth. Likewise, individual teeth can have multiple sites examined.

Specimen Preparation and Imaging

Because some specimens were too large to examine directly in the scanning electron microscope (SEM), cut portions of high resolution casts of a few specimens were analyzed rather than the actual fossil. Specifically, UA 10606, PR2232, 9-11-98-553, and 8-22-98-182 (see Table 1 for explanation of abbreviations) were molded with Polygem Novasil #737 tin-based silicone rubber. Casts were poured using Eager Plastics EP 5340 epoxy resin, without pigment. Pigment within the casting resin created inconsistencies visible in the SEM during initial attempts. Casts were mounted on aluminum specimen holders using either standard double-sided tape or carbon conductive tabs (Ted Pella Inc., CA), to reduce charging. A gold coating of approximately 20 nm was applied to a cast of one specimen (PR 2232) to prevent electron scattering and subsequent charging of the specimen. Original specimens were not coated.

Specimens were imaged using an Amray 1810 SEM operating with a tungsten filament and accelerating voltage of 2kV for uncoated specimens and 5kV for the coated specimen. Images were examined at ×300 magnification. Labial, lingual, and occlusal views were examined in all specimens. Digital photographs were captured using ScionImage 4.0.1 for Windows. Microwear sites were compared qualitatively to assess potential postmortem and taphonomic damage, as described in Teaford (1988b) and King et al. (1999). Microwear sites with suspect features were discarded to avoid potential inclusion of pseudofeatures created by postmortem, taphonomic, or preparatory damage. The taphonomic effects of weathering, transport, and acid etching appear to have obliterated microwear features in many of the examined specimens, as discussed above.

Images were analyzed using Microware 4.0.1, developed by P. Ungar (Ungar, 1995). For each wear feature, four endpoints (two for length and two for breadth) were digitized. Pit and scratch density, length and breadth measurements, means and standard deviations, and orientation consistency were automatically computed. Orientation consistency is the unit r described by Zar (1999) as the length of the mean vector of circularly distributed data:

$$r = \frac{1}{n}\sqrt{\left(\sum_{i=1}^{n}\cos\theta_i\right)^2 + \left(\sum_{i=1}^{n}\sin\theta_i\right)^2}$$

r varies inversely with the dispersion of circularly distributed data in this study, providing a measure of the regularity of orientations of microwear features. Grine et al. (2002) examined feature measurement errors associated with use of the Microware software for dental microwear quantification from scanning electron microscope images, and found that errors did not significantly affect results for analysis of scratch length and orientation when a common technique was used. As only this quantification program (Microware 4.0.1.) was used, it is unlikely that error in data collection significantly affects the results of this study.

Dietary Inference

Of the various measures employed in microwear analysis, discussed above, we consider two, scratch length and orientation heterogeneity, as independent means of inferring the material properties of food. Longer scratch lengths correlate with the consumption of soft food items, and it has been suggested that higher orientation consistency also relates to softer foods (Ungar, 1996). Likewise, shorter scratch lengths, and possibly, lower orientation consistencies are indicative of a diet richer in hard

food items (Ungar, 1996). Analyses of variance were conducted on scratch length and orientation consistency to determine if significant differences occur between isolated microwear sites within a single individual, between individuals, and between taxa. Because a Shapiro-Wilk W test (p < .001) documented that scratch length data were not normally distributed, nonparametric Kruskall-Wallis tests were employed to test for differences between groups. Orientation consistency data were normally distributed, and ANOVA analyses were used to determine differences among groups. A 99% level of significance was employed in interpretation of results, with a Bonferroni correction for nonindependence. Following Gordon (1988), individuals were initially analyzed separately for variance across teeth and surfaces, as opposed to simply pooling all specimens into a single analysis, to account for non-independence of data and for potential variance due to random variation or positional influences rather than systematic differences across taxa.

Pitting was rare to absent in all specimens examined in this study, precluding consideration of the pit-to-scratch ratio. As pits are the dominant microwear features in carnivores, the lack of pitting in these taxa supports previous interpretation of herbivory for both the traversodontid cynodonts and the 'prosauropod' archosaur. Because scratch width is sometimes uninformative in studies of paleodiet (Teaford and Runestad, 1992), and is influenced by differences in enamel microstructure, we do not consider scratch width in this study. Previous studies have demonstrated significant differences in the enamel microstructure of archosaurs and synapsids. Sander (1997, 2000) reported that nearly all non-mammalian synapsids, including the traversodontid *Boreogomphodon*, are characterized by a specific enamel structure, synapsid columnar enamel, consisting of short columnar units with irregular, polygonal cross-sections. In constrast, the prosauropod *Plateosaurus* has parallel crystallite enamel with poorly developed incremental lines (Sander, 1999). Additionally, scratch width was below 0.0005 mm in all microwear features examined in this study and was not systematically or significantly different among taxa. We also did not consider feature density in this study, due to taphonomic effects. Comparison of tooth surfaces examined in this study and experimentally weathered tooth surfaces analyzed by King et al. (1999) showed qualitatively similar effects. Furthermore, microwear features were rare in studied specimens, with only 29 out of 76 examined teeth displaying any microwear features at all.

Analysis of Masticatory Mechanics

We used Fiorillo's (1998) approach of assessing dominant directions of wear via rose diagram plots, and interpreting these as reflecting directions of jaw movements within the traversodontid cynodonts and the 'prosauropod' archosaur. Rose diagrams, which describe frequencies of circularly-distributed data, were employed to assess the distribution of dominant orientations across wear sites and among taxa, using Oriana 1.0.6 (Kovlach Computing Services). Statistical analyses were carried out for raw scratch length data and summary orientation consistency data for each microwear site.

Rose diagram plots of mean orientations were developed for grouped 'prosauropod' specimens, grouped cynodont specimens, and separately for cynodont upper dentition and lower dentition. In addition, specimens of *Dadadon besairiei* and three currently taxonomically unassigned traversodontid specimens were plotted separately.

RESULTS

Pits were observed in six sites on traversodontid specimens and only one on a 'prosauropod' specimen. Of these occurrences, one traversodontid specimen displayed two pits, whereas the

other occurrences were singular; accordingly, pitting was excluded from further analysis.

Sixty teeth from nine traversodontid specimens were examined. Two were isolated lower teeth, and the remaining 58 were from seven specimens with multiple teeth in place. Of these 60 teeth, 18 retained features that fulfill the criteria described in Teaford (1988b) for determination of original microwear. Figure 1 shows examples of examined microwear sites and traversodontid teeth. A total of 53 microwear sites from these 18 teeth were examined, with a total of 1572 microwear features observed and analyzed. Of the 53 sites, 13 occur on upper dentitions and 40 occur on lower dentitions (Table 1). Four sites are located on grinding surfaces, all on lower dentitions, while the remaining 49 occur on shearing surfaces of both upper and lower dentitions. Of the sites on shearing surfaces, 4 are on labial surfaces, 11 are on mesial surfaces, and 34 are on lingual surfaces. Twenty-seven microwear sites were oriented along the sagittal plane, while 26 sites were oriented along the coronal plane.

Sixteen teeth from eight 'prosauropod' specimens were examined. Five teeth were isolated specimens, whereas the remaining eleven were from three jaw fragments containing multiple teeth. Eleven teeth displayed microwear features suitable for analysis. Figure 2 shows examples of examined microwear sites and a prosauropod tooth. Some 31 sites in total were examined, with a total of 786 microwear features analyzed. Of the 11 teeth, the labial and lingual surfaces of 10 were distinguishable morphologically by comparison with tooth-bearing mandibles and maxillae. Specimen 8-30-98-352, with eight microwear sites, could not be oriented definitively. Of the remaining 23 examined sites, 14 clearly were on labial surfaces, and nine were on lingual surfaces.

Microwear Length

Cynodonts—Kruskall-Wallis tests of raw scratch length data showed significant differences between sites on teeth within a single specimen for half of the traversodontid specimens. Specimen 8-2-96-39 exhibited only one microwear site and, therefore, was excluded from statistical analyses. Traversodontids exhibit significant differences in scratch length and orientation consistency between individuals (Table 2). There are also significant differences when traversodontid specimens are grouped by taxon and by tooth position. The upper dentitions of *Dadadon* [specimens UA 10606 and PR 2232] were significantly different from the unnamed traversodontid 9-3-98-430 (p-value << .001). *Dadadon* (specimen 9-11-98-553) and unnamed traversodontids (8-2-96-43, 8-22-98-183, 8-22-98-182 and 9-4-98-444) also differ significantly in scratch length (p-value << .01) on the lower teeth. There are no significant microwear differences between specimens 8-22-98-182 and 9-4-98-444, nor between specimens 8-2-96-43 and 8-22-98-183, although there are significant differences across these groups (p-value << .01). All of these specimens and groupings differ significantly from the *Dadadon* lower dentition, specimen 9-11-98-553. When sites are grouped by tooth position (upper vs. lower), there are significant differences between groups in scratch length (p-value < .01), but not in orientation heterogeneity (p-value > .01). However, because no single specimen that includes both an upper and a lower dentition exhibited microwear, the high variability of scratch length across specimens indicates that this result should be interpreted with caution. No significant differences were observed when comparing groups based on position of microwear sites within specimens (labial vs. lingual, p-value > .01).

'Prosauropod' Archosaur—Analysis of raw scratch length data showed significant differences between sites within three individual prosauropod specimens (Table 3). One of these, 8-28-97-140, was a specimen from a multi-toothed jaw, whereas the other specimen, 8-22-97-92-4, was an isolated tooth. The third specimen, 8-22-97-92-2, also showed significant differences between sites, but this result is possibly attributable to a single outlier site with several unusually large scratches. Significance values are generally much lower than in the analysis of traversodontid specimens, possibly due to lower sample sizes of the 'prosauropod'. Scratch lengths are significantly different among 'prosauropod' specimens (p-value << .01). Scratch lengths are not significantly different between sites on labial and lingual surfaces. Because tooth position was unknown for most specimens, comparisons of upper versus lower dentitions could not be made.

Microwear Orientation

Traversodontid Cynodonts—Whereas scratch length is an independent measure for each microwear feature, orientation consistency is a summary feature of each microwear site. Because some specimens display only a small number of microwear sites (range: three to eleven), and because each site contributes a single measure of orientation consistency, orientation consistency could not be statistically tested for differences within individual specimens. For this reason, difference in orientation consistency is only considered between specimens. Orientation consistency is not significantly different among traversodontid specimens (p > .001) or groupings based on tooth or site position (Table 2). Orientation consistency is extremely variable among sites within most individual specimens; because samples sizes are smaller than for scratch length, this result should be considered preliminary.

Rose diagrams are displayed as half-hemispheres, with features oriented to a common plane, as shown. Though shown as vectors for simplicity, each feature is actually a scalar, without directionality (i.e., antero-ventral is the same as postero-dorsal in the direction of jaw motion). Twenty-seven measurements specify rostral or caudal orientation (Fig. 3), whereas 26 measurements indicate lingual or labial orientation (Fig. 4).

Figure 3A displays the scratch orientations of all cynodont specimens. A wide range is evident, with a slight dominance of features in a postero-dorsal orientation. A second mode exists in the orthal plane, as well as another concentration in an antero-posterior orientation. There may also be a minor antero-dorsal component, though this may not be substantially different from the antero-posterior direction.

Figure 3B shows the orientation distribution for upper molariform teeth of all the cynodont specimens. There is a clear bimodality that is not symmetric about the dorso-ventral axis. A postero-dorsal orientation and a nearly antero-posterior orientation (again with a possible slight antero-dorsal tendency) dominate.

Rose diagrams of lower dentitions of all the cynodont specimens (Fig. 3C) show an asymmetric bimodal distribution, although not parallel to that displayed by the upper dentitions. A postero-dorsal orientation again dominates, but a second mode is present in a dorso-ventral orientation.

When only *Dadadon* specimens (both upper and lower dentitions) are examined (Fig. 3D), a bimodal distribution is still evident, although weaker than in other groupings. A postero-dorsal orientation dominates, with a secondary antero-posterior mode. The dorso-ventral component is small in the pooled lower dental specimens. Although this distribution resembles that of the upper dentition for all cynodont specimens (Fig. 3B), nearly half of these *Dadadon* measurements (five of 12) are from lower dentitions.

When the unnamed traversodontid specimens are considered separately (Fig. 3E, F, G), the large dorso-ventral component seen in the pooled lower dentition specimens, and missing from the *Dadadon* specimens, is evident in the lower dentition specimens 8-22-98-182 (Fig. 3E) and 9-4-98-444 (Fig. 3G). However, upper dentition specimen 9-3-98-430 (Fig. 3F) shows the same distribution of orientations as *Dadadon*.
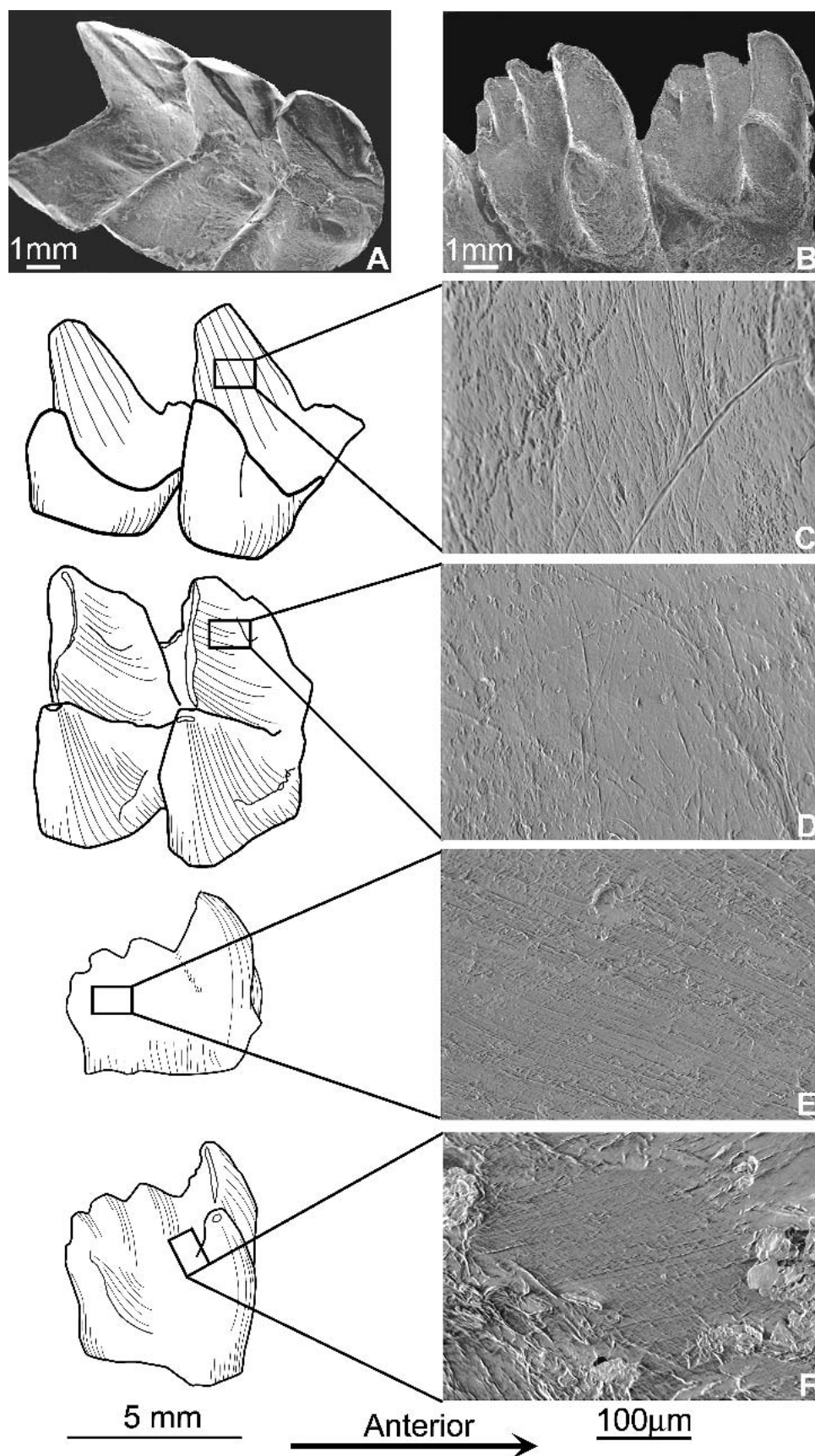
FIGURE 1.   Scanning electron microscope images of slightly worn traversodontid cynodont specimens bearing microwear: **A**, upper left dentition of *Dadadon*, UA 10606 (8×), ventral view, mirrored for consistency with line drawings, anterior to lower right, lingual to lower left; **B**, lower right dentition of unnamed traversodontid, 8-22-98-182 (14×), lingual view, anterior to right; examples of dental microwear (300×), **C**, UA 10606, upper dentition, lingual view; **D**, PR2232, ventral view, labial to bottom; **E**, 8-22-98-182, labial view; **F**, 8-2-96-43, lingual view.
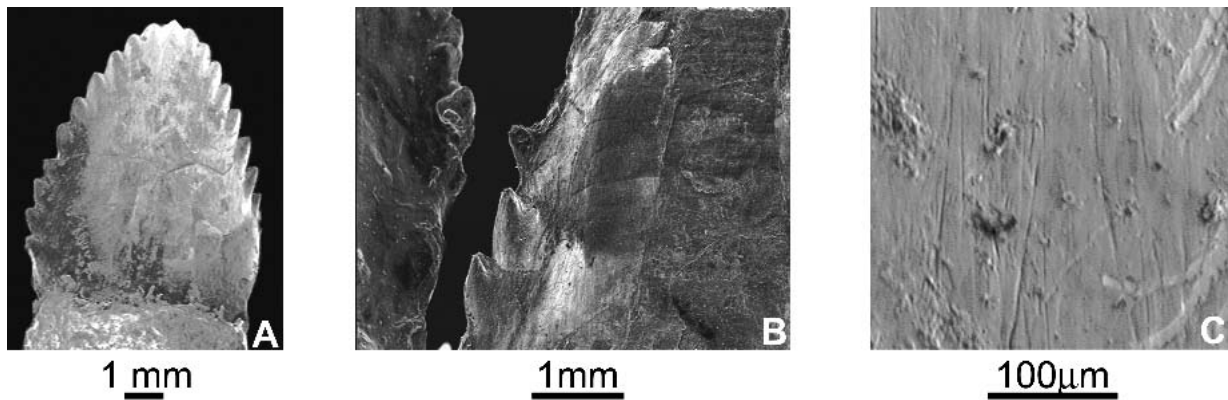
FIGURE 2. Scanning electron microscope images of 'prosauropod' archosaur teeth: **A**, 8-22-97-92-1 (10×), lingual view; **B**, specimen 8-30-97-156, view of area along serrations where microwear features are concentrated in most 'prosauropod' specimens (22×); **C**, 8-30-98-352, (300×), lingual view.

Analysis of lingual-labial orientations (Fig. 4) from all cynodont specimens (upper and lower dentitions) shows minor variation with a single dominant mode, near the dorso-ventral axis, angled dorso-laterally, suggesting potential lateral motion during mastication.

'Prosauropod' Archosaur—There are no significant differences in orientation heterogeneity among all of the 'prosauropod' specimens (p-value > .001), although this is possibly an artifact of small sample sizes within the individual groups (Table 3). There are no significant differences in orientation heterogeneity between labial and lingual surfaces. Analysis of 'prosauropod' orientations (Fig. 5) reveals little variation and a close conformity to the orthal plane, with a negligible antero-posterior component.

'Prosauropod' Archosaur versus Traversodontid Cynodonts

Both scratch length and orientation consistency differ significantly when all traversodontid specimens are compared to all 'prosauropod' specimens (Table 4). The 'prosauropod' teeth show greater average scratch length (0.087 mm) than traversodontids (0.053 mm). Furthermore, 'prosauropod' teeth show greater mean orientation consistency (0.871) than traversodontids (0.714). While traversodontids show a bimodal distribution of microwear orientations, supporting dominant postero-dorsal

and antero-posterior components to their jaw motion, the 'prosauropod' archosaur specimens examined show jaw motion only in the orthal plane.

DISCUSSION

Dietary Reconstruction

Tougher plant material could potentially influence scratch length and consistency, without causing pitting as harder material would, although toughness of plant material has never been explicitly tested for its impact on dental microwear features. Modern herbivores feed predominantly on angiosperm fruits and leaves, making it difficult to determine which plant parts or taxa may have contributed to the diet of these Triassic (pre-angiosperm) herbivores. Among the common gymnosperms of Triassic Gondwana are several species of cycadophytes, glossopterids (seed ferns), and conifers. Non-seed plants include lycopods (club mosses), sphenopsids (horsetails), and ferns. Many of these groups experienced rapid diversification in the Triassic (Willis and McElwain, 2002), providing ample taxonomic and morphological diversity to support distinct diets in coexisting herbivores. In particular, modern cycads are characterized by extremely tough leaves and stems, possibly as much as two to four times as tough as those of angiosperm dicots (N. J. Dominy, University of Chicago, pers. comm., 2003). Similar, but more ancient cycads may have contributed to a substantial portion of the diet of the taxa studied here. In addition, mechanical prop-

TABLE 2. Results from statistical analysis of scratch length (Kruskall-Wallis test) and orientation consistency (one-way ANOVA) within and between traversodontid specimens

Specimen number	Scratch length	Orientation consistency
8-2-96-43	–	N/A
8-22-98-183	*	N/A
9-11-98-553	–	N/A
PR 2232	–	N/A
UA 10606	*	N/A
8-22-98-182	*	N/A
9-3-98-430	*	N/A
9-4-98-444	–	N/A
Among all individuals	*	*
Among taxa	*	–
Among *Dadadon* specimens	*	–
Upper vs. Lower dentition	*	–
Labial vs. Lingual	–	N/A

Because orientation consistency is a summary statistic for each microwear site, it does not have adequate sample sizes for comparison within individuals. Significant differences (p < .01) are denoted by *, and lack of significant differences (p > .01) are denoted by – .

TABLE 3. Results from statistical analysis of scratch length (Kruskall-Wallis test) and orientation consistency (one-way ANOVA) within and between 'prosauropod' specimens

Specimen number	Scratch length	Orientation consistency
8-22-97-92-1	–	N/A
8-22-97-92-2	*	N/A
8-22-97-92-3	–	N/A
8-22-97-92-4	*	N/A
8-28-97-140	*	N/A
8-29-97-156	–	N/A
8-30-98-352	–	N/A
9-8-98-524	–	N/A
Among all individuals	*	–
Labial vs. Lingual	–	–

Because orientation consistency is a summary statistic for each microwear site, it does not have adequate sample sizes for comparison within individuals. Significant differences (p < .01) are denoted by *, and lack of significant differences (p > .01) are denoted by – .
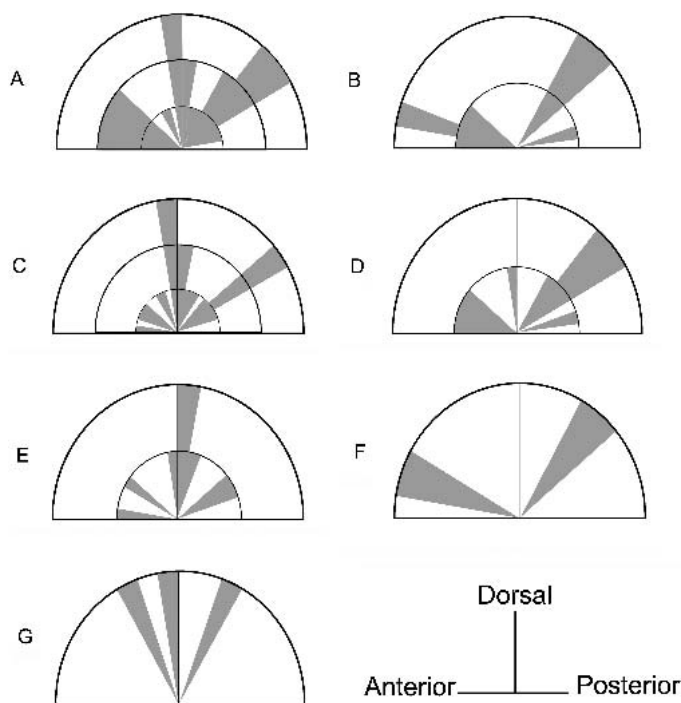
FIGURE 3. Rose diagrams of microwear feature orientations distributions in cynodont specimens. **A**, all cynodont specimens (n = 9); **B**, all cynodont upper dentitions (n = 3); **C**, all cynodont lower dentitions (n = 6); **D**, all *Dadadon* specimens (n = 3); **E**, specimen 8-22-98-182 (lower dentition only); **F**, specimen 9-3-98-430 (upper dentition only); **G**, specimen 9-4-98-444 (lower dentition only). Partitions in the rose diagrams denote frequencies of various orientations, with frequency increasing with distance from the center. Plots with more data will tend to have more partitions, as there is a greater range in frequency of various orientations.

erties vary across plant parts (N. J. Dominy, University of Chicago, pers. comm., 2003), with stems and scale leaves being tougher than foliage.

The analysis of dental microwear features present in the Isalo II traversodontid cynodonts and the 'prosauropod' bear on inference of both the probable diet of these animals and the determination of overlap in resource utilization between the two groups. Pitting was rare, with a total of eight pits found in the 82 microwear sites. Abundant pitting generally reflects a diet incorporating hard objects, such as seeds (typically from fruit), or potentially bone. The near absence of pitting from examined specimens indicates that seeds, bone, or any other hard food substance did not comprise a significant component of the diet
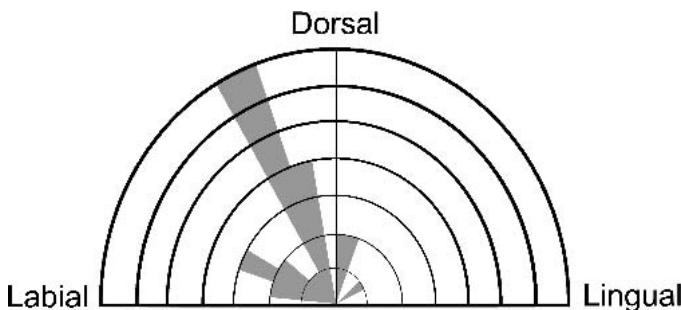

FIGURE 4. Rose diagram of orientation distribution of laterally-directed microwear features in all cynodont specimens (upper and lower dentition; n = 26).
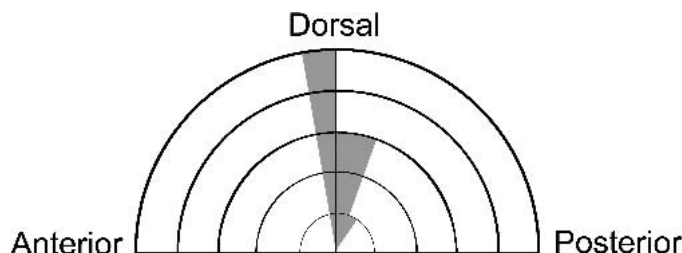

FIGURE 5. Rose diagram of microwear feature orientation distribution in 'prosauropod' specimens (n = 8).

for the traversodontid cynodonts or the 'prosauropod' archosaur. Both the traversodontid cynodonts and the 'prosauropod', then, probably were feeding on softer plant material. Within this narrower range of potential diet (non-seed parts of plants), significant differences in scratch length and orientation consistency between grouped cynodonts and the suite of 'prosauropod' specimens suggest that these taxa did not overlap extensively in diet.

'Prosauropod' teeth display longer scratch lengths and higher orientation consistencies than traversodontid cynodonts. Both of these factors may relate to the material properties of food items, as discussed above. Longer scratch lengths have been shown to relate to shearing rather than crushing mastication, and suggest softer food items. Likewise, higher orientation consistency has been suggested to indicate a softer diet. These two different features are consistent in their implications for diet, indicating a harder or tougher diet for the traversodontids and a softer diet for the 'prosauropod' archosaur. These interpretations are also consistent with morphological evidence for mechanical processing in these taxa. Wear facets and complex occlusion in traversodontid cynodonts indicate a high degree of oral processing (Crompton, 1972), and potentially a more fibrous or resistant diet. In contrast, the lack of wear facets (Barrett, 2000) and the simple jaw mechanics, discussed below, argue against extensive oral processing, and potentially for a softer diet, in the 'prosauropod' archosaurs.

Due to the limited motion in shearing planes during mastication, Gordon (1982) suggested that variation in feature orientation is greater on grinding than on shearing surfaces. Van Valkenburgh et al. (1990) further suggested that variation in feature orientation along shearing planes relates to the hardness of food items, because jaw motion is generally limited to a single or a few dominant directions along the shearing plane. Of the total 53 microwear sites observed in cynodonts, only four were from grinding surfaces. The remainder occurred on shearing surfaces. It is possible that high variability in jaw motion alone can account for the observed variability in feature orientation, as the arguments by Grine (1986) and Van Valkenburgh et al. (1990)

TABLE 4. Mean, range, and significance of Kruskall-Wallis test for scratch length and one-way ANOVA analysis of orientation consistency between traversodontid cynodont specimens (n = 9) and 'prosauropod' archosaur specimens (n = 8)

	Mean	Maximum	Minimum	*P*-value of means
A				
'Prosauropod'	0.087	0.518	0.011	p << .001
Cynodonts	0.053	0.263	0.006	
B				
'Prosauropod'	0.886	0.991	0.592	p << .001
Cynodonts	0.752	0.982	0.189	

A, scratch length (in mm); **B**, orientation consistency.

are based on mammals with well-established and constrained masticatory mechanics. Likewise, shorter scratch lengths may result from more variable chewing. However, dominant modes are clearly evident in the distribution of feature orientations, arguing against high variability in jaw motion as the sole cause of variability in feature orientation. While the existence of multiple dominant modes in jaw motion, displayed in rose plots (Fig. 3), account for some of the variation in feature orientation, the low consistency of orientations and the high dispersion of orientations beyond the dominant modes observed in the microwear features of the traversodontid cynodonts may suggest that they were feeding on more-resistant food items. Furthermore, the differences in microwear feature lengths and orientations exhibited by the traversodontids and 'prosauropod' also occur in modern mammals, which have very similar masticatory mechanics but differ in diet (Teaford and Walker, 1984; Teaford and Lytle, 1996; Ungar, 1996; Ungar and Teaford, 1996; Ungar and Spencer, 1999).

As extensive microwear studies for extant nonmammalian tetrapods are not available, it is impossible to fully gauge the potential effect of the distinct chewing mechanisms exhibited by the traversodontid cynodonts and 'prosauropod' examined in this study. However, the combined analysis of scratch length, orientation consistency, and rose diagrams of feature orientation suggest that the traversodontids and 'prosauropod' in this study did not consume the same resources. The combination of shorter scratch lengths, lower orientation consistency, and more complex and precise masticatory mechanics support the conclusion that traversodontids fed on more resistant vegetation than the 'prosauropod'. For example, the traversodontid cynodonts could have been feeding on a variety of plant parts, such as stems or scale leaves, rather than simply on the foliage, or they could have fed on "tougher" plants, such as cycads.

Although it currently is impossible to determine exactly which plants these animals were eating, this study displays the potential of dental microwear analysis in paleoecological studies of ancient faunas lacking close modern analogues or living representatives. It is possible to determine the degree of dietary overlap among coexisting species and make broad inferences on the material properties of dietary items (hardness, softness, and possibly toughness).

Masticatory Mechanics

Traversodontid Cynodonts—Analysis of microwear features also lends insight into the masticatory biomechanics of these animals. A wide range of microwear orientations is displayed by the cynodont specimens, as indicated by the low levels of orientation consistency. The addition of positional context for individual microwear sites and teeth within the maxillary and mandibular tooth row provides the ability to interpret microwear orientations in terms of masticatory motion and direction. Most groupings (all specimens, tooth type, tooth position, individual taxa) reveal a clear bimodal distribution of orientations (Fig. 3). Whereas both upper and lower teeth show a dominant dorso-posterior orientation, upper teeth also display a second dominant mode in an antero-posterior orientation. In contrast, the second dominant mode in the lower dentition is near the dorso-ventral axis.

Examined separately, *Dadadon* specimens display a wide range of scratch orientations, again with two dominant modes corresponding to those displayed by the upper dentition. When the unnamed traversodontid specimens are considered separately, it is clear that the dorso-ventral component seen in the pooled lower-dentition specimens is contributed solely by the two specimens 8-22-98-182 and 9-4-98-444. In specimen 8-22-98-182, feature orientations are concentrated in the dorso-ventral direction, with only a minority of features oriented in the pos-

tero-dorsal or the antero-posterior directions. In specimen 9-4-98-444, there is again a concentration in the dorso-ventral orientation, as well as in high-angle antero-dorsal and postero-dorsal orientations. The differences in orientation are not due to position, as shown by the upper and lower dentitions of *Dadadon*. These two specimens are much smaller than those of *Dadadon* (but not than 9-3-98-430), and the observed differences may reflect size-related or allometric aspects of jaw movement, or they may pertain to phylogenetically earlier-diverging forms, resembling *Scalenodon*. Further study of these specimens and other smaller traversodontid specimens is required to address whether these anomalous results are due to size or whether they represent significant and previously unrecognized diversity in masticatory mechanics among traversodontid cynodonts. Further discussion of masticatory mechanics, thus, is limited to *Dadadon* and the unnamed traversodontid 9-3-98-430.

Rose diagram analysis of microwear features oriented in the lateral plane, across all cynodont specimens, shows a single high-angle dominant mode in the dorso-labial direction (Fig. 4). Close inspection of these features, however, suggests that their orientations are predominantly affected by their position on the tooth surface (e.g., basin margin, labial or lingual wall). Because most sites examined lie on or along tooth surfaces at a high angle to the dorso-ventral plane, their orientations may be more influenced by the slight angle of these tooth surfaces, rather than by complex patterns of mastication. For this reason, while the dorso-labial mode may reflect regular lateral movement during mastication, it may also be simply a consequence of the angles of tooth surfaces. As tooth occlusion and jaw motion are not independent of each other, their respective influences on microwear orientation are difficult to isolate further.

The postero-dorsal orientation of many wear features in *Dadadon* specimens and in specimen 9-3-98-430 suggests substantial posterior retraction of the jaw during the chewing cycle (Fig. 6). The distribution of microwear orientations observed in these taxa agrees with Hopson's (1966) suggestion that the reduction in skull height and development of the coronoid process along the synapsid lineage progressively re-oriented the external adductor musculature, such that it pulled the jaw more posteriorly, instead of in a predominantly dorsal direction. Crompton (1972) further described jaw movement and post-canine occlusion in traversodontid (gomphodont) cynodonts, stating that the jaw was directed postero-dorsally as it closed. The dominance of postero-dorsally oriented microwear features described here for the new Malagasy traversodontids match Crompton's observations closely (see Figs. 5B, 6D; Crompton, 1972).
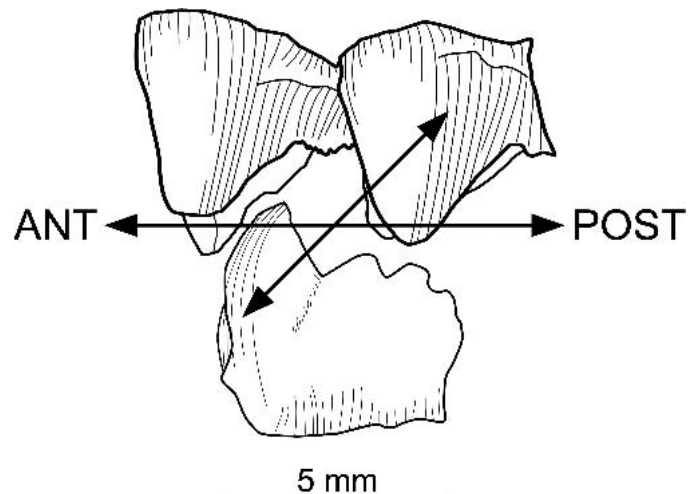

FIGURE 6. Model of occlusion in *Dadadon besairiei*, as indicated by rose diagrams of microwear feature orientation, in lateral view.

Crompton (1972) also suggested, based on wear facets, that traversodontid (gomphodont) cynodonts may have been capable of an antero-dorsally directed power stroke. Microwear feature orientations from these specimens are less supportive of this hypothesis. Although there may be a minor low-angle antero-dorsal component within the antero-posterior direction that is a secondary mode in *Dadadon* specimens and in specimen 9-3-98-430, this component may not be significantly different from horizontal. This secondary mode suggests that significant fore-aft jaw motion occurred in the horizontal plane during mastication in these taxa (Fig. 6). Crompton (1972) suggested that greater antero-posterior jaw movement distinguished *Massetognathus* from *Scalenodon*. Although the relationships of the traversodontid cynodonts *Massetognathus* and *Scalenodon* to the taxa studied here are not yet precisely understood (Flynn et al., 2000), the substantial antero-posterior jaw motion exhibited by the Malagasy taxa suggests that they share the condition of jaw motion seen in *Massetognathus*. The dominance of the postero-dorsal direction, however, possibly is a more inclusive trait of the traversodontid cynodonts, as suggested by Crompton (1972).

The anomalous distribution of orientations in the two specimens of small unnamed traversodontid taxa 8-22-98-182 and 9-4-98-444, however, does not fit this scenario. More specimens and analyses are required to determine if this model of masticatory evolution is broadly applicable to adults across all traversodontids, or if these specimens represent greater diversity of jaw mechanics within the traversodontid cynodonts.

'Prosauropod' Archosaur—In stark contrast to the complexity of orientations and the bimodality of orientations of jaw movement displayed by the cynodonts, analysis of the 32 microwear sites from 'prosauropod' specimens showed very low variation and a tight conformity to the dorso-ventral axis. These early archosaurs thus did not process food through elaborate mastication, but by simple shear in a dorso-ventral plane. Though this result is not unexpected given the simple jaw mechanics of most reptiles (Carroll, 1987), it contrasts with complexity observed in later herbivorous dinosaurs, as discussed by Fiorillo (1998) and Rybczynski and Vickaryous (2001).

Herbivory is generally thought to have arisen only in some lineages of Dinosauria, and arguably in a few species of crocodilians, within the dominantly carnivorous Archosauria, although a recent study suggested that herbivory (inferred from gross tooth and jaw morphology) may have occurred in a basal dinosaur or 'predinosaur' archosaur in the early Late Triassic (Dzik, 2003). If the Malagasy taxon examined here is determined not to be a prosauropod, but rather a more basal archosaur, than these new microwear data would definitively document the occurrence of herbivory in a non-dinosaurian archosaur, and the existence of a greater diversity of herbivores among archosauromorphs in the mid-Late Triassic than previously thought. Furthermore, this would suggest that its prosauropod craniodental features (e.g., leaf-shaped teeth, position of the ascending process of the maxilla, etc.) have been achieved convergently by this taxon, and that, at least in this taxon, this dental morphology is associated with a purely herbivorous diet. Along with prosauropods and basal ornithischian dinosaurs, this new taxon then would represent the third independent evolution of leaf-shaped cuspidate teeth among Triassic taxa (Sues, 2000). As the association between prosauropod dental morphology and diet has been widely discussed (Barrett, 2000), an evolutionarily independent example of this distinctive tooth morphology, and its definitive association with herbivory (as demonstrated by our analysis of dental microwear) would provide an important departure point for future studies. Leaf-shaped cuspidate teeth have arisen independently in several groups, first appearing in Permian pareiasaurs, caseids, and basal anomodonts (Sues, 2000). Rybczynski and Reisz (2001) used dental microwear analysis, in conjunction with morphological analysis, to provide

evidence for the association of this distinctive tooth morphology with an herbivorous diet and precise occlusion in a basal anomodont with leaf-shaped cuspidate teeth. Analysis of dental microwear in additional groups that converge on this distinctive morphology could provide valuable insight into the association between tooth morphology and diet.

Dental microwear analysis is a valuable tool for paleoecological and biomechanical studies, even in taxa without modern representatives or analogues. This study demonstrates the utility of microwear analysis in determining potential diet and resource partitioning of coexisting taxa, and in reconstructing dominant directions of jaw motion in the analyzed traversodontid cynodonts and 'prosauropod' archosaur.

LITERATURE CITED

Barrett, P. M. 2000. Prosauropod dinosaurs and iguanas: speculations on the diets of extinct reptiles; pp. 42–78 in H.-D. Sues (ed.), Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record. Cambridge University Press, Cambridge.

Barrett, P. M. 2001. Tooth wear and possible jaw action of *Scelidosaurus harrisonii* Owen and a review of feeding mechanisms in other thyreophoran dinosaurs; pp. 25–52 in K. Carpenter (ed.), The Armored Dinosaurs. Indiana University Press, Bloomington.

Besairie, H. 1936. Recherches géologiques à Madagascar, première suite; la géologie du nordouest. Mémoires de l'Académie Malgache 21: 1–259.

Biknevicius, A. R. 1986. Dental function and diet in the Carpolestidae (Primates, Plesiadapiformes). American Journal of Physical Anthropology 71:157–171.

Carroll, R. L. 1987. Vertebrate Paleontology and Evolution. W. H. Freeman & Co, New York, 698 pp.

Crompton, A. W. 1972. Postcanine occlusion in cynodonts and tritylodonts. British Museum of Natural History Bulletin of Geology 21: 27–71.

Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. Journal of Vertebrate Paleontology 23:556–574.

Fiorillo, A. R. 1998. Dental microwear patterns of the sauropod dinosaurs, *Camarasaurus* and *Diplodocus*: evidence for resource partitioning in the Late Jurassic of North America. Historical Biology 13:1–16.

Flynn, J. J., J. M. Parrish, B. Rakotosamimanana, L. Ranivoharimanana, W. F. Simpson, and A. R. Wyss. 2000. New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar. Journal of Vertebrate Paleontology 20:422–427.

Flynn, J. J., J. M. Parrish, B. Rakotosamimanana, W. F. Simpson, R. L. Whatley, and A. R. Wyss. 1999. A Triassic fauna from Madagascar, including early dinosaurs. Science 286:763–765.

Gordon, K. D. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. American Journal of Physical Anthropology 59:195–216.

Gordon, K. D. 1983. Taphonomy of dental microwear: can fossil microwear be studied productively? American Journal of Physical Anthropology 60:200.

Gordon, K. D. 1988. A review of methodology and quantification in dental microwear analysis. Scanning Microscopy 2:1139–1147.

Grine, F. E. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. Journal of Human Evolution 15:783–822.

Grine, F. E., P. S. Ungar, and M. F. Teaford. 2002. Error rates in dental microwear quantification using scanning electron microscopy. Scanning 24:144–153

Hopson, J. A. 1966. The origin of the mammalian middle ear. American Zoologist 6:437–466.

King, T., P. Andrews, and B. Basak. 1999. Effects of taphonomic processes on dental microwear. American Journal of Physical Anthropology 108:359–373.

Krause, D. W. 1982. Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*. Paleobiology 8:265–281.

Maas, M. C. 1991. Enamel microstructure and microwear: an experimental study of the response of enamel to shearing force. American Journal of Physical Anthropology 85:31–50.

Maas, M. C. 1994. A scanning electron-microscopic study of in vitro abrasion of mammalian tooth enamel under compressive loads. Archives of Oral Biology 39:1–11.

Reisz, R. R., and H.-D. Sues. 2000. Herbivory in late Paleozoic and Triassic terrestrial vertebrates; pp. 9–41 in H.-D. Sues (ed.), Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record. Cambridge University Press, Cambridge.

Rensberger, J. M. 1982. Patterns of dental change in two locally persistent successions of fossil aplodontid rodents; pp. 415–438 in B. Kurten (ed.), Teeth: Form, Function, and Evolution. Columbia University Press, New York.

Rybczynski, N., and R. R. Reisz. 2001. Earliest evidence for efficient oral processing in a terrestrial herbivore. Nature, 411:684–687.

Rybczynski, N., and M. K. Vickaryous. 2001. Evidence of complex jaw movement in the Late Cretaceous ankylosaurid *Euoplocephalus tutus* (Dinosauria: Thyreophora); pp. 299–317 in K. Carpenter (ed.), The Armoured Dinosaurs. Indiana University Press, Bloomington.

Sander, P. M. 1997. Non-mammalian synapsid enamel and the origin of mammalian enamel prisms: the bottom-up perspective; pp. 41–62 in W. V. Koenigswald and P. M. Sander (eds.), Tooth Enamel Microstructure. A. A. Balkema Publishers, Rotterdam.

Sander, P. M. 1999. The microstructure of reptilian tooth enamel: terminology, function, and phylogeny. Münchner geowissenschaftliche Abhandlungen (Reihe A) 38:1–102.

Sander, P. M. 2000. Prismless enamel in amniotes: terminology, function, and evolution; pp. 92–106 in M. F. Teaford, M. M. Smith, and M. W. J. Ferguson (eds.), Development, Function, and Evolution of Teeth. Cambridge University Press, Cambridge.

Solounias, N., and L. A. C. Hayek. 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. Journal of the Zoological Society of London 229:421–445.

Strait, S. G. 1991. Dietary reconstruction in small-bodied fossil primates.

Unpublished Ph.D. dissertation, State University of New York at Stony Brook, Stony Brook, 374 pp.

Sues, H.-D. 2000. Herbivory in terrestrial vertebrates: an introduction; pp. 1–8 in H.-D. Sues (ed.), Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record. Cambridge University Press, Cambridge.

Teaford, M. F. 1985. Molar microwear and diet in the genus *Cebus*. American Journal of Physical Anthropology 66:363–370.

Teaford, M. F. 1988a. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. Scanning Microscopy 2:1167–1175.

Teaford, M. F. 1988b. A review of dental microwear and diet in modern mammals. Scanning Microscopy 2:1149–1166.

Teaford, M. F., and J. A. Runestad. 1992. Dental microwear and diet in Venezuelan primates. American Journal of Physical Anthropology 88:347–364.

Teaford, M. F., and A. Walker. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. American Journal of Physical Anthropology 64:191–200.

Teaford, M. F., and J. D. Lytle. 1996. Diet-induced changes in rates of human tooth microwear: a case study involving stone-ground maize. American Journal of Physical Anthropology 100:143–148.

Teaford, M. F., M. C. Maas, and E. L. Simons. 1996. Dental microwear and microstructure in early Oligocene primates from the Fayum, Egypt: implications for diet. American Journal of Physical Anthropology 101:527–544.

Ungar, P. S. 1995. A semiautomated image analysis procedure for the quantification of dental microwear II. Scanning Microscopy 17:57–59.

Ungar, P. S. 1996. Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. Journal of Human Evolution 31:335–366.

Ungar, P. S., and M. A. Spencer. 1999. Incisor microwear, diet, and tooth use in three Amerindian populations. American Journal of Physical Anthropology 109:387–396.

Ungar, P. S., and M. F. Teaford. 1996. Preliminary examination of nonocclusal dental microwear in anthropoids: implications for the study of fossil primates. American Journal of Physical Anthropology 100:101–114.

Van Valkenburgh, B., M. F. Teaford, and A. Walker. 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. Journal of Zoology 222:319–340.

Willis, K. J., and J. C. McElwain. 2002. The Evolution of Plants. Oxford University Press, Oxford, 378 pp.

Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall Inc, Upper Saddle River, New Jersey, 663 pp.