Morphometry of the teeth of western North American tyrannosaurids and its applicability to quantitative classification

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Gross tooth morphology and serration morphology were examined to determine a quantifiable method for classifying tyrannosaurid tooth crowns from western North America. From the examination of teeth in jaws, tyrannosaurid teeth could be qualitatively assigned to one of five types based on the cross-sectional shape of the base of the tooth and characteristics of the mesial carina. A principal component analysis (PCA) revealed that much of the variance in tooth shape was a result of isometry, but some gross morphological variables exhibited strong positive allometry. Non-size associated factors were also important in determining tooth shape, particularly when data on denticle dimensions were considered in the analysis. While PCA identified important factors in variation, PCA ordination plots did not cluster the teeth into distinct, separate groupings based on taxon or bone of origin. The group classification functions determined by discriminant analysis, though not universally successful for classifying unidentified isolated teeth of all tyrannosaurids, do identify bone of origin of adult *Albertosaurus*, *Daspletosaurus*, and *Gorgosaurus* teeth at a statistically acceptable level.

Key words: Theropoda, Tyrannosauridae, dentition, classification, quantitative analysis, Cretaceous, North America.

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Introduction

The teeth of theropod dinosaurs are diverse and relatively abundant in Upper Cretaceous sediments of western North America. Many features of theropod teeth allow identification at high taxonomic resolution, sometimes down to species level (Currie et al. 1990). Diagnostic features of the tooth crown include cross-sectional shape, presence of mesial and/or distal denticles and their locations, and the size and shape of each denticle. These have been described and utilized in classification for various North American taxa, including tyrannosaurids (Currie et al. 1990; Farlow et al. 1991; Fiorillo and Currie 1994; Baszio 1997; Sankey 2001; Sankey et al. 2002). These studies demonstrate that isolated tyrannosaurid tooth crowns can be identified to the family level.

The teeth of most theropod dinosaurs are contained in the premaxilla, maxilla, and dentary. In most theropods, the largest maxillary teeth are larger than the largest dentary teeth (Currie 1987). The denticles are complex structures (Abler 1997), aligned on carinae that sometimes bifurcate in tyrannosaurids (Erickson 1995).

Tyrannosauridae is a lineage of large-bodied Late Cretaceous coelurosaurs (Holtz 1994, 1996, 2000); Sereno 1997; Norell et al. 2001). The generic and specific taxonomy of the tyrannosaurids is unstable, and the relationships among these taxa are controversial (Currie 2003b; Currie et al. 2003). Several genera, including *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*, and *Tyrannosaurus* (Russell 1970; Currie 2003a) are found in the Upper Cretaceous sediments of southern Alberta and the northwestern United States.

The crown of a tyrannosaurid tooth (Fig. 1) is a semi-conical structure made up of a stack of nested dentine cones with a thin external layer of enamel on the crown (Abler 1992). The premaxillary tooth is D-shaped in basal cross section, with two serrated ridges (carinae) located on the lingual side. Maxillary and dentary teeth are more laterally compressed, less recurved than in other theropods, with a round to ovoid cross-sectional outline and stout saddle- or chisel-shaped serrations (denticles) (Fig. 1) on both the mesial and distal (see Smith and Dodson 2003) margins of the tooth crown. These serrations are sometimes angled towards the apex of the tooth, and are generally aligned along carinae that curve lingually. Further, the denticles on the maxillary and dentary teeth have the following additional characteristics: (1) they are relatively large (Farlow et al. 1991), (2) they are more widely spaced than in many other theropods (Sankey et al.

2002), (3) they have mesial and distal serrations that are equivalent in size (Chandler 1990), (4) they are wider labially-lingually than they are long proximodistally, (5) they generally decrease in size towards the base and apex of the tooth, (6) they possess sharp ridges of enamel along the midline, and (7) they are smaller relative to tooth length in larger individuals, but are absolutely larger in basal diameter and denticle height (Chandler 1990; Currie et al. 1990). The internal and external morphologies of tyrannosaurid teeth are described in detail by Abler (1992). The microstructure and chemical composition of *Tyrannosaurus* teeth are discussed by Dauphin et al. (1989).

Continual replacement (polyphyodonty) of teeth occurred throughout the life of a dinosaur (Edmund 1960; Chandler 1990; Erickson 1996), with one or two replacement teeth developing at any given time for each tooth position (Edmund 1960). As the growth rate of the animal decreases over time, its tooth replacement rates also slow down (Erickson 1996), and the influence of wear and tear on the replacement of teeth increases.

Abler (1992) described three types of dental wear surfaces for tyrannosaurids that were characterized by shape and location on the tooth crown. Farlow and Brinkman (1994) reported wear on the lingual sides of dentary teeth, an unusual feature given the way tyrannosaurid jaws fit together (Schubert and Ungar 2005). Jacobsen (1996) observed the presence of wear on the mesial, distal, labial, and lingual sides of teeth, with a number of teeth exhibiting more than one type of wear. Wear features have recently been attributed to two different etiologies, 1) occlusal attrition, resulting in elliptical shaped facets with microscopic parallel wear striations, and 2) abrasion, often resulting in conchoidal shaped spalled surfaces with microscopic striations that are heterogeneous (Schubert and Ungar 2005). Attritional wear facets are found on only one side of a given tooth crown, never on the mesial or distal surfaces (Schubert and Ungar 2005). Thus, one might expect to find occlusal wear facets on the lingual side of a maxillary tooth crown, and on the labial side of a dentary tooth crown (Lambe 1917), which could potentially serve as an indicator of bone of origin for isolated teeth (Schubert and Ungar 2005).

Currie (1987) determined that the teeth of a small theropod, *Troodon*, vary in structure according to position in the jaw, and can be separated into four types, similar to Hungerbühler's (2000: 33) "dental sets": (1) premaxillary, (2) maxillary, (3) mesial dentary, and (4) distal dentary. Similarly, a distinction between the premaxillary and maxillary/dentary teeth of tyrannosaurids is easily made from the examination of teeth in jaws (Chandler 1990; Carr 1999; Brochu 2003) but thus far, the characteristics that separate these types have not been quantified.

The feasibility of quantifiably distinguishing taxon of origin below the family level, or bone of origin for tyrannosaurid teeth, has not been investigated. Quantifiable distinctions would be useful for identifying isolated teeth, as they are commonly found in North American Mesozoic strata, and are useful for tracking geographical and evolutionary occurrences in paleoecological studies (Brinkman 1990; Farlow and Pianka 2002).

This study is an attempt to quantify tooth variation within a restricted co-familial group of dinosaurs from ecologically similar settings. The viability of two multivariate statistical methods to discriminate between tooth samples is assessed using a relatively restricted sample. The efficacy of a given technique for distinguishing subtle variation within a restricted sample would demonstrate its potential as a method for tracking ecological and evolutionary shifts within any stratigraphically well-represented clade. Our exploratory statistical approach will serve as a methodological baseline for studying ontogenetically, taxonomically, and stratigraphically more divergent samples.

To quantify the positional and taxonomic variation of tyrannosaurid teeth (specifically, tooth crowns) we studied teeth in tyrannosaurid jaws to determine if there were trends in serration and gross tooth morphology that can be used to identify isolated tyrannosaurid teeth. We used principal component analysis (Pimentel 1979; Chapman et al. 1981; Weishampel and Chapman 1990) to examine the quantitative morphometry of tyrannosaurid teeth, as an adjunct to their descriptive morphometry. In addition to quantifying the scaling relationships among the different dimensions of the teeth and examining the effects of isometry on these, we ordinated the results of this analysis in order to examine the relationship of tooth morphometry to bone of origin. This last objective is also pursued through the use of discriminant analysis based upon tooth morphometry.

Institutional abbreviations.—BHI, Black Hills Institute, Hill City, South Dakota, USA; MOR, Museum of the Rockies, Bozeman, Montana, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Methods

Specimens.—In situ teeth (in the original alveolar position in the jaw) from various western North American taxa were examined (Appendix 1). Of the many isolated tyrannosaurid teeth in the collections of the TMP, the majority are from the Judith River Group of southern Alberta. These isolated teeth consist mainly of shed tooth crowns, the most complete of which were examined for this study (Appendix 2).

Measurements.—For consistency of measurement, the base of the tooth crown was defined as a plane that extends horizontally at the level of the base of the distal carina when the tooth is positioned in approximate life orientation (Fig. 2), which is roughly parallel to the termination of enamel at the base of the tooth crown. Measurements (in mm) follow the methods of Farlow et al. (1991) and Sankey et al. (2002): (1) fore-aft basal length (FABL); (2) tooth crown height (THEIGHT), measured from the base of the distal carina; (3) cross-sectional thickness (XSTHICK), measured at the

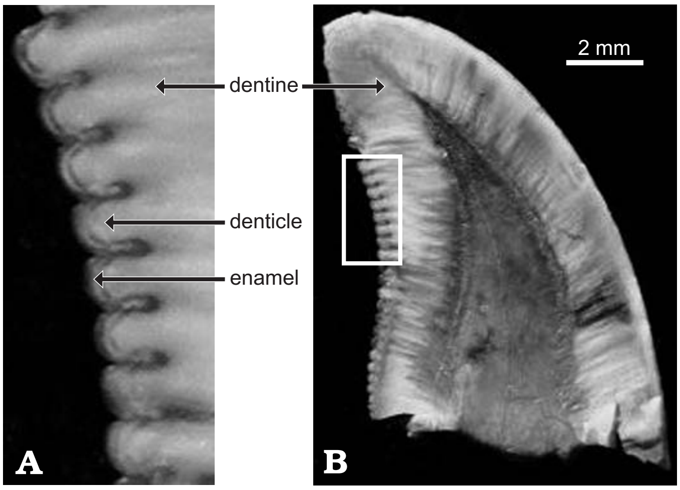

Fig. 1. Longitudinal section through the crown of a small, broken, tyrannosaurid tooth (TMP 86.130.214, Judith River Group, Campanian, Alberta, Canada). The plane of the break resulted in the loss of the mesial carina, so only the distal carina is preserved on the tooth. **A**. Enlargement of the area outlined in B shows the enamel and the denticles. **B**. Photograh of the whole specimen showing dentine (light-colored area).

base of the tooth crown; (4) curvature (CURVATUR); and (5) distance from the base of the mesial carina (end of the denticles) to the base of the tooth crown (DMCTOB). The mesial (M) and distal (D) carinae were each divided approximately into basal (B), middle (M), and apical (A) thirds (*sensu* Chandler 1990). As denticles tend to diminish in size towards the base and apex of the tooth, denticle width (DW) and denticle height (DH) were measured for average-sized denticles in the middle of each section (Fig. 2). Tooth measurements 1, 2, 3, and 5 were taken with dial calipers, whereas tooth measurement 4 (except for exceptionally large teeth) and the denticle measurements (6 and 7) were taken with a calibrated ocular micrometer through a binocular microscope.

For comparative purposes, ratios calculated for in situ teeth are (Farlow et al. 1991; Carr 1996): (1) XSTHICK/FABL; (2) XSTHICK/THEIGHT; and (3) DMCTOB/THEIGHT. A subjective approximation of the last ratio was used to estimate *a priori* the bone of origin for the isolated teeth, based on the relative lengths of the maxillary and dentary mesial carinae in *Dromaeosaurus* (Fiorillo and Currie 1994).

Measurement error.—A single-factor (in situ or isolated) repeated-measures ANOVA was used to examine the contribution of measurement error to the total variance of the sample. For a subset of the entire sample (12 isolated teeth and 5 in situ teeth [4 *Gorgosaurus libratus*, 1 *Daspletosaurus torosus*]), each of the measurements was repeated three times for each tooth; each replicate was considered as a repeated measurement in the ANOVA. The departure of the variance-covariance matrix of each set of repeated measurements from sphericity was evaluated by calculation of the Greenhouse-Geisser ε; a value near 1.0 was taken to indicate little departure, but in all cases the ε value was used to calculate the appropriate approximation of F for that portion of the ANOVA (Quinn and Keough 2002). An F-max test was used to examine each series of repeated measurements for homoscedasticity (Sokal and Rohlf 1969), and normality within each series was tested for using a Lilliefors' modification of the Kolmogorov-Smirnov one-sample test (Wilkinson 1990); these tests of the model's assumptions determined the acceptance of the results of the ANOVAs.

In addition, in situ teeth are rarely pristine, and the measurement of THEIGHT is sometimes hampered by slight apical chipping or wear at the base of the distal carina. Farlow et al. (1991: 163) experienced similar difficulties with incompletely preserved teeth, and measured tooth crown height vertically from the outer rim of the tooth socket to the tooth apex, noting that their method overestimated tooth height in some cases. In the present study, our measurement for the more poorly preserved teeth would tend to slightly underestimate the value of THEIGHT. However, only teeth with very minimal damage were considered, and can therefore be considered to be reasonable and representative of the height of the tooth.

Statistical analysis.—To assess the sizes and shapes of the teeth, a sub-sample (n = 35) of isolated teeth as well as a sub-set of in situ teeth (n = 71) were chosen for statistical analysis. For the isolated tooth sample, over 1700 specimens were examined, 196 were measured, but only the 35 used in the study were pristine and had all mensural characters (denticles included). The carinae were not always well preserved or complete on the examined in situ teeth, and in order to maximize the sample size for statistical analysis, denticle data were not included. Of the ~161 measured in situ teeth, data from only the 71 best-preserved teeth were used.

Simultaneous size-dependent shape changes in two or more anatomical dimensions are best considered in terms of multivariate scaling (Jolicoeur 1963a; Cock 1966; Morrison 1976; Pimentel 1979; Shea 1985; Rohlf and Bookstein 1987; Strauss 1987; Voss 1988; McKinney and McNamara 1991; Jungers et al. 1995; Klingenberg 1996). The principal component generalization of the allometric equation, derived from $\log_{10}$-transformed mensural data (Jolicoeur 1963b), describes multivariate scaling (Jolicoeur 1963a; Pimentel 1979; Shea 1985; Strauss 1987; Voss 1988; McKinney and McNamara 1991). When derived from $\log_{10}$-transformed mensural data from a single taxonomic group, the first component—the size-determined shape vector (McKinney 1990)—can be taken to represent the variance incident upon differences in size (Somers 1986; Tissot 1988; McKinney 1990; McKinney and McNamara 1991), whether isometric or allometric. Subsequent components thus describe variance in shape that is not associated with size (Tissot 1988; Marcus 1990; McKinney 1990; McKinney and McNamara 1991).

The logarithmic spiral manifests itself in the shape of the vertebrate tooth to a greater or lesser degree (Thompson 1961), and the element of tooth shape (particularly THEIGHT and CURVATUR) incorporating this cannot be expected to vary with size over a wide size range according to allometric

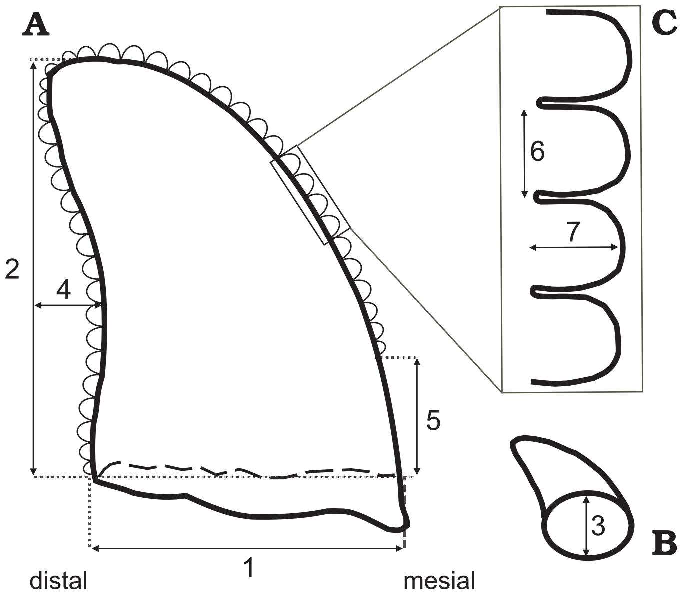

Fig. 2. Schematic illustration of tooth and denticle measurements obtained for this study. Diagram is an outline of tooth specimen TMP 86.130.214. Denticles on tooth outline in lateral (**A**), basal (**B**), and enlarged (**C**) views, not to scale. For measurements, tooth is aligned so that the basal termination of enamel (broken line in A) is approximately horizontal. 1, fore-aft basal length (FABL); 2, tooth crown height (THEIGHT); 3, cross-sectional thickness (XSTHICK); 4, curvature (CURVATUR); 5, distance from the base of the mesial carina to the base of the tooth (DMCTOB); 6, denticle width (DW); 7, denticle height (DH).

rules (Batschelet 1979). However, the tyrannosaurid tooth describes a sufficiently short segment of the logarithmic spiral that the allometric relationship can be assumed without a loss in explicatory power over the size range of teeth examined.

In situ and isolated teeth were analyzed separately. Further subdivisions of these sample groups were not done because identified taxa are represented by unequal numbers of individuals and/or the bone of origin (Appendix 1). In addition, the isolated teeth could not be assigned with certainty to either sub-familial level taxon or bone of origin (Appendix 2), though the familiarity with tyrannosaur teeth of the first author, gained from examining many hundreds of specimens, made educated *a priori* estimations for bone of origin possible. All teeth in each sample were grouped initially as tyrannosaurid dinosaurs, and within each principal component analysis there was no taxonomic subdivision, nor subdivision by bone of origin. We assume that the allometric vector does not differ significantly among any such groupings (Klingenberg 1996), and in any case, principal component analysis will segregate variance not directly explained by size, whether due to systematic or physical position, from that explained by size. All of the measurements were $\log_{10}$-transformed to minimize possible inherent heteroscedasticity (Kerfoot and Kluge 1971; Zar 1984; Tissot 1988), to better approximate the multivariate normal distribution (Pimentel 1979), and to better approximate the linear PCA model (Jolicoeur 1963a; Pimentel 1979; Shea 1985; Strauss 1987; Voss 1988). Biological data generally conform to the assumption of multivariate normality (Marcus 1990). PCA is in any case robust to minor deviations from the multivariate normal distribution, which are of lesser importance when PCA is being used to ordinate the data (Reyment 1990).

Principal component analysis was performed on variance-covariance matrices derived from the $\log_{10}$-transformed data using SYSTAT (Version 5.0, 1994, SYSTAT, Inc.). The entire suite of components from each analysis, ranked by eigenvalue, and incrementally-decreasing subsets of each suite, were tested for isotropicity of length by Bartlett's χ^2 test for sphericity (Morrison 1976). As the sample sizes were small, the decision of how many components to retain was based upon the results of this iterative application of Bartlett's approximation of χ^2 (Quinn and Keough 2002). Acceptance levels for each set of tests were determined by a stepwise Bonferroni adjustment (Rice 1989). The first component (PC I) of each analysis was interpreted as the size-determined shape vector, whereas the remainder of those retained were examined for evidence of morphological changes not strongly determined by overall size (Tissot 1988; Marcus 1990; McKinney and McNamara 1991; Jungers et al. 1995). The correlations of each of the morphological variables with each of the components, and the percent of the total variation of each morphometric variable explained by each of the components, were calculated as described by Pimentel (1979). The first component was tested for isometry (i.e., all possible ratios of PC I loadings approximating 1.0, or an isometric slope for reduced major axis slopes calculated for any pairwise combination of morphometric variables in the variable suite—Cheverud 1982, Klingenberg 1996) by comparing it to a theoretical "isometric vector" (Leamy and Bradley 1982; Cheverud 1982; Voss 1988). The individual loadings of an isometric vector are computed as ($1/\sqrt{p_i}$) where p_i equals the number of variables in the analysis (Jolicoeur 1963b). In the case of the present analyses, the loadings on the theoretical isometric vector equal ($1/\sqrt{5}$ = 0.447214) (excluding the denticle variables), and ($1/\sqrt{17}$ = 0.242536) (including the denticle variables). The difference between the observed size-dependent shape components and the appropriate theoretical isometric vectors was tested by means of Anderson's (1963) χ^2 approximation (Pimentel 1979). A variable loading that approximates the value of the isometric loading exhibits isometry—i.e., equality of relative growth rate (Jolicoeur 1963a)—relative to an overall measure of size (i.e., when multiplied by $1/\sqrt{p_i}$, against the weighted geometric mean of all variables—Klingenberg 1996). Variable loadings considerably greater than the isometric loading can thus be interpreted to indicate positive allometry, whereas variable loadings well below the isometric loading indicate negative allometry (Voss 1988).

The size-associated variance predicted to be explained by isometry was removed from the original data matrix of the in situ teeth (restricted to the five gross anatomical variables) by a modification of the Burnaby method for size-removal (Burnaby 1966; Rohlf and Bookstein 1987; Marcus 1990). Here we use the theoretical isometric vector (with loadings

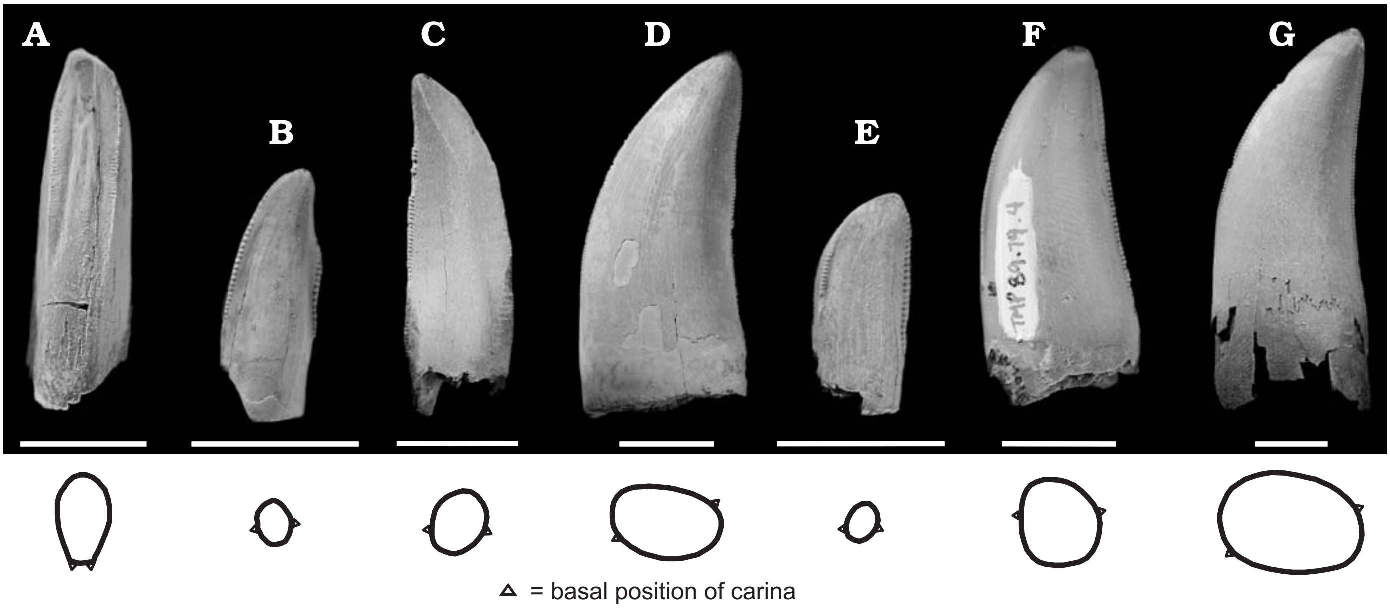

Fig. 3. The five major types of teeth found in the tyrannosaurid jaw, Judith River Group, Campanian, Upper Cretaceous, Alberta, Canada. **A**. Premaxillary, TMP 65.26.3. **B**, **C**. Mesial maxillary, MM1 TMP 98.68.65 (**B**), MM2 TMP 66.31.36 (**C**). **D**. Distal maxillary, TMP 85.36.342. **E**, **F**. Mesial dentary, MD1 TMP 79.14.538 (**E**), MD2 TMP 89.79.4 (**F**). **G**. Distal dentary, TMP 97.12.43. Cross-sectional shape and location of carinae are as indicated, and are to scale relative to each other. Scale bars 10 mm.

of $1/\sqrt{5} = 0.447214$) in place of the usual PC I derived from the data (Burnaby 1966; Rohlf and Bookstein 1987; Marcus 1990). We assumed that any significant intra-group variance here (due to bone of origin, individual representation, or taxonomic grouping below the family level) was additive to variance due to size. As PC I in the original PCA would account for the variance produced by common allometry (Klingenberg 1996) as well as that due to isometry, it can be replaced by the isometric vector. Variance from other sources would remain in the modified data set and be susceptible to further analysis. A new data matrix with this variance removed was generated and subjected to a principal component analysis. The principal components extracted from this analysis are interpreted as describing aspects of tooth shape that are not dependent upon isometric scaling.

To classify the teeth to a bone of origin, the origins of the isolated teeth were first determined subjectively, based on the length of the mesial carina relative to the length of the distal carina. These assignations were first tested by subjecting the isolated tooth sample to discriminant analysis, a technique that has been used by other researchers to distinguish tooth morphs for various animals (e.g., Palmqvist et al. 1999; Smith 2002). Using SYSTAT (Wilkinson 1990), the $\log_{10}$-transformed gross mensural data from the isolated tooth sample were used to derive canonical coefficients for the five gross morphological variables, and two discriminant functions for the two putative bones of origin, maxillary and dentary (Morrison 1976, Pimentel 1979). The Wilks' λ and its associated F from the MANOVA generated in this process were used post hoc to evaluate the discriminant analysis (Morrison 1976). The consistency of the author-assigned groupings with the discriminant scores of all of the cases was tested by means of a χ^2 test for independence of association of the discriminant function's classification results against an expected homogeneous distribution (arrayed in a 2×2 contingency table—Steel and Torrie 1980). The values of the canonical coefficients were compared to those of the corresponding PCA factor loadings in order to further clarify the relationships among the gross mensural characters of the teeth and their mode of variance depending upon bone of origin.

As an independent and more powerful test of the discriminant function derived from the isolated tooth data, the gross mensural data from the in situ tooth sample were used together with the group classification functions to provisionally classify the in situ teeth to bone of origin. The differences between the scores determined for the in situ teeth were compared to the distributions of the differences in group classification scores established for the isolated teeth, and predicted group membership assigned on that basis. The distributions of predicted *versus* actual bone of origin (arrayed as a 2×2 contingency table) were tested for independence of association by means of a χ^2 test for interaction (Steel and Torrie 1980). Correct classification by the group classification functions of teeth already unequivocally known to bone of origin would support the importance of the variables used to describe tooth morphology, and validate the subjective judgement of the first author.

Results

Empirical description.—There are 4 premaxillary, 11 to 17 maxillary, and 13 to 17 dentary teeth in tyrannosaurids (Currie et al. 2003). Five qualitative types of teeth can be observed in the tyrannosaurid jaws (Fig. 3). Premaxillary teeth

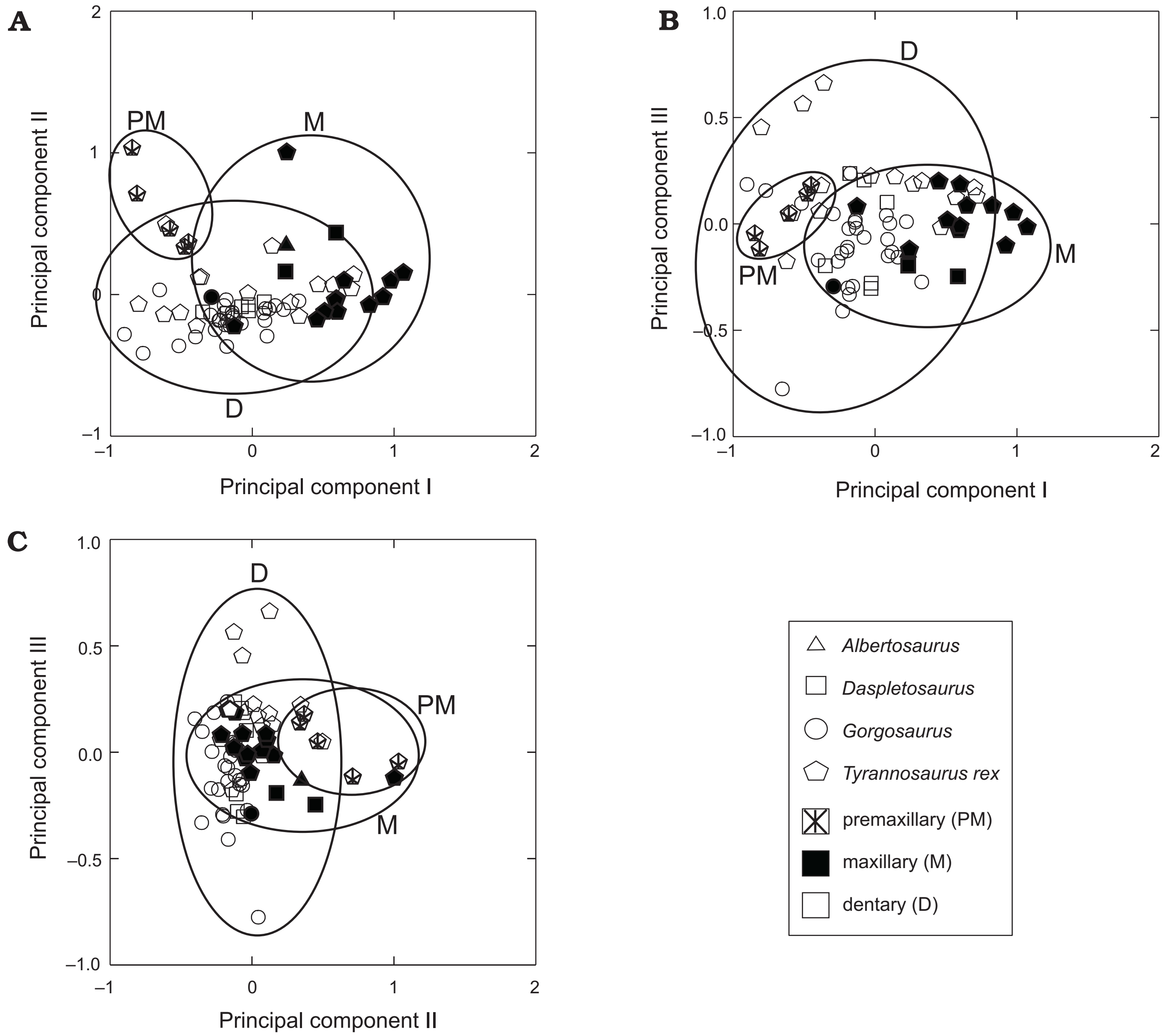

Fig. 4. **A**. Ordination plot for PC I *versus* PC II for the teeth in jaws. **B**. Ordination plot for PC I *versus* PC III for the teeth in jaws. **C**. Ordination plot for PC II *versus* PC III for the teeth in jaws.

are smaller than all but the most distal maxillary and dentary teeth, and are D-shaped in cross-section. The mesial (first one or two) maxillary and dentary teeth are more rounded in cross-section (personal observation). These correspond to the incisiform and sub-incisiform tooth shapes mentioned by Carr (1999). Brochu (2003) also noted a difference in the location of the carinae on the first few dentary teeth, which would result from this difference in cross-sectional shape. The remainder (distal) of the maxillary and dentary teeth are more ovoid and labio-lingually compressed in cross-section. Mesial dentary teeth are procumbent, but curve distally. All maxillary teeth and distal dentary teeth are more vertical in orientation, but also curve distally. These distinctions are obvious for in situ teeth, but are more difficult to determine for isolated teeth because their original alveolar positions are unknown.

Except in *Tyrannosaurus rex*, the mesial denticles on the maxillary teeth start closer to the base of the tooth than those of the dentary, just as in *Dromaeosaurus* (Fiorillo and Currie 1994). The widths of both the mesial and distal denticles are approximately equivalent in both the maxillary and dentary teeth (Chandler 1990 and personal observation). In the dentary teeth, however, the heights of the distal denticles are generally slightly larger than those of the mesial denticles (personal observation); finer mesial than distal denticles are generally considered typical of tyrannosaurids (Carr 1996). The direction of the deviation of the mesial carina from the midline can be used to distinguish teeth from the left or right sides of the jaw in tyrannosaurids, as the carina always shifts towards the lingual side of the tooth. If the tooth is viewed mesially with the base down, a deviation to the left, for example, indicates either a right maxillary or left dentary tooth. Also, as tyrannosaurid dentaries are not as curved as the maxillae, the basal deviation of the mesial carina from the midline is typically greater in the dentary teeth.

In some isolated tooth specimens (TMP 94.12.313, 94.12.209, 94.12.4), the first two preserved teeth of the right dentary of TMP 86.144.1 (*Gorgosaurus libratus*), and the first five dentary teeth of TMP 94.143.1 (*Daspletosaurus torosus*), there are no discernable denticles on the mesial apex of the tooth. The enamel is smooth and intact, and there does not appear to be any evidence of wear. The absence of apical denticles is likely genetic and not taphonomic in these samples.

Measurement error.—The distributions of none of the repeated measures taken from isolated teeth or from in situ teeth were significantly non-normal in distribution. The three repetitions for each measurement, isolated and in situ, were all homoscedastic. For both of these tests the stepwise Bonferroni adjustment acceptance levels were 0.004 and 0.01, respectively. The Greenhouse-Geisser ε varied but was generally high (THEIGHT: 0.784; FABL: 0.846; XSTHICK: 0.938; CURVATUR: 0.996; DMCTOB: 0.912), indicating moderate to small departures from compound symmetry for the data. Assumptions for the repeated-measures ANOVA were thus supported, or could be adjusted for. At a stepwise Bonferroni-adjusted acceptance level of 0.01, the ANOVAs showed no significant differences between measurements at different times for any of the variables, and no significant interaction effect between time of measurement and situation of tooth. We can thus dismiss measurement error as a significant factor in this analysis. Additionally, the measurements used are replicable and should be of use in other studies of tyrannosaurid teeth.

Statistical analysis.—In the interpretation of the morphometric principal component results, the first principal component is interpreted as describing size-related shape differences, whereas subsequent components describe non-size-related shape differences (Somers 1986; Tissot 1988; McKinney 1990; McKinney and McNamara 1991). Additionally, variables that show maximum variance explained by, and strong correlations with, the same principal component display variance in shape controlled by the same factor, whether it be size-associated or otherwise.

Interpreting PCA of the in situ tooth sample for the gross morphological variables requires only the first four components, which collectively account for 99.45 percent of the sample variance (Appendix 3). PC I differs significantly from the isometric vector. FABL, THEIGHT, and XSTHICK display negative allometry, DMCTOB positive allometry, and CURVATUR strong positive allometry. This reflects how the teeth become relatively thinner and more recurved with increasing size, as the base of the mesial carina moves up the slope of the tooth. The opposing trends of THEIGHT and CURVATUR reflect the contribution of the logarithmic spiral element of tooth shape in the recurved shape of the tooth. The size-associated shape vector explains almost two-thirds of the total variance (Appendix 3), but only accounts for the majority of the variance of CURVATUR. The remaining gross morphological variables have their variances more evenly spread among the first three components (Appendix 3). Likewise, the strongest positive correlation is between CURVATUR and PC I. The other variables, although having positive correlations with PC I, also have strong correlations with PC II and PC III (Appendix 3). Because PC II and PC III describe shape variance that cannot be attributed to size, these large correlations and amounts of variation described must be ascribed to such factors as bone and taxon of origin. It must also be pointed out that relatively few individual animals contributed teeth to this sample (Appendix 1), so individual variation will make a disproportionate contribution to PC II and PC III. Unfortunately these factors cannot easily be teased apart.

Removing the variance attributable to isometry from these data (Appendix 4) reduces the sum of the eigenvalues by approximately 55 percent, indicating that isometry is responsible for slightly more than half of the total variance in the unmodified sample. The first two components derived from the modified data matrix account for 96.78 percent of its total variance (Appendix 4). The variance due to allometry and non-size-associated factors such as systematic position, bone of origin, and individual idiosyncrasy will be distributed through this total variance. Most of the variance in FABL, THEIGHT, and XSTHICK, variables which were negatively allometric in the first PCA (Appendix 3), are explained by PC I in this analysis (Appendix 4). The majority of the variance of CURVATUR, a strongly positively allometric variable in the first analysis (Appendix 3), is explained by PC II in this analysis (Appendix 4). DMCTOB shows a similar distribution of variance across PC I and PC II in both analyses (Appendices 3, 4). Both CURVATUR and DMCTOB are negatively correlated with PC I (Appendix 4). Overall, the PCA from the modified data set suggests that the remaining allometric variation left after the removal of the variation due to isometry is distributed across PC I and PC II. However, this also implies that some aspects of tooth allometry are not correlated with one another in the absence of size. The sum of the eigenvalues derived from the data set after the removal of isometric variance (Appendix 4) is not greatly in excess of the sum of the eigenvectors for PC II–PC IV in the original PCA (Appendix 3). Therefore, an additional implication is that allometry contributes a relatively small amount of variance to the whole.

The sample of isolated teeth (Appendix 2) is much smaller than that of in situ teeth (Appendix 1), which may account for some of the differences in the PCAs of the two samples (Appendices 3, 5), especially if this entails a difference in taxonomic representation. In addition, unlike the limited number of individuals in the in situ sample, the isolated tooth sample likely represents as many individuals as teeth. Again, the first four components, explaining 99.11 percent of the total variance, are non-isotropic (Appendix 5). The loading for THEIGHT is close to isometric in PC I (Appendix 5), as opposed to its negatively isometric PC I loading in the in situ tooth PCA (Appendix 3). The pattern of loadings for this vector are otherwise fairly similar for both analyses, although FABL, THEIGHT, and XSTHICK have much more of their total variances explained by PC I in the isolated tooth PCA (Appendices 3, 5). PC II of this analysis is poorly correlated with these three variables, and explains little of their total variance. Instead, it is largely defined by the non-size associated shape variances of CURVATUR and DMCTOB (Appendix 5). Most of the remnant variance of FABL, THEIGHT, and XSTHICK is explained by PC III, which also has fairly strong correlations with this component (Appendix 5). In contrast to the analysis of in situ teeth (Appendix 3), the analysis of isolated teeth shows non-size-associated variance in CURVATUR and DMCTOB that is not correlated with the non-size-associated variance in the other gross morphological variables (Appendix 5). For DMCTOB, this is likely due to the presence of *Tyrannosaurus rex* teeth in the in situ tooth sample. In contrast to the teeth of the other genera examined, the mesial denticles of both examined specimens of *T. rex* teeth start farther away from the base of the teeth in the maxilla. This would introduce variance in this variable not necessarily associated with size but definitely attributable to systematic position.

In the PCA of isolated teeth incorporating denticle data (Appendix 6), the first three components, accounting for 79.46 percent of the total variance of the data, are the most strongly associated with the gross morphological variables. PC I, the size-associated shape vector, explains most of the variance in FABL, THEIGHT, and XSTHICK with the inclusion of denticle data. Significant amounts of non-size-associated variance in CURVATUR and DMCTOB are still explained by the subsequent two components (Appendix 6). A much larger amount of variance in DMCTOB is explained here by PC III, and this variable is also highly correlated with PC II (Appendix 6). This contrasts with what was found for DMCTOB in the PCA of this sample using only the gross morphological variables (Appendix 5). PC I and PC II also generally explain significant amounts of variance in denticle dimensions (Appendix 6). Although much of this variance is size-associated, some is not, and is associated instead with the variance of CURVATUR (and to a lesser degree DMCTOB) explained by PC II (i.e., for denticle dimensions DDWB and DDHA). Most of the size-associated change in denticle shape is negatively allometric, or in the case of MDHB and MDHM, roughly isometric (Appendix 6). The remaining 20.54 percent of the sample variance explained by the subsequent six components is distributed largely among the denticle variables. They therefore contain a significant portion of non-size-associated variance. DDHB, DDHM, and DDHA have relatively large amounts of variance explained by PC IV, whereas MDHA has a significant amount explained by PC V. Generally patterns in the explanation of variance by components IV–IX are difficult to discern, and the component correlations do little to elucidate them (Appendix 6).

Ordination diagrams for the principal components that explain the greatest amount of variance (PC I, II, and III) in the unmodified data for in situ teeth allow visual evaluation of tooth distribution by taxon and bone of origin (Fig. 4). Distribution of teeth along PC I (Fig. 4A, B) can be attributed to tooth size (and, to a lesser degree, dinosaur size). Neither the taxa nor bone of origin separate well into clear, distinct groupings. This quantifiably supports Carr and Williamson's (2000) qualitative observation that the teeth of western North American tyrannosaurids are not diagnostic below the family level. To a limited degree, the maxillary teeth separate from the dentary teeth, as do the premaxillary teeth, in the plot of PC II against PC III (Fig. 4C).

The discriminant analysis of the isolated teeth using gross morphology indicated a significant difference in mean between the two groups by subjectively-assigned bone of origin (Wilks' $\lambda = 0.451$; $F = 7.051$, 29, 5 df, $P < 0.001$). Upon examination of the absolute values of the standardized canonical coefficients (Table 1), it was evident that the most important variable was DMCTOB, followed in decreasing order by FABL, THEIGHT, XSTHICK, and CURVATUR.

Table 1. Canonical coefficients for the dependent variables for the isolated teeth from the discriminant analysis. FABL, fore-aft basal length; THEIGHT, tooth crown height; XSTHICK, cross-sectional thickness; CURVATUR, curvature; DMCTOB, distance from the base of the mesial carina to the base of the tooth.

Variable	Canonical coefficient
FABL	–0.810
THEIGHT	–0.810
XSTHICK	0.532
CURVATUR	0.167
DMCTOB	1.160

Two group classification functions were generated from this analysis, which can be used to identify western North American tyrannosaurid teeth as either maxillary or dentary:

(1) 136.637(FABL) + 62.049(THEIGHT) – 84.760(XSTHICK) – 32.940(CURVATUR) – 17.367(DMCTOB) – 76.762

(2) 121.353(FABL) + 50.957(THEIGHT) – 75.817(XSTHICK) – 31.400(CURVATUR) – 3.829(DMCTOB) – 62.176

Each of the groups has a characteristic distribution for the difference between the products of these two functions. The assignations to maxillary or dentary were originally made on a subjective basis. Still, the majority of the isolated teeth separate into two relatively distinct groups based on bone of origin. If the predictions determined by the discriminant analysis are compared to the *a priori* classification (Appendix 2), only one (pathologically anomalous) tooth (TMP 88.36.61) out of the 35 in the data set was misclassified (Table 2). The *a priori* assessment classified it as a dentary tooth, but the discriminant equations predicted it to be a maxillary tooth. The distribution of predicted against actual bone of origin is significantly different from what would be expected by chance (Table 2); the discriminatory functions correctly assign isolated teeth to their bone of origin.

In order to test the classificatory reliability of the group classification equations, the equations were used to generate new scores from the gross morphological values of the in situ teeth, which were classified as either maxillary or dentary on this basis (Appendix 1). These scores were compared to the score distributions derived from the isolated teeth and assigned to maxillary or dentary on this basis. When all taxa are included in the test, the group classification functions are not sufficient to accurately classify all teeth to bone of origin (Table 3). With the removal of *Tyrannosaurus rex*, the distribution of tooth assignment is significantly different from what would be expected by chance, with only one tooth misclassified (Table 3). This small tooth belonged to a small juvenile specimen (TMP 94.12.155) of *Gorgosaurus libratus* (Currie 2003a). The *T. rex* sample was not classified to a significantly different degree from what would be expected by chance (Table 3).

Discussion

Empirical analysis.—It is reasonable to surmise that few individual animals are represented by more than one tooth in a random sampling of isolated teeth (Farlow et al. 1991). Taxonomic and ontogenetic variation is undoubtedly present in the sample of isolated teeth examined. These teeth are generally not identified beyond the family level. The in situ teeth, however, can be used to assess taxonomic variation.

A comparison of the ratio XSTHICK/FABL and XSTHICK/THEIGHT for distal tooth alveolar position 8 (or close if not present) in the maxillae and dentaries of several taxa revealed slight taxonomic differences, and contrary to Currie et al. (1990), slight ontogenetic differences (Table 4). The teeth in jaws of small juvenile specimens (dentaries, TMP 94.12.155) of *Gorgosaurus libratus* (Currie 2003a), were thinner labio-lingually relative to fore-aft basal length of the tooth crown, but were comparable relative to tooth crown height in cross-sectional thickness to larger specimens of the same taxon (Table 4). The values for these ratios generally showed a similar range among taxa as they did within a taxon. Thus, the cross-sectional thickness of a tyrannosaurid tooth does not appear to be a reliable generic identifier.

Farlow et al. (1991) noted that fore-aft basal length is linearly related to cross-sectional thickness, as well as tooth crown height. For theropods in general, tooth serration basal length increases with increasing tooth size (Farlow et al. 1991). Tyrannosaurid teeth show greater variability in the range of serration size along the mesial carina than other theropods (Chandler 1990). Large individuals of *Tyrannosaurus rex* have absolutely larger denticles (and thus lower denticle densities) than other tyrannosaurids (Carr and Williamson 2000), meaning that the largest tyrannosaurid teeth may be identifiable as *T. rex*. The number of denticles is cor-

Table 2. Comparison of predicted *versus* "true" (based on *a priori* assessment) classification of the isolated teeth from the group classification analysis. Only one (anomalous) tooth of the 35 (sample 14) was misclassified.

		Predicted		
		Maxillary	Dentary	Total
"True"	Maxillary	11	0	11
	Dentary	1	23	24
	Total	12	23	

Test for homogeneity of classification: $\chi^2 = 26.64$, 1 df, $P < 0.005$.

Table 3. Comparison of predicted *versus* actual classification of the in situ teeth as determined by the group classification equations. For taxa other than *Tyrannosaurus rex*, the predictions of the equations were fairly accurate. Note that the five premaxillary teeth from *T. rex* were consistently classified as maxillary teeth; they are not included in this table.

All taxa

		Predicted		
		Maxillary	Dentary	Total
True	Maxillary	5	12	17
	Dentary	6	43	49
	Total	11	55	

Test for homogeneity of classification: $\chi^2 = 1.585$, 1 df, $P > 0.1$.

All taxa except *T. rex*

		Predicted		
		Maxillary	Dentary	Total
True	Maxillary	4	0	4
	Dentary	1	33	34
	Total	5	33	

Test for homogeneity of classification: $\chi^2 = 21.623$, 1 df, $P < 0.005$.

Only *T. rex*

		Predicted		
		Maxillary	Dentary	Total
True	Maxillary	1	12	13
	Dentary	5	10	15
	Total	6	22	

Test for homogeneity of classification: $\chi^2 = 1.410$, 1 df, $P > 0.1$.

Table 4. Comparison of cross-sectional thickness/fore-aft basal length and cross-sectional thickness/tooth crown height for posterior tooth position ~8 (TMP specimens/casts), showing slight differences reflective of ontogeny and taxonomy for tyrannosaur teeth in jaws. Note that tooth numbering begins at the front of the mouth and proceeds caudally.

Taxon	XSTHICK/FABL		XSTHICK/THEIGHT	
	Maxilla	Dentary	Maxilla	Dentary
Gorgosaurus libratus	0.54	~0.41, 0.57, 0.72, 0.77	0.29	~0.33, 0.32, 0.34, 0.43
Daspletosaurus sp. 1	0.55	0.56	0.28	0.32
Tyrannosaurus rex	~0.7	0.74, 0.76	~0.4	0.48

related with tooth size (Chandler 1990; Farlow et al. 1991), making this a difficult feature upon which to rely for identification purposes (Chandler 1990; Baszio 1997). In an attempt to overcome this problem, Rauhut and Werner (1995) proposed that a measurement of the denticle size difference index (DSDI, the difference between a set length of the mesial and distal carinae) could be used as a taxonomic identifier. However, DSDI varies along the carina, and the range of DSDIs in *Tyrannosaurus rex* encapsulates the DSDI range of Theropoda, excluding the outliers: troodontids and *Richardoestesia* (Carr and Williamson 2004). In different theropod taxa, the number of denticles is correlated with tooth size in a variety of ways. The analysis of shape features unrelated to size makes identification possible (Baszio 1997). The principle that non-size-related shape features can be used to distinguish between tooth specimens is integral to the present study.

Statistical analysis.—The disproportionate contribution of a small number of individuals to the in situ tooth sample (Appendix 1), with the resulting lack of independence among these data, lessens the power of the analyses based upon them (Appendices 3, 4; Table 3). However, the perspective that they enabled upon the characteristics of teeth in the context of their bone of origin justifies their use, and relevant test statistics have sufficiently low probabilities (Appendices 3, 4; Table 3) that they can be accepted regardless. If our assumption concerning the homogeneity of any possible intra-group variance-covariance matrices in any subset of the data is incorrect, it will render our interpretations of the PCA results suspect, as we have interpreted PC I to describe size-associated shape variance and subsequent PCs non-size-associated variance. This is difficult to test for, given the sizes and natures of our samples. However, the effect of removing the variance due to isometry (Appendix 4), and the high degree to which most morphometric variables are explained by and correlated with PC I in the other PCAs (Appendices 3, 5, 6), support this assumption. Further work along these lines, however, should restrict samples more closely by phylogeny. The differences in sample size among the taxa examined here (*Gorgosaurus*, 8 individuals; *Albertosaurus*, 1 individual; *Daspletosaurus*, 3 individuals; *Tyrannosaurus*, 2 individuals; Appendix 1) precluded any isolation of the variance attributable to phylogeny.

The first principal component is the size-determined shape vector (McKinney 1990). The maximum variance explained by PC I in any of the sub-sets of the data is 64.6 percent, for the in situ teeth (Appendix 3). The smallest amount (48.8 percent) of variance explained by PC I is for the isolated teeth with denticle data included (Appendix 6), whereas for the isolated teeth with denticle data excluded (Appendix 5), it explains 59.07 percent of the total variance. Even though the denticles generally had large amounts of their total variance explained by PC I, their inclusion introduced large amounts of non-shape associated variance (Appendix 6). Differences in shape associated with size thus contribute less to variance in tooth shape than in other osteological features (e.g., Chapman et al. 1981), although when tooth shape is quantified by gross morphology alone (Appendices 3, 5), it is still the greatest contributor.

The removal of variance that could be explained by a theoretical isometric vector (in place of the empirically-derived size-associated shape vector for the in situ teeth) reduced the total amount of variance in that data set by roughly 55 percent, indicating a large contribution by isometry to total variance in tooth shape. Nonetheless, strong positive allometry in CURVATUR and DMCTOB when only gross morphological variables are included in the analysis (Appendices 3, 5) show that some aspects of tooth shape change disproportionately with size; larger teeth are proportionately more curved, and have a greater distance between the base of the mesial carina and the base of the tooth, than smaller teeth. All of the gross morphological variables are positively allometric when the denticle data are included in the analysis (Appendix 6), due to the influence of the largely negatively allometric denticles. The changes in gross morphological shape associated with size are proportionately greater than those in denticle dimensions, which rapidly become relatively smaller as teeth increase in absolute size.

The contribution to variance of the denticles was only considered for the isolated teeth, as preservation of denticles on in situ teeth was poor. With the exception of MDHM, the maximum loadings of the normalized data for the denticles was concentrated in principal components IV, V, VI, VII, VIII, and IX. Cumulatively, these variables account for 17.3 percent of the total variance in the data. However, the denticle parameters, except for MDHA (PC V), DDHB (PC IV), and DDHA (PC II), show maximum variation explained by, and correlation with, PC I. Thus, aside from the denticle variance attributable to size (PC I), the contribution of denticle morphometry to total tooth shape variance is difficult to interpret. Further investigation of the influence of phylogeny or function on non-size associated variance in denticle shape may shed light on the distribution of this portion of the total variance. The frequently incomplete preservation of denticles does not facilitate their use in morphometric analysis, especially if the carina is divided into sections, and equivalent sections compared. As the size of denticles usually changes along the carina, this division is necessary. However, the measurement of the largest denticle on each tooth could provide better comparative control, as it would be a consistent and equivalent parameter for each tooth. Thus, further analysis is recommended in order to determine the significance of the contribution of the denticles to the variance in tyrannosaurid teeth.

Examination of the patterns of variance per component and component correlations revealed some interesting trends. For all sub-sets of the data, the variable that had the most variance explained by a particular component generally had the highest correlation (not necessarily positive) with that particular component (Appendices 3, 4, 5, 6). For PC I (with the exception of the analysis for the isometry-removed data—Appendix 4), this indicates which dimensions of the teeth were most strongly influenced by the size of the tooth;

CURVATUR for the PCA of the in situ teeth (Appendix 3), THEIGHT for the PCA of the gross measurements of the isolated teeth (Appendix 5), and to a lesser extent, for the PCA of the isolated teeth including denticle dimensions (Appendix 6). The sampling problems with the in situ tooth sample, particularly the influence of *Tyrannosaurus rex* specimens (Appendix 1), probably account for this switch in the identity of the most prominent variable, in addition to accounting for the non-size-associated prominence of DCMTOB in PC II of the in situ tooth PCA (Appendix 3). CURVATUR and DCMTOB both have significant non-size-associated influences on PC II, in the presence of denticles or not, for the isolated teeth, showing strong correlations with, and high variance explanation by, this component (Appendices 5, 6). We hypothesize that the variance of these two features can be attributed to phylogeny, but further analysis of a larger sample of teeth identified to genus, at least, is necessary to test this hypothesis.

DMCTOB demonstrated the highest variability and strongest correlation for PC III in the PCA for the isolated teeth including the denticle variables (Appendix 6). However, in the PCA using only the gross morphometric variables, the component thus influenced became PC II, and the correlation became negative (Appendix 5). This pattern was the same for PC II in the PCA for the in situ teeth (Appendix 3), which also did not include any denticle variables. This suggests a more complex relationship between DMCTOB and the denticle dimensions; to be expected as DMCTOB describes an aspect of the mesial carina, which is composed of denticles (Fig. 2). Again, the contribution of denticle dimensions to total variance is obscure, although DMCTOB and the denticle dimensions describe different aspects of carina morphometrics (Fig. 2).

Despite the reduced statistical independence in the data, the analysis for the in situ teeth allowed for a comparison of the relative position of data points of known taxon and bone of origin in an ordination plot. PC I tended to separate the teeth by size, but also suggested separation of maxillary and dentary teeth into two overlapping groups (Fig. 4A, B). PC III spread out the maxillary teeth and the dentary teeth but did not show any separate clustering of the two types of teeth (Fig. 4B, C). PC II grouped the maxillary and dentary teeth together in a tighter cluster (Fig. 4A, C). Distinction between teeth originating in these bones must then be due to non-size-associated shape characteristics. For the most part, however, no clear grouping of tooth type occurred in any of the plots.

The separation of maxillary and dentary teeth suggested by PC I was also evident in the results of the discriminant analysis. By the absolute values of the canonical coefficients, the most important variables for distinguishing the teeth were DMCTOB, FABL, and THEIGHT (Table 1). From the results of the PCA for the in situ teeth (Appendix 3), FABL and THEIGHT exhibited strong negative allometry, whereas DMCTOB was positively allometric. The most strongly positively allometric variable, CURVATUR, also has most of its variance explained by PC I and is most strongly correlated with this factor (Appendix 3), and is of relatively little importance in the discriminant function (Table 1). Evidently non-size-associated variance was more important in distinguishing tyrannosaurid teeth than size-associated variance, which is to be expected. In addition, this supports the common size-associated scaling relationships among sub-groups posited by us and used as a necessary assumption for the PCA. The strong contribution of DMCTOB to PC II, and its negative correlation with this factor (Appendix 3) indicate that this feature contributes the most important non-size-associated variance useful in discriminating among teeth.

The discriminant analysis generated two discriminant functions that theoretically allow the determination of the bone of origin of an isolated tooth. From the *a priori* assignments of the isolated teeth, the discriminant functions correctly classified 34 of the 35 teeth. The misclassified tooth (TMP 88.36.61) exhibited a structural abnormality. In most teeth the enamel ridge of the carina does not extend proximally beyond the denticles. In this tooth, the ridge of enamel extended beyond the end of the denticles at the base of the tooth crown. This discrepancy resulted in the tooth being classified *a priori* as a dentary tooth. However, as the measurement was taken from the base of the mesial carina to the base of the tooth, this affected the value of DMCTOB, causing it to be classified as a maxillary tooth by the discriminant functions. As this was an abnormal tooth, the correct classification cannot be known, and this tooth should be disregarded. However, the discriminant functions produced predictions of bone of origin for these data acceptable at a significant statistical level (Table 2), indicating that they would be useful in classifying a similar sample of teeth with at least the same acuity as an informed observer.

In order to test the predictive accuracy of the discriminant functions, they were applied to the data for the in situ teeth, which had a known bone of origin. For *Albertosaurus*, *Daspletosaurus*, and *Gorgosaurus*, the predictions of the discriminant functions were statistically accurate (Table 3). Only one tooth for these taxa was misclassified. This tooth came from the dentary of TMP 94.12.155, a small, juvenile *Gorgosaurus* (Currie 2003a). Another *Gorgosaurus* specimen (TMP 86.144.1) and a *Daspletosaurus* specimen (TMP 94.143.1) were larger juveniles (Currie 2003a), and their teeth were correctly classified. This suggests that the predictive abilities of the discriminant functions derived from our data (Appendix 2) may only be applicable to larger, relatively more mature specimens of these taxa. However, if more small juvenile specimens were available for study, the data set could be expanded and re-analyzed, potentially producing discriminant functions with greater discriminatory power.

The accuracy of the predictions generated by these discriminant functions for *Tyrannosaurus rex* was not statistically significant (Table 3). Of the 28 maxillary and dentary teeth from MOR 555 and TMP 98.86.1 (high quality research casts of BHI 3033), only 11 were correctly classified. The poor fit of the discriminant predictions to the *T. rex* data could be due to either of two factors. First, it was observed while measuring the teeth that, unlike the other taxa, the mesial denticles of *T. rex* teeth start closer to the base of the teeth in the dentary. This means that the significance of the DMCTOB would generally be the opposite for *T. rex* than for *Albertosaurus*, *Daspletosaurus*, and *Gorgosaurus*. In addition, *T. rex* teeth demonstrate a trend towards a greater tooth cross-sectional thickness relative to both fore-aft basal length and tooth crown height relative to other tyrannosaurid taxa. Thus, the discriminant functions derived from taxonomically mixed data are not suitable tools for accurately identifying the bone of origin of *T. rex* teeth. However, as *T. rex* does not co-occur stratigraphically with the other taxa (Eberth et al. 2001) this is not a great concern.

In general, it is difficult to quantifiably distinguish the teeth of tyrannosaurid taxa. Principal component analysis determined that the denticles do contribute to the morphological variance of tyrannosaurid teeth. However, the significance of this contribution, other than that explained by the size-associated shape vector, requires further study. The removal of the variance due to isometry revealed that much of the variance in tooth shape is due to this, although positive allometry is important in determining the aspects of shape described by CURVATUR and DMCTOB, and negative allometry strongly influences denticle shape over much of the two carinae. PCA ordination plots demonstrated that the teeth did not unambiguously cluster into distinct groups based on either taxon or bone of origin. More promisingly, discriminant functions were effective for classifying the bone of origin of teeth of relatively mature examined specimens of *Albertosaurus*, *Daspletosaurus*, and *Gorgosaurus*, although less accurate in classifying the teeth of *Tyrannosaurus rex*.

Conclusions and future directions

The teeth of tyrannosaurids can be divided into five types based on cross-sectional shape and the characteristics of the mesial carina: (1) premaxillary, (2) mesial maxillary, (3) distal maxillary, (4) mesial dentary, and (5) distal dentary. The ratio of the distance of the base of the mesial carina to the base of the tooth crown/tooth crown height can be useful for distinguishing between maxillary and dentary teeth. The mesial denticles for relatively mature specimens of *Albertosaurus*, *Daspletosaurus*, and *Gorgosaurus*, start closer to the base of the tooth in the maxilla, which is not true for the teeth of *Tyrannosaurus rex*.

PCA and sphericity tests demonstrated the contribution of the denticles to the morphometric variance of tyrannosaurid teeth. However, the significance of the denticles' contribution to this variance requires further study.

PCA determined that most of the variance for any of the sub-sets of the data analyzed was accounted for in the first three principal components. Removal of the influence of the predicted effects of variance associated with isometry in shape quantified in the first principal component revealed that much of the variance in tooth shape is due to isometric growth, but some gross aspects of tooth shape can be attributed to allometry. PCA ordination plots demonstrated that the teeth did not cluster unambiguously into distinct groupings based on taxon or bone of origin.

Discriminant functions were effective for classifying the teeth of relatively mature examined specimens of *Albertosaurus*, *Daspletosaurus*, and *Gorgosaurus*. This may result from variation in denticle or carina morphology that would reflect functional differences in maxillary and dentary teeth. As it was possible to assign teeth to bones in the animals but not to discriminate between taxa, *Albertosaurus*, *Daspletosaurus*, and *Gorgosaurus* likely shared aspects of tooth function. Discriminant functions generally did not accurately classify the teeth of examined specimens of *Tyrannosaurus rex*. The functional implications of this difference require further study. DFA thus suggests similarities and differences of tooth function in adult tyrannosaurids that are amenable to future biomechanical testing.

In summary, although the teeth of tyrannosaurid dinosaurs must belong to one of five types based on position of teeth in the bones of the jaws, it is difficult to quantifiably distinguish these teeth reliably by taxon. However, for larger, relatively mature specimens (apart from *T. rex*), discriminant functions can be used to separate maxillary and dentary teeth. This method proved more effective for assigning teeth to bones than did PCA, and suggests the informative discriminatory power of DFA for moderate and larger sample sizes.

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Appendix 1

Log_{10}-transformed data for the gross mensural characters, and known tooth position for specimens of in situ tyrannosaurid teeth (n = 71). Negative values for CURVATUR indicate teeth that do not recurve. (j) indicates juvenile specimen (see Currie 2003a). All specimens are from the Judith River Group, Alberta, Canada, except those marked with an *: TMP 81.10.01 is from the Horseshoe Canyon Formation of the Edmonton Group, Alberta, Canada, MOR specimens are from the Two Medicine Formation, Montana, U.S.A and the original of TMP 98.86.1 (high quality research casts of BHI 3033) is from the Hell Creek Formation, South Dakota, USA.

Specimen	Position	FABL	THEIGHT	XSTHICK	CURVATUR	DMCTOB
Gorgosaurus libratus						
TMP 67.9.164	D	1.348	1.613	1.246	0.368	1.124
TMP 83.36.100	M	1.182	1.509	0.959	0.322	0.740
TMP 83.36.134	D	1.396	1.680	1.236	0.491	1.170
TMP 83.36.134	D	1.354	1.609	1.238	0.041	1.100
TMP 86.144.1 (j)	D	1.130	1.464	0.929	0.362	0.944
TMP 86.144.1 (j)	D	1.146	1.467	0.940	0.380	0.968
TMP 86.144.1 (j)	D	1.130	1.375	0.886	0.415	0.863
TMP 94.12.155 (j)	D	0.991	1.217	0.633	0.380	0.362
TMP 95.5.1	D	1.045	1.387	1.049	–0.477	0.778
TMP 95.5.1	D	1.305	1.645	1.161	0.766	1.086
TMP 95.5.1	D	1.301	1.625	1.041	0.230	1.025
TMP 95.5.1	D	1.283	1.599	1.134	0.222	0.996
TMP 95.5.1	D	1.286	1.606	1.140	0.368	1.255
TMP 95.5.1	D	1.255	1.526	1.114	0.301	1.068
TMP 95.5.1	D	1.233	1.480	1.104	0.263	0.934
TMP 95.5.1	D	1.137	1.330	0.954	0.114	0.944
TMP 99.55.170	D	1.230	1.628	1.170	0.230	0.892
TMP 99.55.170	D	1.290	1.660	1.072	0.204	1.021
TMP 99.55.170	D	1.250	1.574	1.104	0.079	0.944
TMP 99.55.170	D	1.243	1.531	1.079	0.279	0.886
TMP 99.55.170	D	1.230	1.496	0.991	0.230	0.949
TMP 99.55.170	D	1.176	1.391	1.004	0.230	0.973
TMP 99.55.170	D	1.146	1.350	0.934	–0.398	0.949
ROM 1247	D	1.053	1.435	1.097	–0.155	1.013
ROM 1247	D	1.236	1.627	1.170	0.431	1.134
ROM 1247	D	1.322	1.672	1.053	0.491	1.049
ROM 1247	D	1.326	1.655	1.121	0.556	1.064
ROM 1247	D	1.316	1.632	1.124	0.505	1.068
ROM 1247	D	1.093	1.336	0.903	0.362	1.061
*Albertosaurus sarcophagus**						
TMP 81.10.1	M	1.493	1.822	1.274	0.690	0.778
Daspletosaurus sp.1 (see Currie 2003a)						
TMP 97.12.223	M	1.537	1.895	1.386	1.045	0.845
TMP 97.12.223	M	1.377	1.666	1.288	0.699	0.898
TMP 94.143.1 (j)	D	1.114	1.465	1.025	0.204	0.820
TMP 94.143.1 (j)	D	1.223	1.507	1.045	0.519	0.914
TMP 94.143.1 (j)	D	1.260	1.501	1.009	0.491	0.959
Daspletosaurus sp.2* (see Horner et al. 1992)						
MOR 590	D	1.356	1.750	1.270	0.342	1.083
MOR 590	D	1.354	1.755	1.241	0.146	1.061
MOR 590	D	1.342	1.718	1.204	0.041	1.057

Specimen	Position	FABL	THEIGHT	XSTHICK	CURVATUR	DMCTOB
*Tyrannosaurus rex**						
MOR 555	M	1.603	1.857	1.449	0.806	1.260
MOR 555	M	1.558	1.828	1.393	0.653	1.442
MOR 555	M	1.501	1.751	1.375	0.531	1,412
TMP 98.86.1, high quality research cast	PM	1.500	1.711	1.312	0	–0.301
TMP 98.86.1, high quality research cast	M	1.691	1.980	1.465	1.061	1.417
TMP 98.86.1, high quality research cast	M	1.661	1.914	1.491	1.117	1.450
TMP 98.86.1, high quality research cast	M	1.592	1.850	1.441	0.898	1.484
TMP 98.86.1, high quality research cast	M	1.474	1.746	1.400	0.806	1.301
TMP 98.86.1, high quality research cast	M	1.446	1.693	1.358	0.708	1.340
TMP 98.86.1, high quality research cast	M	1.316	1.501	1.176	0.176	1.111
TMP 98.86.1, high quality research cast	D	1.408	1.601	1.246	0	0.740
TMP 98.86.1, high quality research cast	D	1.566	1.829	1.462	–0.301	0.898
TMP 98.86.1, high quality research cast	D	1.498	1.754	1.360	0.732	1.152
TMP 98.86.1, high quality research cast	D	1.439	1.626	1.310	–0.398	0.991
TMP 98.86.1, high quality research cast	D	1.155	1.233	0.978	0	0.708
TMP 98.86.1, high quality research cast	PM	1.427	1.562	1.158	0	–0.046
TMP 98.86.1, high quality research cast	PM	1.464	1.618	1.262	0	0.505
TMP 98.86.1, high quality research cast	PM	1.450	1.657	1.182	0	0.322
TMP 98.86.1, high quality research cast	PM	1.490	1.667	1.288	0	0.505
TMP 98.86.1, high quality research cast	M	1.595	1.952	1.668	0.851	0.255
TMP 98.86.1, high quality research cast	M	1.667	1.998	1.508	1.188	1.401
TMP 98.86.1, high quality research cast	M	1.610	1.806	1.373	1.100	1.430
TMP 98.86.1, high quality research cast	M	1.524	1.731	1.326	0.806	1.307
TMP 98.86.1, high quality research cast	D	1.400	1.609	1.274	0	0.279
TMP 98.86.1, high quality research cast	D	1.606	1.863	1.453	0.398	0.845
TMP 98.86.1, high quality research cast	D	1.647	1.880	1.522	0.839	1.272
TMP 98.86.1, high quality research cast	D	1.636	1.857	1.494	0.778	1.356
TMP 98.86.1, high quality research cast	D	1.595	1.782	1.476	0.724	1.253
TMP 98.86.1, high quality research cast	D	1.462	1.744	1.377	0.431	1.215
TMP 98.86.1, high quality research cast	D	1.507	1.683	1.360	0.447	1.330
TMP 98.86.1, high quality research cast	D	1.459	1.658	1.342	0.204	1.021
TMP 98.86.1, high quality research cast	D	1.352	1.474	1.238	–0.523	0.756
TMP 98.86.1, high quality research cast	D	1.246	1.365	1.137	0	0.964

Appendix 2

Log_{10}-transformed data for the gross mensural characters (denticle morphometric data available as supplementary data online), and *a priori* estimated tooth position for specimens of isolated tyrannosaurid teeth (n = 35).

Specimen (TMP)	*a priori* position	FABL	THEIGHT	XSTHICK	CURVATUR	DMCTOB
66.28.5	D	0.991	1.243	0.875	0.058	0.633
67.16.62	D	1.104	1.511	1.000	0.862	1.121
79.8.97	D	1.283	1.520	1.130	0.109	0.944
80.16.1094	D	0.968	1.134	0.763	0.234	0.643
80.20.313	D	1.029	1.111	0.875	0.196	0.892
81.18.126	M	1.303	1.676	1.134	0.686	0.820
81.19.7	M	1.255	1.520	1.093	0.196	0.785
82.16.170	D	1.134	1.422	0.833	0.301	0.806
82.18.214	D	1.130	1.362	0.924	0.301	0.851

Specimen (TMP)	*a priori* position	FABL	THEIGHT	XSTHICK	CURVATUR	DMCTOB
84.163.35	D	1.057	1.258	0.851	0.109	0.929
85.36.325	D	0.944	1.127	0.763	0.234	0.681
85.36.342	M	1.215	1.489	0.982	0.410	0.462
87.36.325	M	1.127	1.346	0.944	0.196	0.477
88.36.61	D	1.193	1.483	1.072	0.477	0.663
89.18.70	D	1.297	1.584	1.134	0.359	0.903
89.36.151	D	1.037	1.204	0.892	0.000	0.724
89.79.4	D	1.000	1.455	1.117	–0.243	0.820
91.144.7	D	1.384	1.691	1.220	0.570	1.290
91.36.188	D	1.100	1.346	0.898	0.196	0.771
91.36.431	D	0.973	1.124	0.845	0.058	0.591
91.50.32	M	1.100	1.283	0.857	–0.243	0.415
91.61.9	M	1.107	1.413	0.820	0.234	0.653
92.36.233	D	1.225	1.464	1.090	0.109	0.869
92.36.823	M	1.233	1.529	0.982	0.570	0.792
92.36.961	M	1.155	1.456	0.987	0.385	0.602
93.36.437	D	1.340	1.594	1.068	0.699	1.083
93.36.610	M	1.286	1.645	1.064	0.497	0.146
94.12.209	D	1.294	1.610	1.179	0.359	0.987
94.12.313	D	1.230	1.576	1.053	0.234	1.025
94.12.42	M	1.408	1.710	1.281	0.234	0.987
94.12.759	D	1.029	1.233	0.903	0.058	0.826
96.12.111	D	1.111	1.365	0.857	0.570	0.839
96.12.379	M	1.196	1.493	1.021	0.385	0.748
97.12.43	D	1.324	1.639	1.199	0.497	1.170
99.55.202	D	1.167	1.481	0.940	0.535	0.851

Appendix 3

PCA of in situ teeth, using gross morphological variables. FABL, fore-aft basal length; THEIGHT, tooth crown height; XSTHICK, cross-sectional thickness; CURVATUR, curvature; DMCTOB, distance from the base of the mesial carina to the base of the tooth. Components subsequent to PC IV isotropic (PC III–PC V: Bartlett's $\chi^2 = 476.963$, 5 df; $P < 0.0001$; PC IV–PC V: Bartlett's $\chi^2 = –400.886$, 2 df; $P = 0.999$). Isometric loading for PC I = 0.447214.

Principal component loadings					
	I	II	III	IV	V
FABL	0.241	0.337	0.372	0.193	–0.808
THEIGHT	0.272	0.306	0.315	–0.843	0.152
XSTHICK	0.252	0.333	0.509	0.495	0.567
CURVATUR	0.733	0.222	–0.636	0.087	0.039
DMCTOB	0.517	–0.795	0.314	–0.01	–0.035
Eigenvalues	0.235	0.075	0.048	0.003	0.002
Percent of variance explained	64.759	20.641	13.258	0.795	0.546
Amount of variance of each variable explained by each component					
	I	II	III	IV	V
FABL	0.452	0.282	0.220	0.004	0.043
THEIGHT	0.557	0.224	0.153	0.065	0.001
XSTHICK	0.402	0.225	0.336	0.019	0.017
CURVATUR	0.845	0.025	0.130	0.000	0.000
DMCTOB	0.547	0.412	0.041	0.000	0.000

Correlations between each component and each variable					
	I	II	III	IV	V
FABL	0.672	0.531	0.469	0.06	–0.207
THEIGHT	0.746	0.473	0.391	–0.256	0.038
XSTHICK	0.634	0.474	0.58	0.138	0.131
CURVATUR	0.919	0.157	–0.361	0.012	0.005
DMCTOB	0.739	–0.642	0.203	–0.002	–0.005

Appendix 4

PCA of in situ teeth derived from variance-covariance matrix with variance due to isometric PC I removed, using gross morphological variables. FABL, fore-aft basal length; THEIGHT, tooth crown height; XSTHICK, cross-sectional thickness; CURVATUR, curvature; DMCTOB, distance from the base of the mesial carina to the base of the tooth. No components isotropic (PC II–PC IV: Bartlett's χ^2 = 750.660, 5 df; P < 0.0001; PC III–PC IV: Bartlett's χ^2 = 406.610, 2 df; P < 0.0001).

Principal component loadings				
	I	II	III	IV
FABL	0.377	0.007	0.061	–0.809
THEIGHT	0.309	–0.017	–0.770	0.333
XSTHICK	0.404	0.073	0.630	0.484
CURVATUR	–0.502	–0.736	0.080	0.013
DMCTOB	–0.589	0.673	–0.001	–0.021
Eigenvalues	0.091	0.066	0.003	0.002
Percent of variance explained	56.020	40.756	1.902	1.322
Amount of variance of each variable explained by each component				
	I	II	III	IV
FABL	0.901	0.000	0.001	0.098
THEIGHT	0.807	0.002	0.170	0.022
XSTHICK	0.877	0.021	0.072	0.030
CURVATUR	0.390	0.610	0.000	0.000
DMCTOB	0.513	0.487	0.000	0.000
Correlations between each component and each variable				
	I	II	III	IV
FABL	0.956	0.016	0.029	–0.315
THEIGHT	0.904	–0.043	–0.415	0.149
XSTHICK	0.943	0.146	0.271	0.173
CURVATUR	–0.629	–0.787	0.019	0.003
DMCTOB	–0.721	0.703	0.000	–0.004

Appendix 5

PCA of isolated teeth, using gross morphological variables. FABL, fore-aft basal length; THEIGHT, tooth crown height; XSTHICK, cross-sectional thickness; CURVATUR, curvature; DMCTOB, distance from the base of the mesial carina to the base of the tooth. Components subsequent to PC IV isotropic (PC III–PC V: Bartlett's χ^2 = 222.400, 5 df, P < 0.0001; PC IV–PC V: Bartlett's χ^2 = –189.687, 2 df, P = 0.999). Isometric loading for PC I = 0.447214.

Principal component loadings					
	I	II	III	IV	V
FABL	0.319	0.008	0.362	0.492	0.725
THEIGHT	0.452	0.050	0.510	0.307	–0.662

XSTHICK	0.308	–0.173	0.456	–0.797	0.179
CURVATUR	0.615	0.625	–0.455	–0.147	0.049
DMCTOB	0.470	–0.760	–0.440	0.086	–0.037
Eigenvalues	0.104	0.039	0.030	0.002	0.002
Percent of variance explained	59.067	21.990	16.933	1.116	0.894
Amount of variance of each variable explained by each component					
	I	II	III	IV	V
FABL	0.670	0.000	0.247	0.030	0.052
THEIGHT	0.709	0.003	0.259	0.006	0.023
XSTHICK	0.532	0.063	0.336	0.067	0.003
CURVATUR	0.649	0.249	0.101	0.001	0.000
DMCTOB	0.449	0.437	0.113	0.000	0.000
Correlations between each component and each variable					
	I	II	III	IV	V
FABL	0.819	0.012	0.497	0.173	0.229
THEIGHT	0.842	0.057	0.508	0.079	–0.152
XSTHICK	0.729	–0.250	0.579	–0.260	0.052
CURVATUR	0.805	0.499	–0.319	–0.027	0.008
DMCTOB	0.670	–0.661	–0.336	0.017	–0.006

Appendix 6

PCA of isolated teeth, incorporating denticle variables. FABL, fore-aft basal length; THEIGHT, tooth crown height; XSTHICK, cross-sectional thickness; CURVATUR, curvature; DMCTOB, distance from the base of the mesial carina to the base of the tooth; MDW, mesial denticle width (basal, middle, apical); DDW, distal denticle width (B, basal, M, middle, A, apical); MDH, mesial denticle height (basal, middle, apical); DDH, distal denticle height (basal, middle, apical). Components subsequent to PC X isotropic (PC IX–PC XVII: Bartlett's $\chi^2 = 68.040$, 44 df; P = 0.012; PC X–PC XVII: Bartlett's $\chi^2 = 48.695$, 35 df; P = 0.062). Isometric loading for PC I = 0.242536.

Principal component loadings										
	I	II	III	IV	V	VI	VII	VIII	IX	X
FABL	0.288	0.031	0.048	–0.234	0.114	–0.293	–0.210	0.093	–0.210	–0.189
THEIGHT	0.417	0.056	0.104	–0.372	0.119	–0.108	–0.167	0.033	0.112	–0.059
XSTHICK	0.305	0.149	–0.114	–0.195	0.244	–0.146	0.182	0.157	–0.137	–0.357
CURVATUR	0.393	–0.690	0.519	0.203	0.060	0.091	0.104	0.063	0.005	0.094
DMCTOB	0.315	–0.405	–0.820	0.196	0.002	–0.032	–0.048	–0.100	0.044	0.038
MDWB	0.231	0.110	–0.019	–0.144	–0.393	0.087	–0.540	0.296	–0.170	0.429
MDWM	0.205	0.088	–0.045	–0.022	–0.124	0.090	0.255	0.107	0.029	0.119
MDWA	0.127	0.060	–0.008	–0.044	0.031	–0.132	0.267	0.122	0.372	0.012
DDWB	0.177	0.228	–0.053	0.032	–0.086	0.301	0.369	0.269	0.158	0.089
DDWM	0.149	0.154	–0.044	0.080	–0.134	0.063	0.299	0.191	–0.291	0.143
DDWA	0.131	0.118	0.012	–0.068	0.101	–0.175	0.196	0.127	0.188	0.186
MDHB	0.237	0.087	0.052	–0.266	–0.231	0.239	–0.083	–0.582	0.379	–0.188
MDHM	0.262	0.166	0.056	0.079	–0.253	0.233	0.217	–0.426	–0.401	0.039
MDHA	0.126	0.211	–0.019	0.144	0.725	0.520	–0.229	–0.057	–0.041	0.177
DDHB	0.196	0.247	0.084	0.614	–0.205	0.043	–0.288	0.228	0.321	–0.400
DDHM	0.125	0.141	0.070	0.315	0.040	–0.242	0.008	–0.162	–0.411	–0.250
DDHA	0.143	0.243	0.080	0.283	0.128	–0.520	–0.005	–0.334	0.179	0.520
Eigenvalues	0.150	0.055	0.040	0.017	0.012	0.009	0.006	0.006	0.004	0.003
Percent of variance explained	48.831	17.790	12.838	5.418	3.759	2.879	2.015	1.888	1.294	1.008

Amount of variance of each variable explained by each component										
	I	II	III	IV	V	VI	VII	VIII	IX	X
FABL	0.828	0.004	0.006	0.061	0.010	0.051	0.018	0.003	0.012	0.007
THEIGHT	0.885	0.006	0.014	0.078	0.006	0.004	0.006	0.000	0.002	0.000
XSTHICK	0.775	0.067	0.029	0.035	0.038	0.010	0.011	0.008	0.004	0.022
CURVATUR	0.381	0.429	0.175	0.011	0.001	0.001	0.001	0.000	0.000	0.000
DMCTOB	0.291	0.176	0.519	0.012	0.000	0.000	0.000	0.001	0.000	0.000
MDWB	0.577	0.048	0.001	0.025	0.128	0.005	0.130	0.037	0.008	0.041
MDWM	0.832	0.056	0.010	0.001	0.024	0.009	0.053	0.009	0.000	0.006
MDWA	0.621	0.051	0.001	0.008	0.003	0.039	0.113	0.022	0.141	0.000
DDWB	0.472	0.286	0.011	0.002	0.009	0.081	0.085	0.042	0.010	0.002
DDWM	0.534	0.210	0.012	0.017	0.033	0.006	0.089	0.034	0.054	0.010
DDWA	0.588	0.172	0.001	0.018	0.027	0.062	0.054	0.021	0.032	0.024
MDHB	0.604	0.029	0.008	0.085	0.044	0.036	0.003	0.141	0.041	0.008
MDHM	0.675	0.099	0.008	0.007	0.049	0.032	0.019	0.069	0.042	0.000
MDHA	0.168	0.173	0.001	0.024	0.431	0.170	0.023	0.001	0.000	0.007
DDHB	0.322	0.187	0.016	0.351	0.027	0.001	0.029	0.017	0.023	0.028
DDHM	0.341	0.160	0.029	0.242	0.003	0.076	0.000	0.022	0.098	0.028
DDHA	0.254	0.267	0.021	0.110	0.016	0.198	0.000	0.054	0.011	0.069
Correlations between each component and each variable										
	I	II	III	IV	V	VI	VII	VIII	IX	X
FABL	0.888	0.058	0.075	–0.241	0.097	–0.219	–0.132	0.057	–0.105	–0.084
THEIGHT	0.931	0.075	0.119	–0.277	0.074	–0.059	–0.076	0.014	0.041	–0.019
XSTHICK	0.869	0.256	–0.167	–0.185	0.192	–0.101	0.105	0.088	–0.064	–0.146
CURVATUR	0.617	–0.655	0.418	0.106	0.026	0.035	0.033	0.019	0.001	0.021
DMCTOB	0.540	–0.419	–0.720	0.112	0.001	–0.013	–0.017	–0.034	0.012	0.009
MDWB	0.754	0.217	–0.032	–0.156	–0.355	0.069	–0.358	0.190	–0.090	0.201
MDWM	0.871	0.226	–0.097	–0.031	–0.146	0.093	0.219	0.089	0.020	0.072
MDWA	0.736	0.211	–0.023	–0.084	0.051	–0.185	0.314	0.139	0.351	0.010
DDWB	0.663	0.516	–0.102	0.039	–0.090	0.274	0.281	0.198	0.096	0.048
DDWM	0.704	0.441	–0.107	0.126	–0.176	0.073	0.288	0.178	–0.224	0.097
DDWA	0.721	0.390	0.033	–0.125	0.154	–0.234	0.219	0.137	0.168	0.147
MDHB	0.770	0.170	0.086	–0.288	–0.209	0.189	–0.055	–0.372	0.201	–0.088
MDHM	0.809	0.309	0.089	0.082	–0.217	0.175	0.136	–0.259	–0.202	0.017
MDHA	0.410	0.415	–0.032	0.156	0.656	0.412	–0.152	–0.037	–0.022	0.083
DDHB	0.565	0.431	0.124	0.591	–0.164	0.030	–0.169	0.129	0.151	–0.166
DDHM	0.553	0.378	0.160	0.466	0.049	–0.261	0.007	–0.142	–0.297	–0.159
DDHA	0.501	0.515	0.144	0.331	0.124	–0.443	–0.004	–0.231	0.102	0.262