SIZE, SHAPE, AND SERRATION DENSITY OF THEROPOD DINOSAUR LATERAL TEETH

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Tooth crown height and tooth mediolateral basal width are linearly (or nearly linearly) related to anteroposterior basal length in lateral teeth (non-incisiform teeth of the maxilla and dentary) of theropod dinosaurs. Comparison of the shape of theropod teeth with canine teeth of mammalian carnivores suggests that theropod teeth were multipurpose implements, used in killing prey, cutting flesh, and—at least in large carnosaurs—possibly even breaking bone. In theropods as a group, the basal length of an individual tooth serration increases linearly with increasing tooth size; serration density (the number of serrations per unit length of tooth carina) decreases allometrically with increasing tooth size. Many predatory vertebrates with serrated teeth show a serration size:tooth size relationship close to that seen in theropods.
KEYWORDS: Theropods, teeth, serrations, functional morphology.

INTRODUCTION

The business end of a carnivorous dinosaur was its mouth (Figure 1; cf. Paul, 1988: 88), and the chief agents of that business were the dinosaur's teeth. Although descriptions of tooth morphology are routinely presented in systematic accounts of theropods (e.g. Osborn, 1912; Lambe, 1917; Gilmore, 1920; Colbert and Russell, 1969; Ostrom, 1969; Russell, 1970; Maleev, 1974; Madsen, 1976; Sues, 1977; Chatterjee, 1978; Charig and Milner, 1986; Gillette *et al.*, 1986; Paul, 1988), there has been no focused effort to explore changes in tooth features across a wide range of theropod taxa. The present paper attempts such an analysis for theropod lateral teeth (non-incisiform teeth of the maxilla and dentary). We will consider aspects of tooth shape and serration size in relation to overall tooth size, and compare these features of tooth morphology between theropods and other predatory vertebrates; we will then use these comparisons to speculate about the functional significance of theropod tooth morphology.
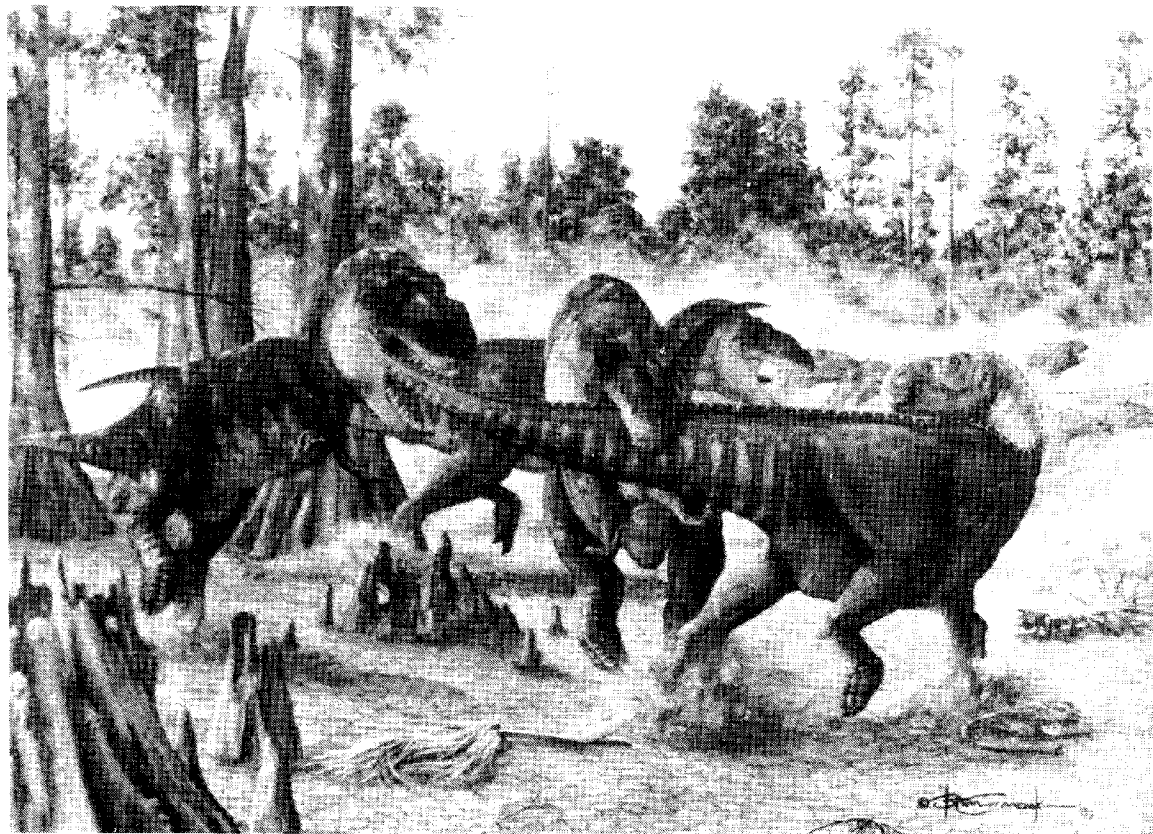
Figure 1 *Tyrannosaurus rex* demonstrating the use of its teeth to *Edmontosaurus regalis*. Paintings used by permission of the artist, Brian Franczak.

MATERIALS AND METHODS

We tried to obtain data from as broad a range of tooth sizes and geologic ages as possible. We measured more than 500 individual theropod teeth, representing the following faunas: Chinle Formation (Late Triassic); Morrison Formation (Late Jurassic); Cloverly Formation, Travis Peak Formation, and Paluxy Sand (Early Cretaceous); Dakota and Straight Cliffs Formations (Mid-Cretaceous); Mifune Group, Black Creek, New Egypt, Two Medicine, Judith River, Iren Dabasu, Nemegt, Mesaverde, Kirtland, McRae, Lance, and Hell Creek Formations (Late Cretaceous). We did not have equal sample sizes of teeth from these units; the vast majority of the teeth we examined are from the Judith River Formation. Most of our teeth were isolated, shed crowns, but where possible we obtained measurements of associated teeth or teeth *in situ* in the jaws of carnivorous dinosaurs.

Taxa herein identified as *Aublysodon*, *Richardoestesia gilmorei*, and cf. *Richardoestesia* constitute supposed tooth associations that require special comment. The *Aublysodon* designation is for relatively small, slender tyrannosaurid teeth that are associated by size with distinctive tyrannosaurid premaxillary teeth; Molnar and Carpenter (1989) described a partial skull of *Aublysodon* with premaxillary and maxillary teeth. Teeth of the holotype of *Richardoestesia gilmorei* (Currie *et al.*, 1990) are all from the dentary. Isolated mandibular teeth of this form are relatively common in the Judith River Formation of Alberta. A second type of tooth, here called cf. *Richardoestesia*, probably is a maxillary tooth of this taxon, although this cannot be confirmed until a maxilla with teeth are found for this animal.

For comparison with our theropod teeth we obtained data for teeth of rauisuchians (Dockum Group and Chinle, Clarens, and Santa Maria Formations; we follow Carroll [1988: 619] in referring both rauisuchids and poposaurids to the rauisuchians), phytosaurs (Dockum Group), unidentified small archosaurs(?) from the Owl Rock Member (here labeled UID Owl Rock Mbr) of the Chinle Formation, *Erythrosuchus* sp., *Ornithosuchus* sp., *Protosuchus richardsoni*, possible sphenosuchians (hesperosuchians) or perhaps small phytosaurs (Owl Rock Member of the Chinle Formation, here labeled sphenosuchians?), ziphodont crocodilians, toothed birds [*Parahesperornis alexi*, *Ichthyornis* cf. *anceps*—here labeled odontognathans], varanid lizards (*Varanus varius*, *V. bengalensis*, *V. salvator*, *V. komodoensis*, *V. dirus*, and *Megalania prisca*), *Mosasaurus princeps*, *Dimetrodon* sp., sabertoothed cats (*Barbourofelis whitfordi*, *B. morrissi*, *B.* cf. *fricki*, *Ischyrosmilus crusifonti*, *Dinictis felina*, *Nimravus debilis*, *Hoplophoneus primaevus*, *Homotherium serum*, *Smilodon neogaeus*, and *S. californicus*), entelodonts (*Archaeotherium* spp.), "Tasmanian devil fish" (*Enchodus ?ferox*), and sharks (*Carcharodon megalodon*, *C. carcharias*, and a sample of small shark teeth of unknown provenance [but probably from the Pliocene of Florida], representing *Galeocerdo cuvieri* and *Carcharhinus* spp. G.R. Case, pers. comm.). The numbers of teeth for each of these taxa varied greatly; some were represented by a single tooth, and some taxa were represented by many teeth from a single animal. A complete set of catalog numbers of the specimens used in our study, and our measurements of each tooth, are available on request from the library of the Royal Tyrrell Museum of Palaeontology. Finally, for some comparisons with theropod teeth we used data on living and extinct canids, hyaenids, and felids taken from Van Valkenburgh and Ruff (1987).

Because theropod teeth as found are frequently broken at the tip, we chose as our routine measurement of tooth size the fore-aft (mesial-distal) basal length (FABL), measured at or near the level of the proximal (basal) end of the posterior tooth keel, perpendicular to the longitudinal axis of the tooth; this level is usually the same as the basal limit of the enamel-covered part of the tooth crown. For *in situ* teeth the tooth crown base defined in this way often coincides with the outer rim of the tooth socket. Tooth crown height (TCH) was measured perpendicular to FABL, and represents the vertical distance from the base of the tooth crown to the tip of the tooth, disregarding any tooth curvature. Due to poor preservation, for some *in situ* teeth we had to measure TCH as the vertical distance from the outer rim of the tooth socket to the tooth tip; in some cases this probably overestimates tooth height (cf. Paul, 1988: 92–93). Tooth basal width (BW) is perpendicular to both FABL and TCH, and was measured at the same level as FABL; BW represents the maximum width of the tooth in this dimension. Some teeth seemed to show slight basal crushing perpendicular to FABL; for these teeth BW as measured here is probably an underestimate. FABL and BW were measured with calipers to the nearest tenth of a millimeter, TCH with a ruler to the nearest millimeter.

In obtaining comparative data on the teeth of other carnivores, we tried to make measurements as comparable to those of theropod teeth as possible, but sometimes had to alter the way in which we defined our measurements. For *Smilodon* sabres the anterior-posterior dimension of the tooth was measured about midway along the length of *isolated* canines; this dimension would be equivalent to the FABL of *in situ* canines (cf. Merriam and Stock, 1932: plate 12). For shark teeth we defined the fore-aft length with reference to the line of the jaw, which due to the jaw's curvature is not necessarily the same as the fish's overall anterior-posterior axis; thus FABL was measured as the distance from the basal limit of one serrated keel to the basal end of the other keel.

We used as our index of tooth serration size a metric often reported in systematic diagnoses of theropod taxa, the number of serrations per 5 mm of anterior (mesial) or posterior (distal) keel (termed serration density by Farlow and Brinkman, 1987), counted as close to half-way along the length of that particular keel as possible. Making denticle counts at a defined level was necessary because denticles often decrease in size toward the tooth base or the tooth tip. Small teeth were frequently too little to have 5 mm of carina length, or 5 mm allowed for so much tooth curvature as to inflate the denticle count. For such teeth we counted the number of serrations per 3, 2, and in some instances only 1 mm of keel, and prorated the count in terms of 5 mm. This procedure has the disadvantage of exaggerating any counting errors, and so for very small teeth the serration count may be only an estimate.

We also employed the reciprocal of the number of serrations per 5 mm of tooth carina, which reduces to the basal length of an individual tooth denticle parallel to the length of the tooth keel.

As with tooth size measurements, we sometimes had to modify the manner in which we did serration counts for non-dinosaurian predators. For some small shark teeth the serrated keel has horizontal and vertical segments connected by an intervening mid-keel. Where possible, our denticle counts were made on the vertical portion of the keel, and otherwise on the mid-keel. We were not always able to distinguish the anterior and posterior keels of isolated shark teeth. Consequently for all shark teeth we took counts for both keels (they were usually very close) and averaged them; in the discussion to follow we arbitrarily treat this averaged count as representing the posterior keel.

We have no way of knowing how many individual dinosaurs are represented by our sample of shed tooth crowns, although it seems reasonable to suppose that few, if any, individual animals are represented by more than one isolated tooth. However, because we include data for *in situ* teeth (for example, most of our *Tyrannosaurus* teeth are from two individual dinosaurs) and for teeth found together, associated with other cranial material (our sample of *Deinonychus* teeth probably represents only a few animals—Ostrom [1969]), there could be confounding influences on our interpretations due to peculiarities of individual dinosaurs whose teeth are over-represented in our sample by virtue of their occurrence together. We examined this possibility by doing parallel analyses in which co-occurring teeth either were or were not included in the data sample; the resulting equations differed very little.

There has been much discussion about the most appropriate statistical model for describing bivariate relationships of morphometric data (cf. Kermack and Haldane, 1950; Imbrie, 1956; Ricker, 1973, 1984; Sokal and Rohlf, 1981; Harvey and Mace, 1982; Seim and Saether, 1983; Rayner, 1985; Leduc, 1987). Many authors have concluded that linear regression is the best structural model for estimating the conditional means of one variable given particular values of another, but that regression is not appropriate for describing the underlying functional relationship between those variables. For the latter task, the reduced major axis (RMA) is a better model, particularly when the distribution of "error" in the two variables (due to inaccuracies of measurement and/or biological variability in the populations sampled) is unknown. In our present study, we cannot with certainty even identify the populations (taxa) to which many of our theropod teeth belong; consequently RMA analysis seems especially appropriate for estimating the functional relationships between theropod tooth shape variables. If the correlation coefficient between two variables is high enough, there is very little difference in the equations based on the two models (Imbrie, 1956 : 231).

We have already noted that our sample is heavily biased toward teeth of Late

Cretaceous age. Furthermore, we have only limited information about the representation of theropod taxa in this Late Cretaceous dental assemblage. For these reasons the regression and reduced major axis equations that we present should be regarded only as approximations to "true" equations based on taxonomically unbiased samples of teeth.

RESULTS

Tooth basal width is nearly linearly related to FABL (Figure 2). The relationship can be described by the RMA equation BW (mm) = [0.71 * FABL (mm)] − 1.26 ($r**2$ = 0.94, $p < 0.0001$, $n = 451$). Unfortunately, there is increasing scatter in the relationship at larger tooth sizes, particularly in teeth of *Tyrannosaurus*. We consequently corrected for this problem of heteroscedasticity by taking the base 10
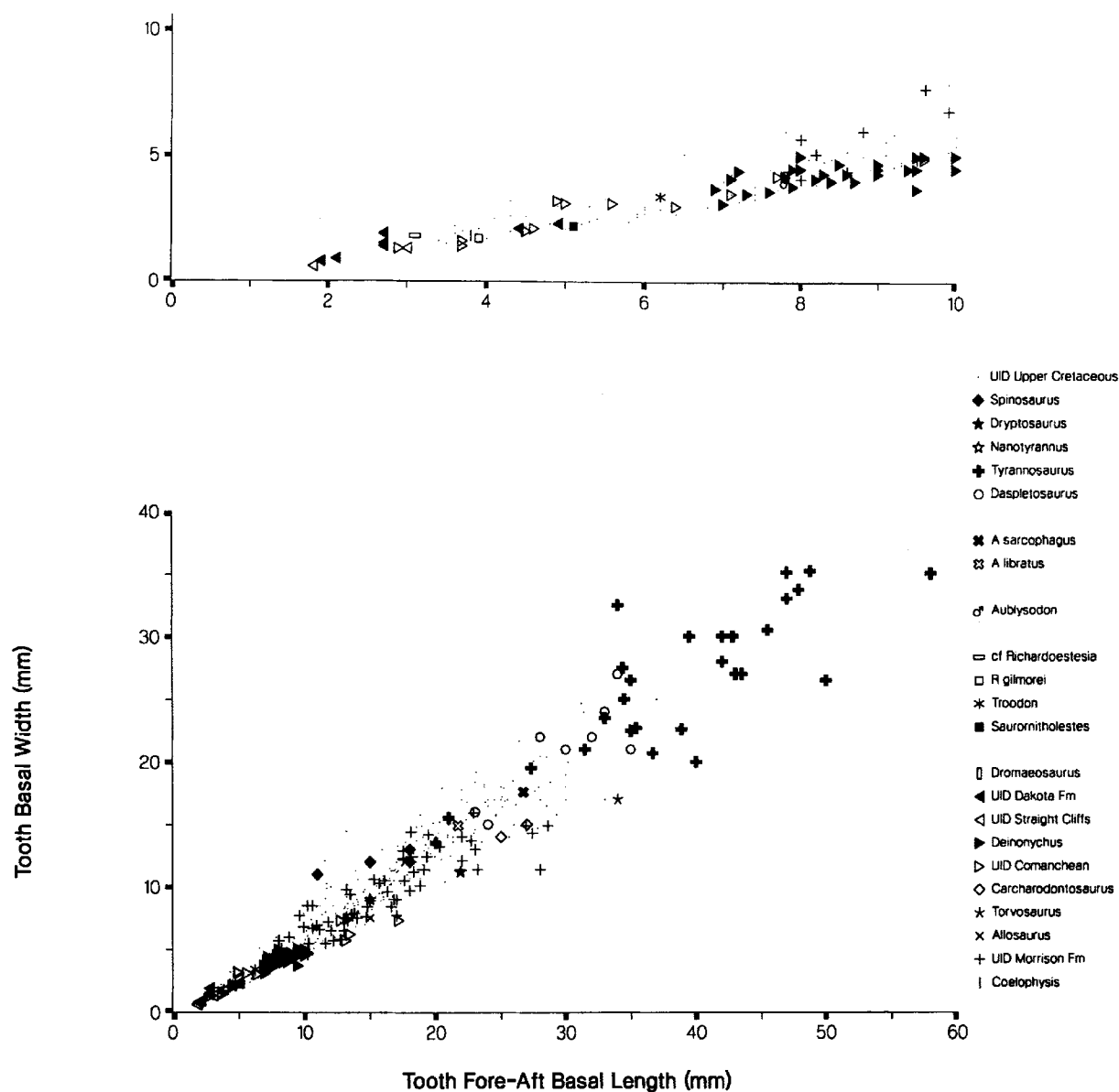

Figure 2 Relationship between tooth basal width and tooth fore-aft basal length in theropods. Insert presents data for very small teeth. Points labeled by stratigraphic names represent unidentified (UID) teeth from the units in question; the same convention applies to other figures.

logarithms of both FABL and BW, obtaining the equation log 10 BW = [1.18 * log 10 FABL] − 0.43 ($r**2 = 0.96, p < 0.0001$). The 95% confidence interval for the slope (calculated as described by Leduc (1987:657)) is 1.14–1.23, suggesting that there may be slight positive allometry in the relationship between BW and FABL, at least when considered over a large range of tooth sizes. However, the slope is close enough to 1 to make us doubt that this positive allometry is biologically meaningful; we suspect that for our purposes the relationship between BW and FABL can be regarded as linear.

Our equations basically describe "Late Cretaceous" lines (the same is true for most other equations given in this paper), given the numerical dominance of teeth of that age in our sample. However, inspection of Figure 2 suggests that theropod teeth of pre-Late Cretaceous age for the most part fall within the scatter of points of Late Cretaceous teeth, although some unidentified Morrison and Comanchean teeth have rather narrower basal widths than Late Cretaceous teeth of comparable FABL.

Our sample from the Morrison Fm is probably dominated by teeth of *Allosaurus*; a large proportion of our Morrison sample comes from the Cleveland-Lloyd Quarry (Madsen, 1976). The RMA equation for Morrison teeth alone is BW = [0.57 * FABL] + 0.27 ($r**2 = 0.78, p < 0.0001$, 95% CI of slope = 0.44–0.75, $n = 64$); examination of the residuals did not indicate any heteroscedasticity that would require transformation of the variables. The lower slope of this equation than that obtained from the linear model for our entire theropod tooth sample suggests that presumed *Allosaurus* teeth are more narrowly based than large Late Cretaceous teeth. However, this result might be an artifact, given that the Late Cretaceous tooth sample is probably not dominated by a single taxon to the extent we think the Morrison sample is; differences in slope might merely reflect differences in a nearly monospecific (Morrison) and a multi- specific sample. We tested this idea by calculating the relationship between BW and FABL for teeth of *Tyrannosaurus*, presumably a single taxon (but see Russell, 1989: 180): BW = [0.69 * FABL] − 0.37; $r**2 = 0.67, p < 0.0001$, 95% CI of slope = 0.38–1.24, $n = 27$); as for the Morrison Fm sample, there is no obvious heteroscedasticity in the relationship. The higher slope of the *Tyrannosaurus* than the Morrison line suggests that large Late Cretaceous (tyrannosaurid) teeth are indeed stouter than their Morrison counterparts, but the slopes of the *Tyrannosaurus* and Morrison lines are not significantly different by the test provided by Imbrie (1956:237).

In situ teeth showed no marked difference in the relationship between BW and FABL for maxillary as opposed to dentary teeth.

Like BW, tooth crown height is also linearly or nearly linearly related to FABL (Figure 3); the RMA equation is TCH (mm) = [2.37 * FABL (mm)] − 5.02 ($r**2 = 0.94, p < 0.0001, n = 278$). Again, however, there is increasing scatter in the relationship with increasing tooth size, especially for *Tyrannosaurus*, and so we once again corrected for heteroscedasticity and obtained the equation log 10 TCH = [1.11 log 10 FABL] − 0.16 ($r**2 = 0.96, p < 0.0001$ 95% CI of slope = 1.06–1.16). As with our interpretation of the relationship between BW and FABL, we suspect that the biologically meaningful relationship between TCH and FABL is really linear.

In situ teeth showed no marked difference in the relationship between BW and FABL for maxillary as opposed to dentary teeth, except that some maxillary teeth of *Tyrannosaurus* are disproportionately tall (cf. Molnar and Farlow, 1990).

For theropods as a whole, tooth serration basal length increases with increasing tooth size (Figures 4 and 5), but *Troodon* and *Spinosaurus* teeth depart markedly from the relationship shown by other theropods: *Troodon* teeth have exceptionally
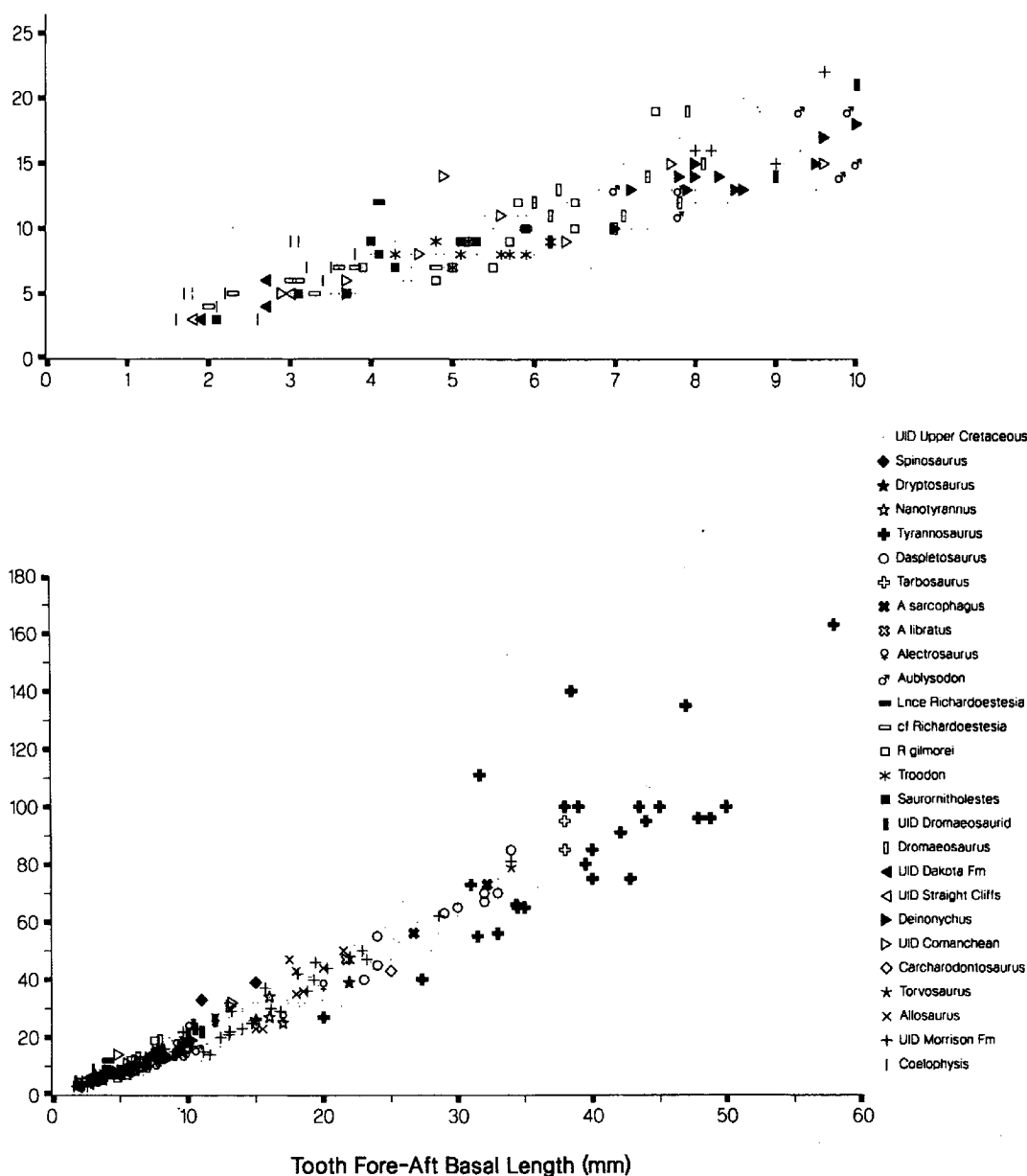
Figure 3 Relationship between tooth crown height and tooth fore-aft basal length in theropods. Insert presents data for very small teeth. "Lnce" refers to the Lance Formation.

coarse denticles for their size, and teeth attributed to Spinosaurus (Bouaziz *et al.*, 1988) are unserrated.

We considered non-linear models (quadratic, exponential, allometric) for the relationship between serration basal length and FABL, but improvements over a linear model in the coefficient of determination were only minor, and so we will assume the relationship to be linear; C.L. Chandler (pers. comm.) has independently come to the same conclusion.

For theropods other than *Troodon* and *Spinosaurus*, the relationship between tooth keel serration basal length and tooth size is given by the following equations:

Anterior Keel:

RMA: Serration basal length (mm) = [0.0167 * FABL (mm)] + 0.101 (95% CI of slope = 0.0152–0.0183).

Regression: Serration basal length (mm) = [0.0150 * FABL (mm)] + 0.126 ($r**2$ = 0.81, $p < 0.0001$, $n = 428$, 95% CI of slope = 0.0143–0.0157).
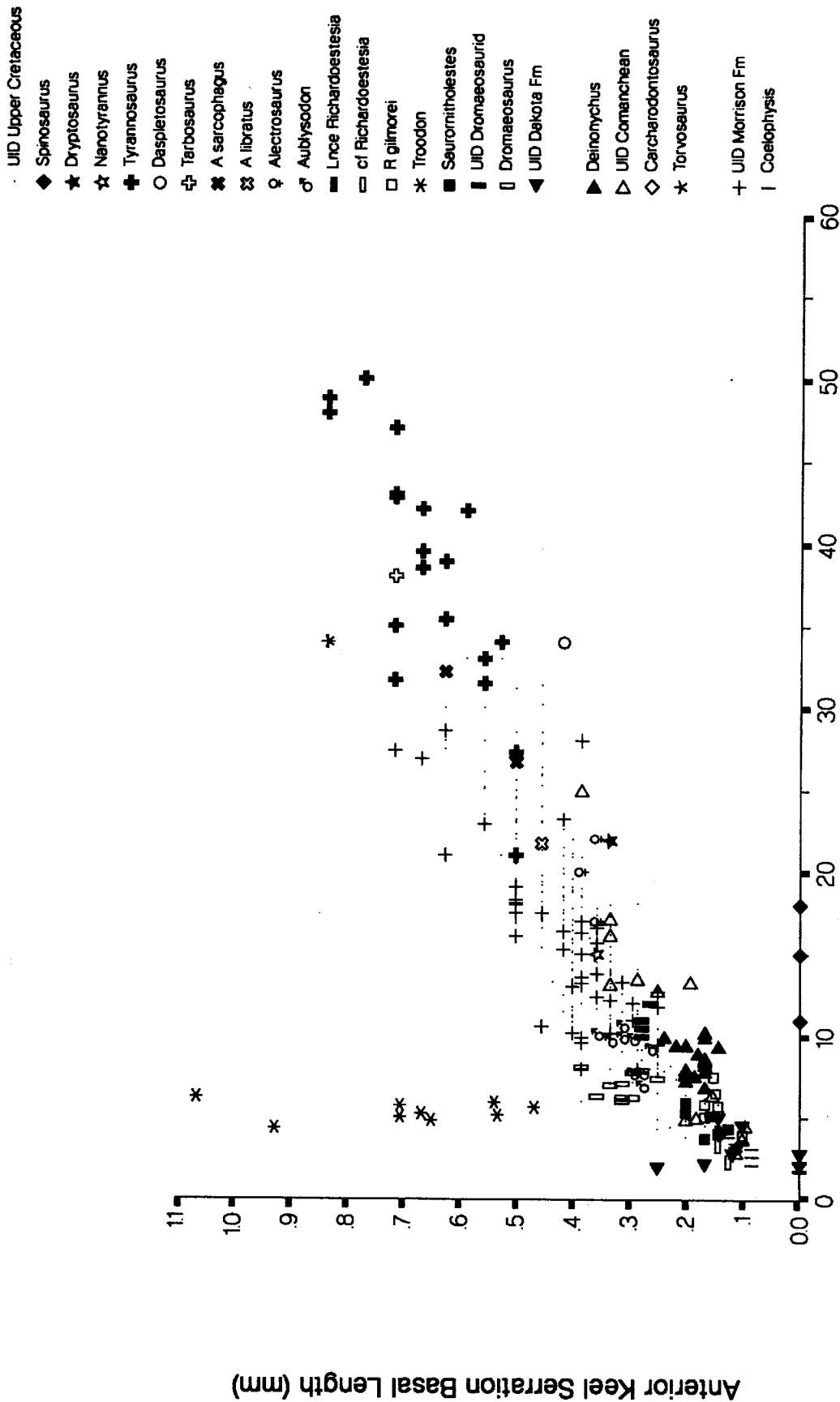
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Figure 4   Relationship between anterior keel serration basal length and tooth fore-aft basal length.
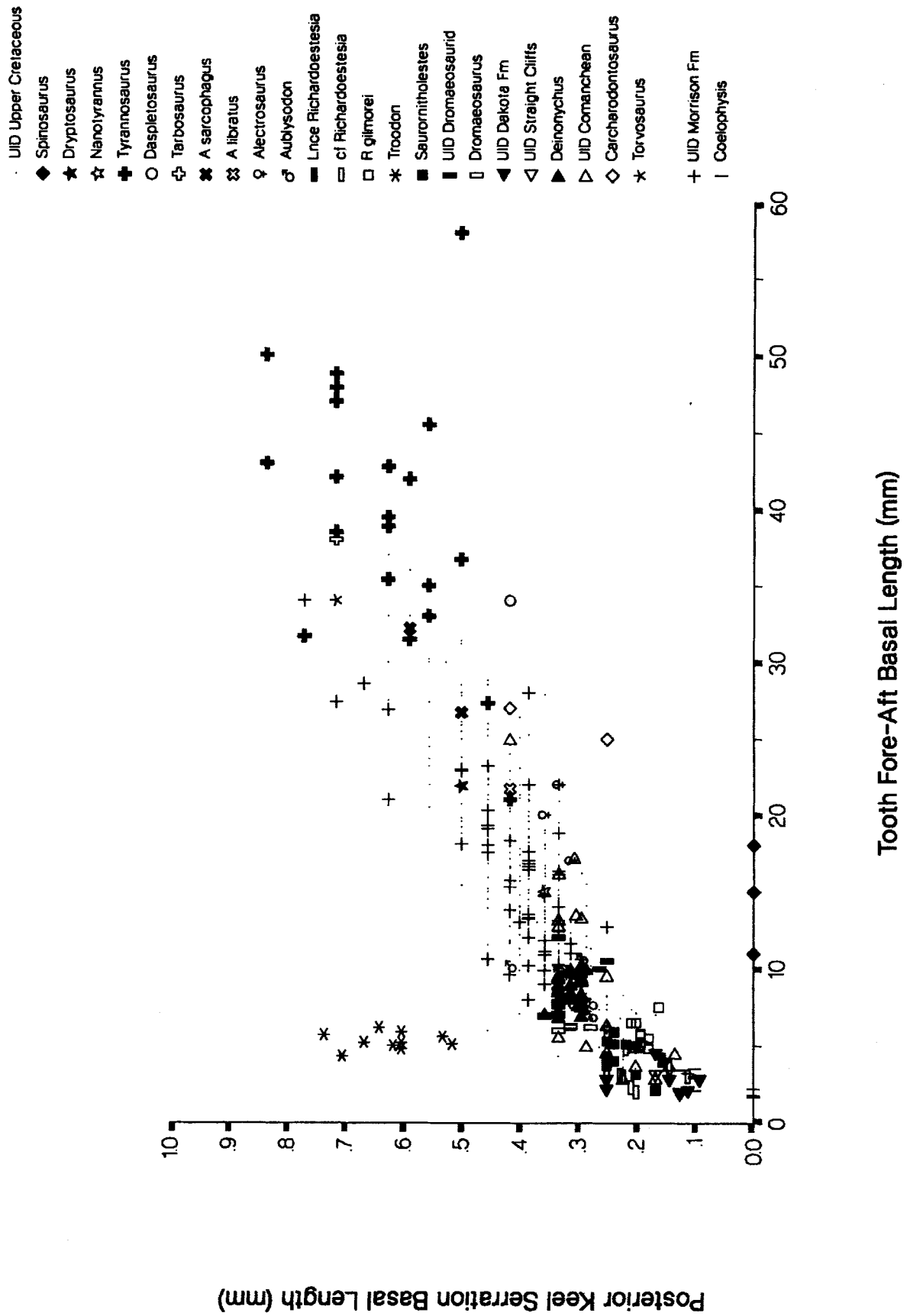
Figure 5 Relationship between posterior keel serration basal length and tooth fore-aft basal length.

Posterior Keel:
   RMA: Serration basal length (mm) = [0.0138 * FABL (mm)] + 0.160 (95% CI of slope = 0.0125–0.0152)

   Regression: Serration basal length (mm) = [0.0119 * FABL (mm)] + 0.187 ($r^{**}2$ = 0.75, $p < 0.0001$, n = 511, 95% CI of slope = 0.0113–0.0125).

Because serration density is essentially the reciprocal of serration basal length, the relationship between serration density and FABL (Figures 6 and 7) takes the form serration density = $1/x$, where x is the linear function of FABL equal to serration basal length. If we try to predict serration density from the regression equations linking serration basal length and FABL (e.g. for the posterior keel, serration density = 5/[(0.0119 * FABL) + 0.187]), however, our model underestimates serration densities for many small teeth. The same problem arises if we assume quadratic, exponential, or allometric models for the relationship between serration basal length and FABL.

The breakdown of our model for small teeth with high serration densities has more than one possible explanation. It may be merely an artifact of the previously mentioned difficulty of measuring serration densities (and thus serration basal lengths) of small teeth; slight errors of measurement—or the scatter of individual data points about the overall relationship between serration basal length and FABL—will be magnified in converting back to serration density from serration basal length. Suppose, for example, that the serration basal length of a tooth is 0.05 mm, while the regression equation predicts a basal length of 0.10 mm for a tooth of that size; the corresponding serration densities will be 100 denticles/5 mm, and 50 denticles/5 mm, respectively.

More interesting is the possibility that the departure of small teeth from the simple linear model has biological significance. Perhaps below some minimum tooth size the relationship between serration basal length and FABL breaks down entirely (W. Coombs, pers. comm.). This might account for the marked departure of *Troodon* teeth from the trend shown by other theropods, but the marked difference in shape between the denticles of *Troodon* and those of other theropods suggests that the extreme coarseness of *Troodon* denticles is related to the manner in which these serrations functioned.

Alternatively, theropod teeth may fall into two populations, large and small, with different slopes in the relationship between tooth size and serration size. Table 1 presents the slopes of regressions of serration basal length against tooth FABL for several taxa of theropods. For most of these the relationship is not significant, but for those in which the limited data suggest such a relationship, the slope is usually larger for dinosaurs with smaller teeth. This suggests that there may well be a different relationship between serration size and FABL for large as opposed to small theropod teeth. Examination of Figures 4 and 5 suggests that the boundary between "small" and "large" teeth occurs at a FABL of about 7 mm.

For teeth (excluding *Troodon*) with FABL less than or equal to 7 mm ("small tooth population"):

Anterior Keel:
   RMA: Serration basal length (mm) = [0.0525 * FABL (mm)] − 0.0803 (95% CI of slope = 0.0315–0.0875)

   Regression: Serration basal length (mm) = [0.0350 * FABL (mm)] − 0.0006 ($r^{**}2$ = 0.44, $p < 0.0001$, n = 82, 95% CI of slope = 0.0263–0.0438)
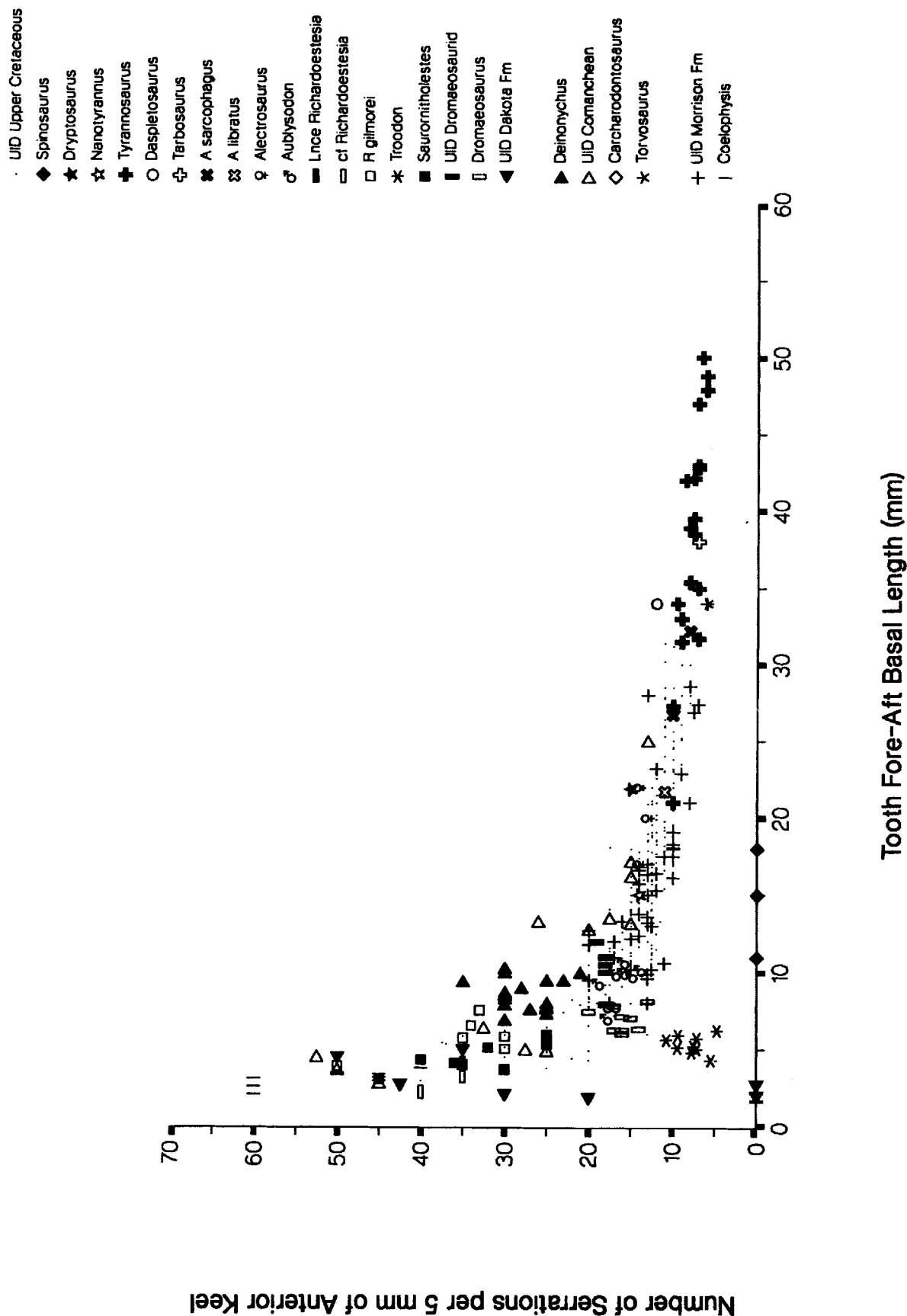
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Figure 6 Relationship between anterior keel serration density and tooth fore-aft basal length in theropods.
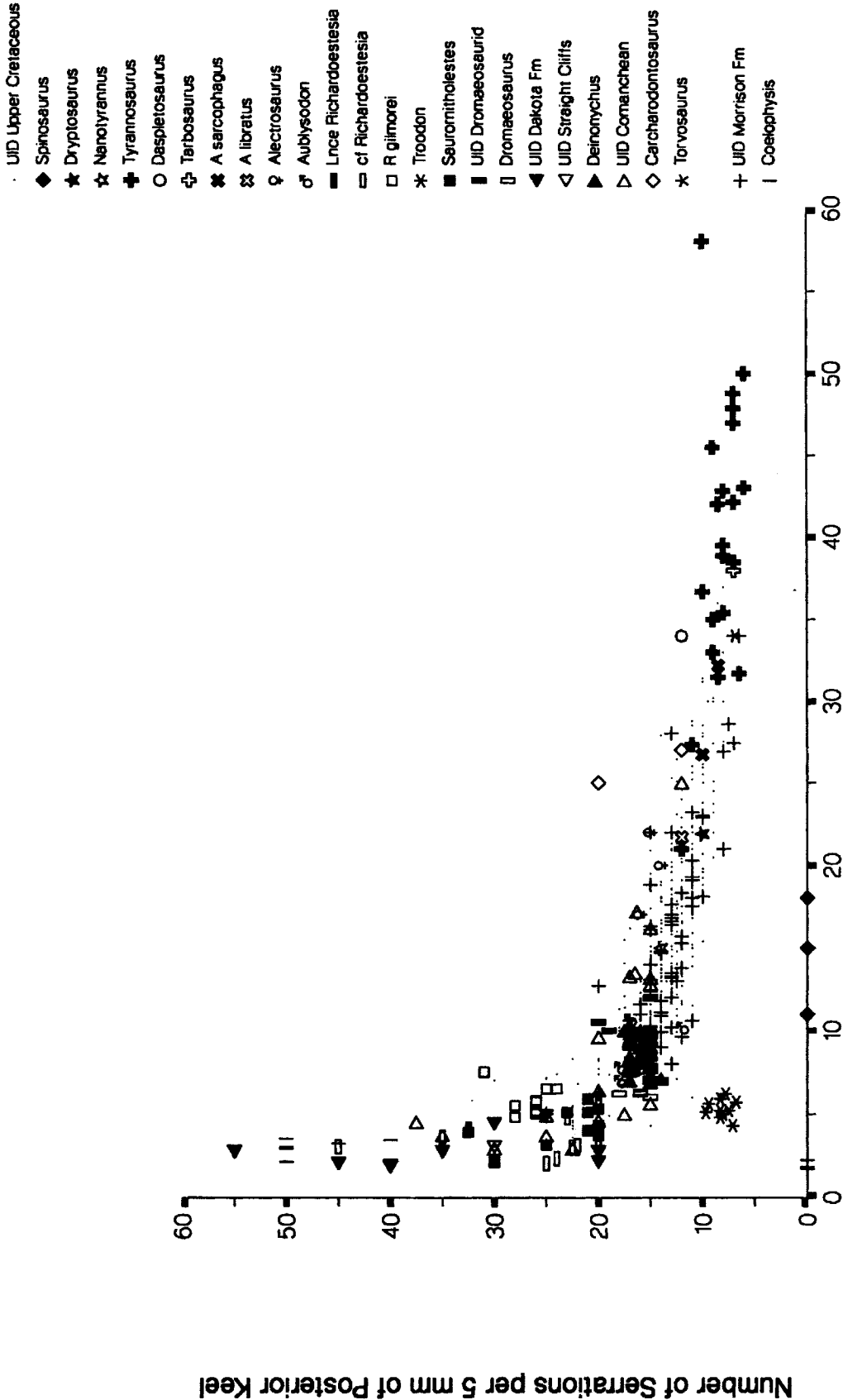
Figure 7 Relationship between posterior keel serration density and tooth fore-aft basal length in theropods.

Table 1 Slopes of regressions of serration basal length on tooth fore-aft basal length for particular taxonomic categories of theropods. "Anterior" and "posterior" designate the anterior and posterior keels

Taxon	Slope	r**2	p	n of teeth
Coelophysis	0.059	0.75	<0.01	11 (anterior)
	0.063	0.69	<0.01	10 (posterior)
Deinonychus	0.004	0.02	0.54	19 (anterior)
	−0.007	0.15	0.04	28 (posterior)
Dromaeosaurus	−0.001	<0.01	0.93	10 (anterior)
	0.003	0.01	0.75	10 (posterior)
Saurornitholestes	0.027	0.62	0.01	9 (anterior)
	0.016	0.44	0.04	10 (posterior)
Troodon	<0.001	<0.01	1.00	10 (anterior)
	−0.010	0.01	0.82	10 (posterior)
Morrison Fm	0.017	0.65	<0.01	44 (anterior)
(mainly *Allosaurus?*)	0.013	0.60	<0.01	64 (posterior)
Aublysodon	0.014	0.41	0.05	10 (anterior)
	0.019	0.34	0.08	10 (posterior)
Tyrannosaurus	0.010	0.61	<0.01	20 (anterior)
	0.006	0.20	0.05	20 (posterior)

Posterior Keel:
  RMA: Serration basal length (mm) = [0.0513 ∗ FABL (mm)] − 0.0179 (95% CI of slope = 0.0315–0.0836)
  Regression: Serration basal length (mm) = [0.0317 ∗ FABL (mm)] + 0.0701 ($r**2 = 0.39$, $p < 0.0001$, $n = 113$, 95% CI of slope = 0.0242–0.0392)
  For teeth (excluding *Troodon*, *Spinosaurus*) with FABL greater than 7 mm ("large tooth population"):

Anterior Keel:
  RMA: Serration basal length (mm) = [0.0153 ∗ FABL (mm)] + 0.1299 (95% CI of slope = 0.0136–0.0172)
  Regression: Serration basal length (mm) = [0.0134 ∗ FABL (mm)] + 0.1631 ($r**2 = 0.76$, $p < 0.0001$, $n = 346$, 95% CI of slope = 0.0126–0.0142)

Posterior Keel:
  RMA: Serration basal length (mm) = [0.0124 ∗ FABL (mm)] + 0.1866 (95% CI of slope = 0.0109–0.0141)
  Regression: Serration basal length (mm) = [0.0104 ∗ FABL (mm)] + 0.2223 ($r**2 = 0.69$, $p < 0.0001$, $n = 398$, 95% CI of slope = 0.0097–0.0110)

The slopes of the RMA equations are significantly different (by the test of Imbrie 1956:237) for small as opposed to large teeth, suggesting that there may well be different trends for theropod teeth of large and small size. We will call this hypothesis the "two population linear model" of the relationship between tooth size and serration size, to distinguish it from the "single population linear model" already presented. If we use the regression equations from the two population linear model to predict serration density from FABL, the problem of underestimating serration densities for small teeth is reduced, but not entirely eliminated.

The similarities in the slopes for anterior as opposed to posterior keels of any given tooth population (single population; teeth with FABL less than or equal to 7 mm;

teeth with FABL > 7 mm) suggests that using separate equations for the two keels is unnecessary. For teeth in the small tooth population, the slopes of the two RMA equations do not significantly differ by Imbrie's test. However, the two RMA equations do have significantly different slopes for teeth in the large tooth population. Furthermore, some theropod teeth (e.g. *Deinonychus*) have anterior and posterior keel serrations of considerably different size. Consequently we will continue to employ separate equations for the anterior and posterior keels in this paper.

Because we do not know the species or even genera of most of the teeth in our sample, we cannot say with assurance whether the single population model or the two population model better corresponds to biological reality. The two models are simply our attempts to describe the relationships between serration size and tooth size in our tooth sample. The true, systematically unbiased relationship(s) may be rather different from either of our models.

For this reason, and because serration density is frequently reported in systematic descriptions of theropods, we also present empirical relationships between serration density and FABL that make no assumptions about the underlying relationship between serration basal length and tooth size. We considered semi-logarithmic, exponential, and allometric (power) models, and decided that the allometric model best fits our data. Because we were mainly interested in predicting serration density from FABL, we only present regression equations:

Anterior Keel:
   Log 10 Serration Density $= (-0.658 * [\text{Log 10 FABL}]) + 1.924$ ($r**2 = 0.821$, $p < 0.0001$, $n = 422$, 95% CI of slope $= -0.629 - -0.688$)

Posterior Keel:
   Log 10 Serration Density $= (-0.478 * [\text{Log 10 FABL}]) + 1.680$ ($r**2 = 0.771$, $p < 0.0001$, $n = 508$, 95% CI of slope $= -0.455 - -0.501$)

Troodon points were excluded from these regression equations, as were teeth with no serrations, the latter due to the impossibility of taking the logarithm of zero.

Coelophysis teeth plot in what seems at first glance a paradoxical fashion, some teeth having no serrations and others among the highest serration densities seen in our theropod tooth sample. The *Coelophysis* teeth with no denticles are among the smaller teeth of this taxon in our sample; given the rapidly increasing serration density at small tooth sizes, one might argue that for *Coelophysis* having no serrations is mathematically equivalent to having an infinite number of infinitely small serrations! Perhaps more realistically, there may be a minimum serration size in the tooth developmental program of any particular species, below which no denticles form; such a hypothesis would be consistent with the steeper slopes for the relationship between tooth size and serration size for small, as opposed to large, teeth in the two-population linear model. This explanation may account for the variable development of serrations in *Compsognathus* (Ostrom, 1978), and the absence of denticles on the teeth of *Walkeria* (Chatterjee, 1987), and *Archaeopteryx* and other toothed birds (Martin *et al.*, 1980; Martin, 1985; Ostrom, 1985).

For the anterior keel, *Deinonychus* teeth and some unidentified Comanchean teeth seem to be more finely serrate than Late Cretaceous teeth of comparable size, and the unidentified Dakota Formation teeth appear to have coarser denticles than similarly-sized Late Cretaceous teeth. In the Late Cretaceous sample, teeth attributed to *Dromaeosaurus* and perhaps cf. *Richardoestesia* seem to be coarsely serrate, and teeth attributed to *Richardoestesia gilmorei* and *Alectrosaurus* more finely serrate, than typical. Teeth of *Saurornitholestes, Aublysodon, Albertosaurus*,

and *Tyrannosaurus* fall roughly in the middle of scatter of values of the anterior keel serration count for teeth in their respective size ranges.

For the posterior keel, *Coelophysis* teeth are more finely serrate, and *Torvosaurus* and many *Deinonychus* and unidentified Dakota teeth more coarsely serrate, than comparably sized Late Cretaceous teeth; unidentified Comanchean teeth occur throughout the scatter of denticle counts for teeth in their size range. Among Late Cretaceous teeth, those identified as *Alectrosaurus, Richardoestesia gilmorei* and *Carcharodontosaurus* have relatively fine denticles, but teeth of cf. *Richardoestesia* can be coarsely serrate. *Dromaeosaurus* and some *Saurornitholestes* teeth have relatively large serrations. Teeth of *Aublysodon, Albertosaurus*, and *Tyrannosaurus* again seem to fall in the middle of scatter for teeth of their respective sizes.

We used the empirical allometric regression equations presented above to predict serration densities for teeth described in the literature; published data for most theropods and other archosaurs are consistent with the trends reported here (Table 2). Although we have no data for this dinosaur, the teeth of *Baryonyx* apparently have unusually fine serrations for their size (Charig and Milner, 1986).

Individual large theropod and *Troodon* teeth tend to have about the same serration density for the anterior and posterior keels, but many small theropod teeth (e.g. *Deinonychus, Richardoestesia gilmorei*, cf. *Richardoestesia*, and *Saurornitholestes*) have coarser posterior than anterior keel denticles. Some of the unidentified Dakota teeth do just the opposite, having finer posterior than anterior keel serrations; other teeth from this fauna lack anterior keel serrations altogether, but do have denticles on their posterior carinae.
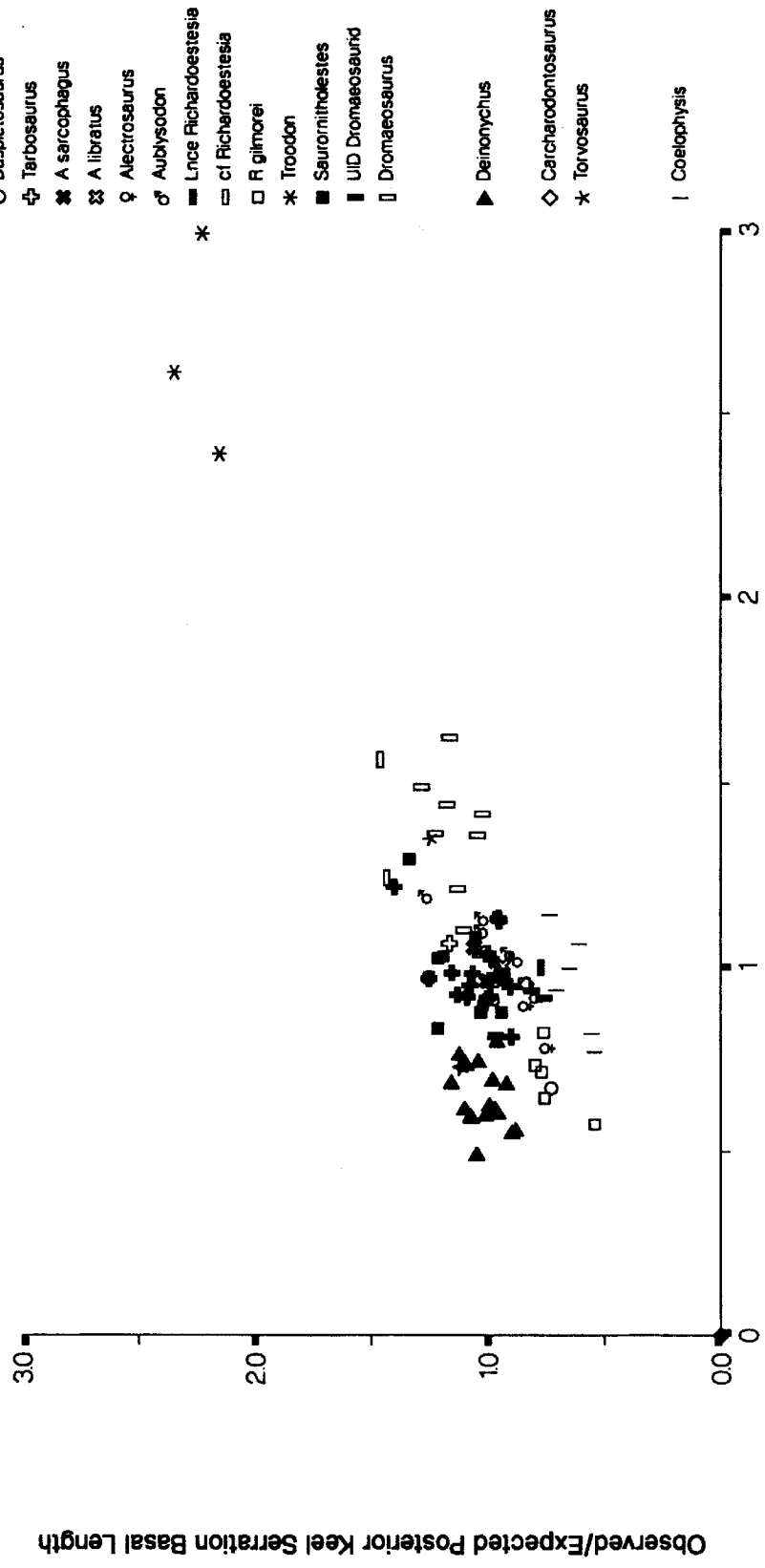
Regression equations presented above can be used to predict serration basal lengths for theropod teeth of given FABL, and these predicted values can in turn be compared with observed values. Most teeth have similar observed/expected ratios for the two keels, but there are some interesting departures from this trend (Figure 8); for example, *Deinonychus* teeth tend to have smaller serrations than predicted for the anterior keel, but about the expected denticle size for the posterior keel. The plot separates other kinds of teeth (*Coelophysis, Dromaeosaurus, Spinosaurus* [points coincident with the origin], and especially *Troodon*) from the main concentration of points as well, suggesting the potential use of this kind of plot (particularly for small theropods) as a more sophisticated way of employing serration size for identification and systematic purposes than the present practice of merely reporting serration densities. However, if teeth of *Richardoestesia gilmorei* do in fact come from the same species as cf. *Richardoestesia*, Figure 8 indicates that teeth from the upper as opposed to the lower jaw of the same species can plot in widely separated regions of such bivariate graphs.

DISCUSSION AND SPECULATIONS

Size, Shape, Bending Strength, and Function

It may be possible to gain insights into functional aspects of theropod tooth morphology by comparing the teeth of carnivorous dinosaurs with those of other predatory vertebrates. Although not entirely similar to theropod teeth in structure—or presumably function—the canine teeth of carnivorous mammals (and even those of as less obviously theropod-like creatures as entelodonts, P. Bjork, pers. comm.) are in some features reminiscent of the lateral teeth of meat-eating dinosaurs.

Van Valkenburgh and Ruff (1987) developed an index for assessing the resistance

Table 2 Fore-aft basal length and serration density for teeth of theropods and other carnivorous archosaurs, based on data from the literature. In most cases FABL is an estimate based on a drawing(s) in the cited reference; exceptions in which the author reported FABL are designated with a *. Predicted values of serration density are made using the empirical logarithmic regression equations between theropod tooth FABL and serration density reported in this paper; the 95% PI is the 95% prediction interval for values of serration density for particular values of FABL

Taxon	FABL (mm)	Number of serrations/5 mm of keel:						Source of data
		Anterior keel			Posterior keel			
		Obs.	Exp.	95% PI	Obs.	Exp.	95% PI	
A) Theropods								
Velociraptor mongoliensis	4	38–40	33	22–48	25–26	25	17–35	Sues (1977)
Lukousaurus yini	4	—	—	—	30	25	17–35	Young (1948)
(Paul [1988] doubts that this is a theropod)								
*Dilophosaurus wetherilli**	10	—	—	—	15	16	11–23	Welles (1984)
Antrodemus valens	18	10	12	8–18	10	12	8–17	Gilmore (1920)
(*Allosaurus fragilis* of Madsen [1976])								
Dryptosaurus incrassatus	18	10–12	12	8–18	10–12	12	8–17	Lambe (1903)
(*Albertosaurus sarcophagus* of Russell [1970])								
Sinosaurus triassicus tooth								
V36	19	—	—	—	16	12	8–17	Young (1948)
Indosuchus raptorius	20	12	11	8–17	12	11	8–16	Chatterjee (1978)
Aublysodon cf. *mirandus*	20	15	11	8–17	12–18	11	8–16	Molnar (1978)
	12	13	16	11–23	13	15	10–21	Molnar and Carpenter (1989)
Ceratosaurus nasicornis	27	10	9	6–14	10	10	7–14	Gilmore (1920)
Gorgosaurus libratus	30	11–12	9	6–13	11–12	9	7–13	Lambe (1917)
(*Albertosaurus libratus* of Russell [1970]. The value of FABL given here may be an overestimate.)								
B) Thecodonts								
Tikisuchus romeri	10	15	18	12–26	15	16	11–23	Chatterjee (1987)
Postosuchus kirkpatricki	20	12	11	8–17	12	11	8–16	Chatterjee (1985)
Teratosaurus suevicus	22	—	—	—	15	11	8–15	Benton (1986)
C) Crocodilians								
*Pristichampsus vorax**	10.1	30	18	12–26	—	—	—	Langston (1975)
Australian ziphodonts								
QM F9220*	10.3	18	18	12–26	19	16	11–23	Molnar (1981: Table 2)
QM F9225*	7.2	27	23	15–33	—	—	—	
Right Maxilla*	4.3	25	33	22–48	27	25	17–35	

(Molnar's "maximum width of crown" is equivalent to FABL; R. Molnar, pers. comm.).

Figure 8 Separation of theropod teeth of known identity on the basis of observed/expected values of serration basal length of the anterior and posterior keels. Expected values were calculated using regression equations presented in the text, assuming the two population linear model. *Troodon* points with high values of relative serration basal length (see Table 3 for the maximum values observed) are excluded to permit better separation of points for other taxa.

to bending stresses of carnivore canine teeth, based on beam theory (Shigley, 1976). Van Valkenburgh and Ruff assumed an elliptical cross section for canine teeth, and computed maximum bending strengths about the anteroposterior (AP) and medio-lateral (ML) axes of the tooth base:

$$\text{Bending strength about AP axis} = \frac{IX}{Fhb}$$

$$\text{Bending strength about ML axis} = \frac{IY}{Fha}$$

where h is the crown height of the tooth, and a and b are one-half the tooth's anteroposterior basal diameter (1/2 FABL), and one-half the mediolateral basal diameter (1/2 BW), respectively; all of these measurements are in millimeters. F represents force, and is assigned a value of 1 in all cases. IX and IY represent the second moments of area about the tooth's AP and ML axes, respectively, and are calculated as:

$$IX = \frac{(pi * ab**2)}{4} \quad IY = \frac{(pt * ba**3)}{4}$$

The units of these strength indices are mm**2.

The basal cross-section of many theropod lateral teeth is more rectangular than elliptical, and we calculated Van Valkenburgh and Ruff's strength indices for theropods using both elliptical and rectangular models. For the rectangular model,

$$IX = \frac{(4ab**3)}{3} \quad IY = \frac{(4ba**3)}{3}$$

With a rectangular model (Figures 9 and 10), theropod teeth have bending strength indices that fall within the scatter for, or are greater than, those calculated for mammalian carnivore canines using the elliptical model; the appearance of greater strength is reduced, but not eliminated, if theropod tooth bending strength is calculated using an elliptical model for tooth base shape. Van Valkenburgh and Ruff (1987) noted that living canids have canines that are basally more mediolaterally compressed than those of living felids, particularly at large tooth sizes. Theropod lateral teeth likewise tend to be flatter than canines of extant felids, although there is much overlap in their relationships between BW and FABL (Figure 11); theropod teeth have considerably greater basal widths than sabercat canines, however. Small theropod teeth tend to be more mediolaterally compressed at their bases than canid teeth, again with overlap in the relationships, but large theropod teeth are less compressed than dog canines of comparable size. The canine teeth of hyaenids plot within the scatter of theropod teeth for both bending strength indices and the relationship between BW and FABL.

If the ML and AP bending strength indices are plotted against each other (Figure 12), teeth that are resistant to bending in one direction also tend to be resistant to bending in the other, but there are some interesting patterns in the relationship. For particular ML bending strength values, extant felids, canids, and hyaenids tend to have relatively high AP strength values, while sabercats have fairly low AP strength indices. As a group, theropods have teeth that plot between the modern carnivores and sabercats in terms of the values of AP bending strength for particular values of ML bending strength, and some theropod teeth are much stouter than canines of any carnivorous mammals with regard to bending about both the AP and ML axes. Tyrannosaurid teeth in particular are very stout, and tend to have both AP and ML bending strengths greater than those of Morrison Fm teeth of comparable FABL.
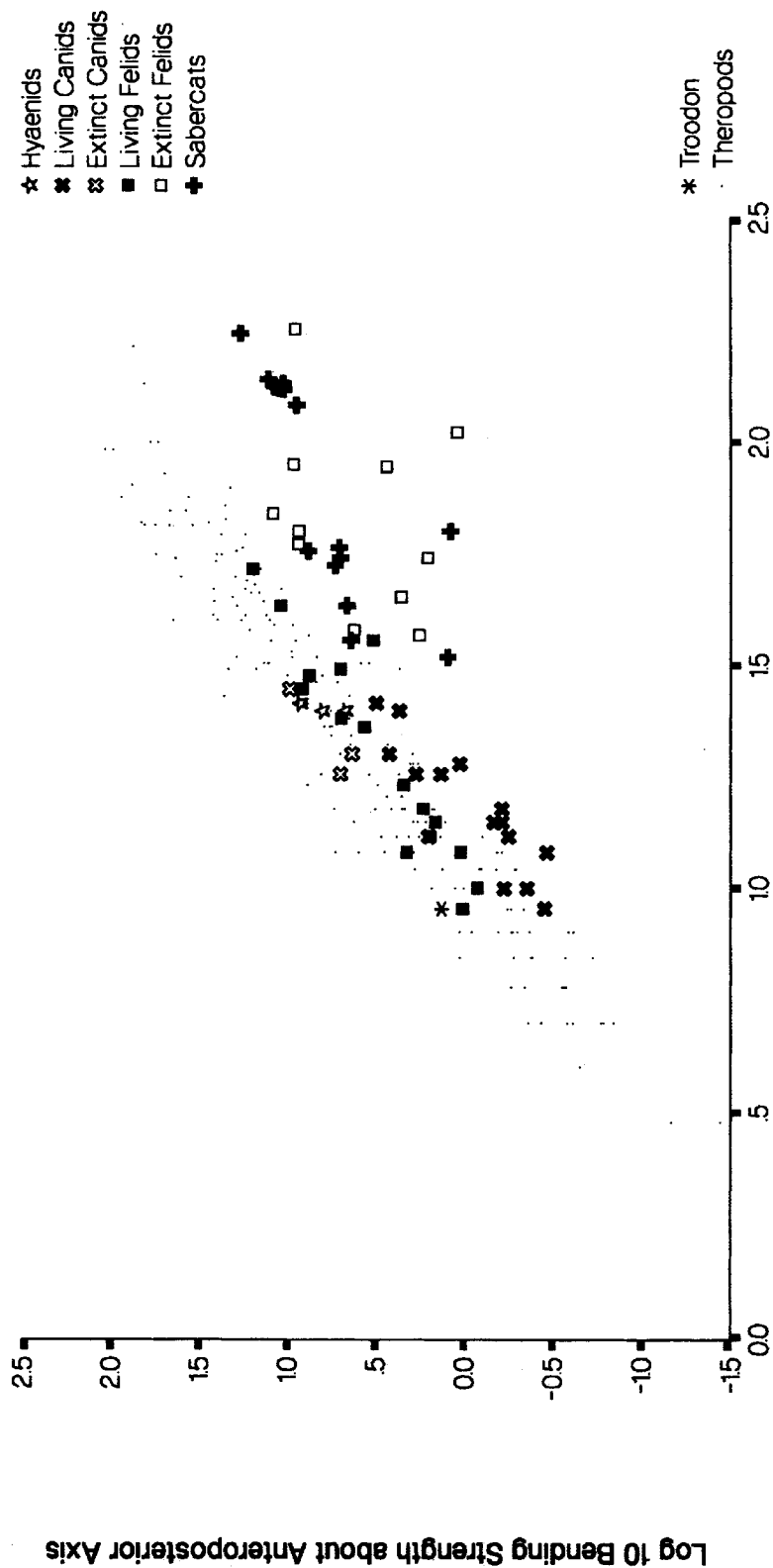
Figure 9 Comparison of the bending strength index about the anteroposterior basal axis of carnivoran canines and theropod lateral teeth, assuming a rectangular shape for the base of theropod teeth, and an elliptical shape for the base of mammalian canines. Points labeled "sabercats" represent measurements obtained by the authors; other felid (including sabercats as "extinct felids") data, as well as canid and hyaenid data, are taken from Van Valkenburgh and Ruff (1987). Data are plotted on logarithmic axes to reduce overlap of points for small teeth.
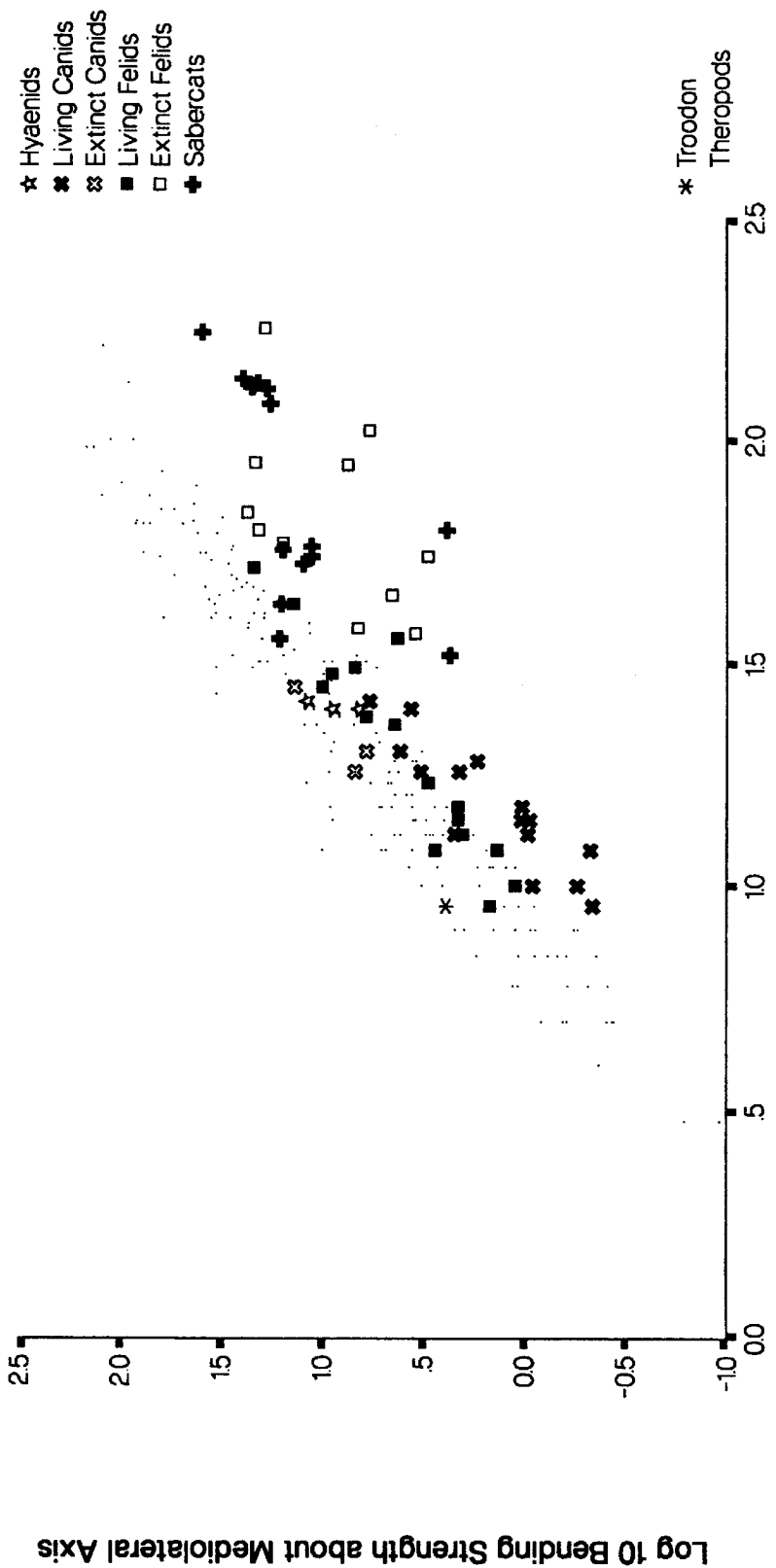
Figure 10 Comparison of the bending strength index about the mediolateral basal axis of carnivoran canines and theropod lateral teeth. Assumptions and plotting conventions as in Figure 9.
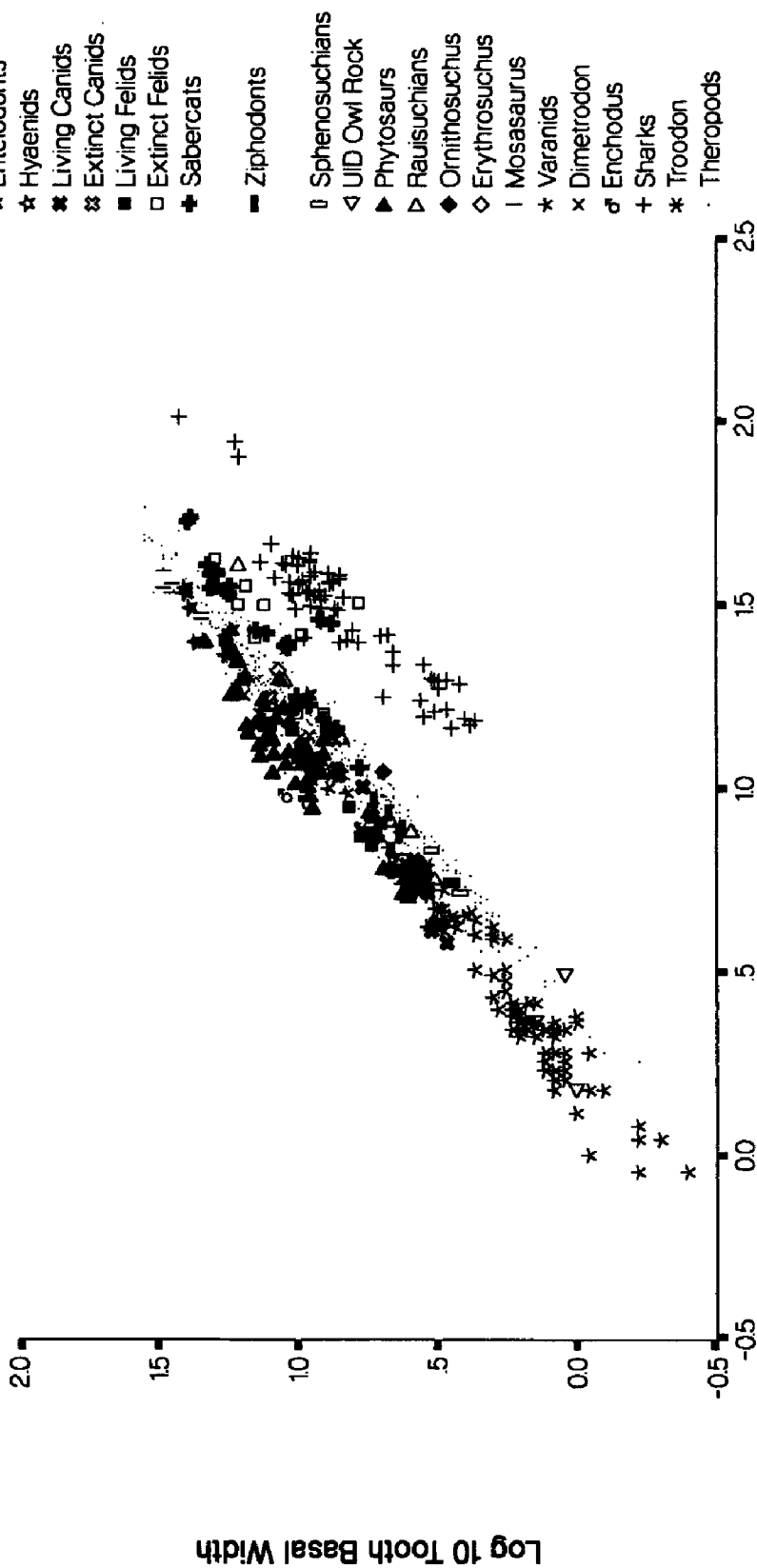
Figure 11 Relationship between tooth basal width and fore-aft basal length in theropods and other predaceous vertebrates. Data are plotted logarithmically to reduce point overlap for small teeth. Points labeled "sabercats" and "entelodonts" were obtained by the authors; all other mammal data are from Van Valkenburgh and Ruff (1987).
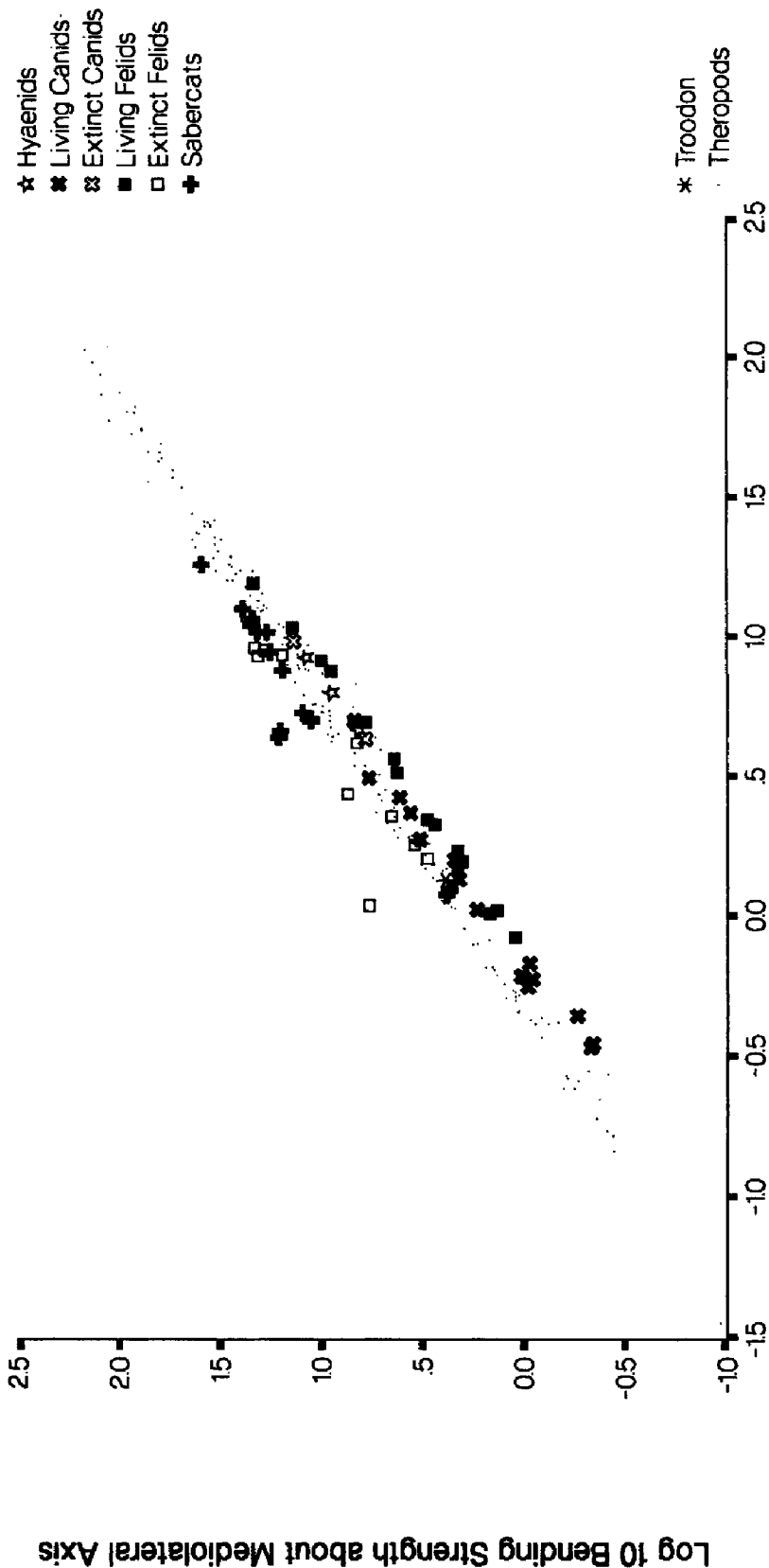
Figure 12 Bending strength about the mediolateral and anteroposterior tooth axes of theropod teeth and the canines of mammalian carnivores.

Entelodont canine teeth and the lateral teeth of most reptilian predators fall within the scatter of theropod values of BW for particular values of FABL. In contrast, *Enchodus, Mosasaurus* and phytosaurs tend to have relatively broader-based lateral teeth than theropods, and shark teeth and sabercat sabers are more blade-like implements than theropod teeth.

For particular values of FABL, most predators have theropod-like values of TCH (Figure 13). Small theropod lateral teeth tend to be shorter, and large theropod teeth taller, than dog canines, however. Nearly all theropod lateral teeth, except for the very tallest and shortest for their basal lengths, fall close to the non-sabercat felid relationship of TCH and FABL. Sharks and (to a lesser extent) ?sphenosuchians and *Mosasaurus* have relatively shorter teeth than theropods, and *Enchodus* and saber-cat teeth are relatively taller; interestingly, however, the tallest carnosaur teeth are about as tall as the biggest sabercat canines. The phytosaur teeth in our sample plot both above and below the scatter of our theropod points, presumably indicative of the rather different shape of teeth in the anterior and posterior regions of the phytosaur jaw.

Van Valkenburgh and Ruff (1987) argued that the relatively greater basal widths of cat than dog canines give these teeth more resistance to mediolateral stresses caused by struggling prey; cats tend to bite more deeply than dogs, and their bites are more likely to encounter bone. The narrow canine teeth of dogs, in contrast, are used to produce shallow wounds during quick attacks.

The canines of carnivorans have to be strong enough to withstand the forces generated during the attack on the prey and the dismemberment and consumption of the carcass. Consequently the canines of hyaenids, for example, are very strongly constructed because the forceful bites required by the bone-crushing habits of their owners put the canines at greater risk of incidental breakage (Van Valkenburgh, 1989).

To the extent that comparisons of shape between carnivoran canines and dinosaur teeth can be used to infer the functions of the latter, theropod lateral teeth seem to have been generalized, perhaps multipurpose, implements; they are not specialized in shape to the degree seen in carnivoran canines. This is not surprising, given that mammalian teeth show much more specialization for particular functions in different regions of the jaw than is typical of reptiles. Large theropod teeth tend to be flatter than modern felid canines, but not as flat as canid or sabercat canines. For particular values of FABL, large theropod teeth are generally taller than dog canines, roughly comparable to non-sabercat felid canines in height, and not as tall as sabertooth sabers. On the other hand, theropod teeth are more doglike than catlike in tooth height relative to skull size; like canids (Van Valkenburgh and Ruff, 1987), flesh-eating dinosaurs (particularly those forms that presumably preyed upon animals their own size or larger) tend to be big-headed predators. The most noteworthy "specialization" seen in large theropod lateral teeth is their great bending strength, which seems to be a function mainly of the size of these teeth.

Paul (1988) suggested that the killing tactics of carnivorous dinosaurs involved sudden surprise attacks in which the predators made deep bites into their victims' bodies, a style of assault that would combine cat-like and dog-like elements. Although such attacks would involve the incisiform as much as the lateral teeth, Paul's hypothesis is consistent with the relatively tall and stout nature of theropod lateral teeth. The stoutness of large theropod teeth—a property simply of their size—may in addition have enabled them to be used fortuitously for biting into and even breaking bone, even without the marked adaptations for the latter function seen in the chewing teeth of hyaenids and other mammalian bone-crushers; Bakker
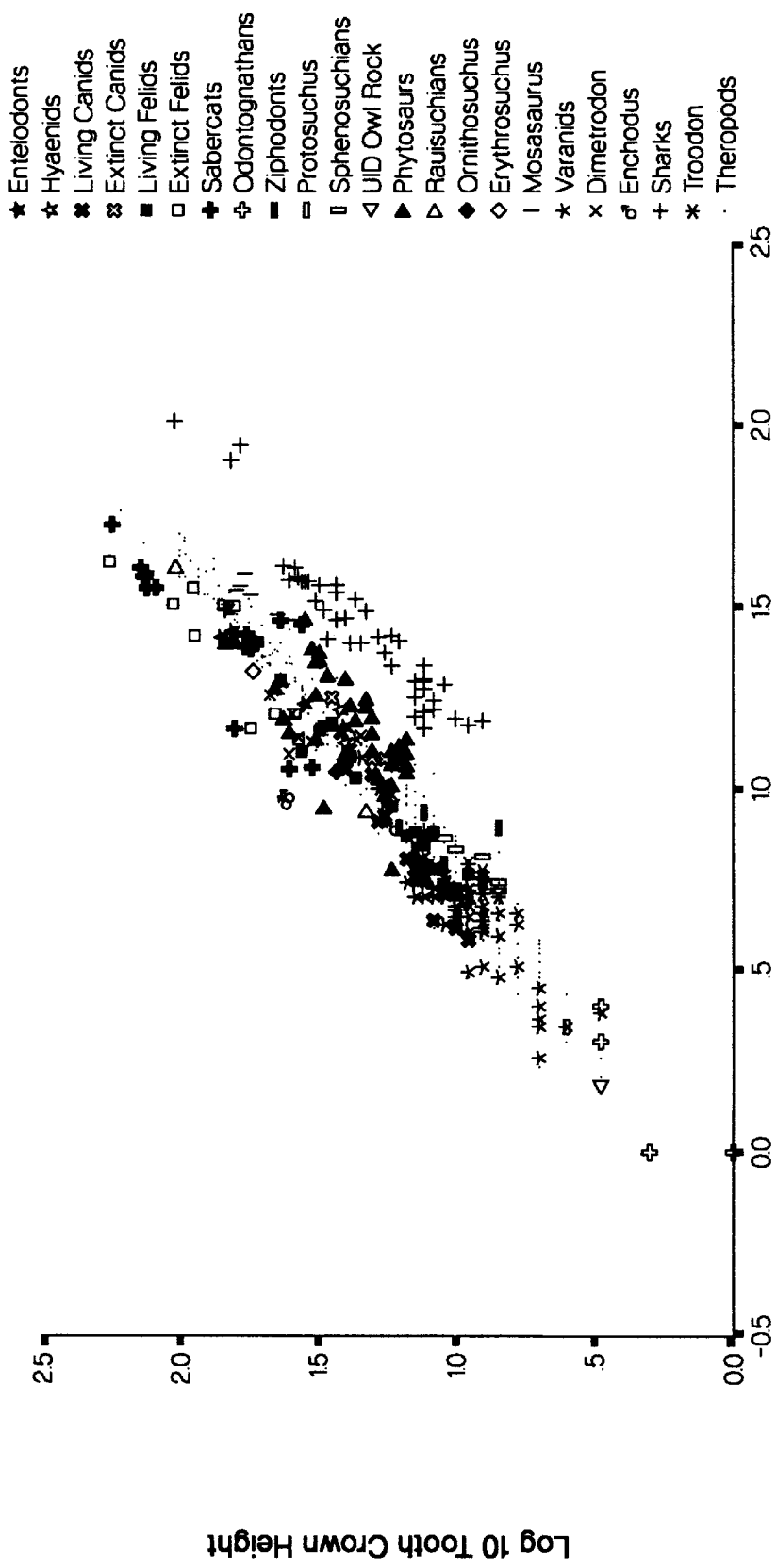
Figure 13 Relationship between tooth crown height and fore-aft basal length in theropods and other carnivorous vertebrates. Data are plotted logarithmically to reduce point overlap for small teeth. We did not obtain data on tooth crown height for the smallest varanid teeth.

et. al. (1988) suggested such a role for the posterior teeth of some tyrannosaurids. Use of theropod teeth for breaking bone may account for the occasional occurrence of tyrannosaur tooth crowns that appear to have shattered while *in situ* in their owners' jaws, after which their broken edges were worn smooth (Carpenter, 1979; Farlow and Brinkman, 1987; Molnar and Farlow, 1990). On the other hand, tooth-marked bones are less abundant in Mesozoic than in Cenozoic bone assemblages (A. Fiorillo, pers. comm.), and so the extent to which carnosaurs intentionally broke bone, or merely did so accidentally in the process of feeding on meat, is questionable.

Unlike theropods, no extant carnivorans have serrated canines, and so interpretations of the function of theropod lateral teeth based on shape comparisons with modern carnivoran canines should not be pushed too far. The canine teeth of living carnivorans presumably function more in holding and subduing prey than in cutting meat from their victims' bodies.

Unlike modern carnivoran canines, and like theropod lateral teeth, however, sabercat canines were serrated, and an analogy between sabertooth sabers and theropod lateral teeth has been made (Paul, 1988; Molnar and Farlow, 1990). Theropod teeth were not as blade-like as sabercat canines, however, and so this analogy is not perfect. Teeth of meat-eating dinosaurs combined an overall shape much like that of a generalized extant mammalian predator's canines with the serrated cutting edges of sabercat canines. This is consistent with our interpretation of theropod lateral teeth as multipurpose structures. Sabercats apparently used their upper canines to deliver a lethal bite to the stomach or throat (Martin, 1980, 1989; Emerson and Radinsky, 1980; Akersten, 1985). The victim was immobilized by the cat's powerful forelimbs during the application of the bite (Gonyea, 1976; Martin, 1980), probably decreasing the likelihood that its struggles would generate lateral stresses that might break the sabers. This in turn may have permitted those sabers to have a more blade-like shape for easier penetration of the prey's body during the attack. Once the victim had been killed, removing meat from its carcass was presumably done by teeth other than the canines.

In contrast, theropod lateral teeth, although undoubtedly used in the act of killing, were not devoted exclusively to that function. Furthermore, in many theropods (especially tyrannosaurs) the jaws, as in canids (Van Valkenburgh and Ruff, 1987), were probably the primary instruments for subduing prey, such that the chances of breaking lateral teeth during the attack may have been greater for dinosaurs than for sabercats.

As quadrupedal animals, sabercats were well positioned for biting their victims' ventral surfaces, whether those ventral surfaces were the prey animals' throats or bellies. As bipeds that were probably as tall or taller than the animals upon which they fed (except in the case of any carnosaurs that killed adult sauropods), theropods were perhaps more likely to have attacked from above (cf. Paul, 1988: 96), and theropods probably bit into bone more frequently than sabercats did.

Any or all of these reasons might explain the greater mediolateral stoutness of theropod lateral teeth than of sabercat canines. Although tooth replacement in theropods may have permitted less caution in the use of their teeth than was possible for sabertoothed cats (Molnar and Farlow, 1990), the great resistance to forces acting perpendicular to the anteroposterior axis of large theropod teeth may have served to keep tooth breakage to a minimum.

Although our data are insufficient to address this in a definitive fashion, the teeth of other reptilian predators in our sample seem very theropod-like in shape. One could argue that this makes sense; given that reptiles generally do not display the

regional specialization seen in the dentitions of carnivorans, the expectation might be that the lateral teeth of most carnivorous reptiles, like those of theropods, should be generalized meat- (and bone?) processing implements. However, the kinds of non-dinosaurian reptilian teeth we examined are not a random selection of teeth of predaceous reptiles, but rather teeth that we examined *because* of their theropod-like features (the same caveat applies to the comparison of serration sizes between theropods and other predators given below). Other kinds of carnivorous reptiles, living and extinct, have lateral teeth that depart markedly from the theropod tooth form; even in our sample, *Mosasaurus* and phytosaur teeth are less theropod-like in shape than the teeth of other reptiles. All that can be said is that most of the reptilian teeth that we studied were quite theropod-like, suggesting that their erstwhile owners used them in a theropod-like fashion.

Shark teeth show the greatest departure from the shape of theropod lateral teeth of any of the carnivores that we studied, being much flatter and shorter for particular values of FABL. Although many shark teeth, like those of theropods, are serrated, the motions made by sharks in using their teeth are presumably very different from those once employed by carnivorous dinosaurs. The flatter shape of shark than of theropod teeth undoubtedly makes the cutting action of a shark's tooth more like that of a true blade than the cutting action of a theropod's tooth was, but may also make shark teeth more susceptible to breakage than dinosaur teeth were. However, tooth replacement in sharks takes place on a roughly 8–10 day cycle (T. Frazzetta, pers. comm.), and at any particular time a shark has more than one tooth generation in operation. Consequently damage to any given tooth may be a very minor problem for a shark.

In modern alligators, in contrast, any given tooth is replaced once every 8–16 months (Edmund, 1962). Although the rate at which theropod teeth were replaced is unknown (and rather controversial—Johnston, 1979, 1980; Bolt and De Mar, 1980; Meinke *et al.*, 1980), the rate of replacement was undoubtedly more alligator-like than shark-like. As already noted, some broken carnosaur teeth seem to have been retained in the jaws long enough for their shattered edges to have been worn smooth, indicating a rather slow rate of tooth replacement. Consequently theropod teeth may have been stouter than shark teeth in the mediolateral dimension to make them last as long as possible. The removal of teeth from the jaws probably occurred more often through normal tooth replacement (with teeth whose roots had been resorbed being lost during feeding—cf. Buffetaut and Suteethorn, 1989) than through breakage.

Cutting-Edge Paleontology: Tooth Size and Serration Size

Teeth of many predatory vertebrates (and even analogous structures in invertebrates—Abler, in press) show serrated edges (Figure 14). There is considerable overlap in the relationship between tooth size and serration size in theropods and other carnivores (Figure 15; Tables 2 and 3), but we cannot offer a definitive assessment of the degree to which other carnivores with serrated teeth show the same relationship between FABL and serration basal length seen in meat-eating dinosaurs. For most of the predator groups our sample is dominated by teeth of only one or a few species—for varanids, in fact, many of the teeth come from only a few individual lizards, and our mosasaur sample comes from a single animal. Only for theropods is the sample size large enough possibly to approximate a taxonomically unbiased sample, and even here our sample is dominated by Late Cretaceous teeth, particularly those of tyrannosaurids. The following remarks about the serration sizes

Table 3 Serration basal lengths of teeth of predatory vertebrates compared with serration basal lengths of theropod teeth. Denticle sizes are expressed in terms of the ratio of the actual denticle basal length to that predicted for theropod teeth of comparable fore-aft basal length. Predicted tooth serration basal lengths were obtained from the regression equations presented in the text. For each group, the first line of data uses expected serration basal lengths obtained from the single population linear model; the second line uses expected serration basal lengths based on the two population linear model. Means are only reported for the theropod sample and for those groups consisting of a single taxon; for other groups there is very uneven sampling of teeth of different taxa. Standard deviations are only reported for the theropod sample

Group	Observed denticle basal length/Predicted denticle basal length							
	Anterior keel				Posterior keel			
	Mean	SD	Range	N	Mean	SD	Range	N
Theropods								
(excluding *Troodon*)*	0.98	0.25	0–1.78	432	0.99	0.21	0–1.76	515
	anterior keel: kurtosis = 3.624, SE kurtosis = 0.234							
	posterior keel: kurtosis = 5.653, SE kurtosis = 0.215							
	0.99	0.28	0–3.79	432	0.99	0.21	0–1.83	515
	anterior keel: kurtosis = 25.025, SE kurtosis = 0.234							
	posterior keel: kurtosis = 6.465, SE kurtosis = 0.215							
Troodon	3.37		2.22–4.85	10	2.49		2.08–2.95	10
	3.79		2.39–6.17	10	2.63		2.15–3.41	10
Sharks							0.55–1.99	71
							0.60–2.07	71
Enchodus	0.90		0.82–0.95	3	0.89		0.71–1.12	3
	0.83		0.75–0.87	3	0.83		0.66–1.05	3
Dimetrodon	1.10		0.99–1.25	7	0.99		0.83–1.24	8
	1.06		0.95–1.20	7	0.96		0.80–1.19	8
Varanids			0–1.32	97			0.27–1.24	111
			0–2.42	97			0.40–1.59	111
Mosasaurus	0.27		0.25–0.29	3	0.31		0.28–0.38	7
	0.28		0.26–0.30	3	0.32		0.29–0.38	7
Erythrosuchus	0.81			1				
	0.81			1				
Ornithosuchus	1.55			1				
	1.45			1				
Rauisuchians			0.68–1.31	8			0.66–0.88	6
			0.67–1.30	8			0.64–0.81	6
Phytosaurs			0.51–1.10	53			0.55–1.02	54
			0.53–1.12	53			0.55–0.97	54
Owl Rock teeth			0.61–0.73	2			0.44–0.59	3
			0.97–1.47	2			0.77–0.87	3
?Sphenosuchians			0.80–1.19	6			0.66–0.94	6
			0.85–1.28	6			0.68–0.91	6
Protosuchus	0.63			1	0.47			1
	1.31			1	0.71			1
Ziphodonts			0.57–0.92	9			0.52–0.67	9
			0.53–0.95	9			0.50–0.63	9
Sabercats			0–1.56	23			0.45–1.37	26
			0–1.58	23			0.45–1.42	26

*We excluded all those teeth that, at the time of measurement, we were sure had come from *Troodon*. At least one of the teeth that at that time were unidentified probably represents *Troodon*, however.
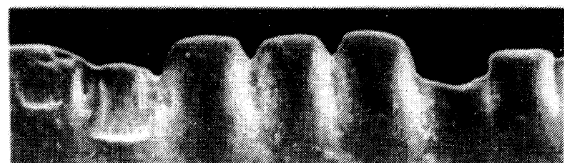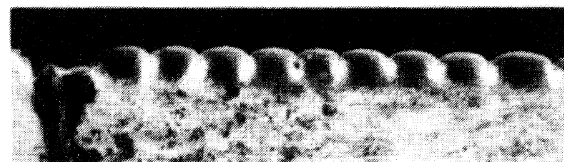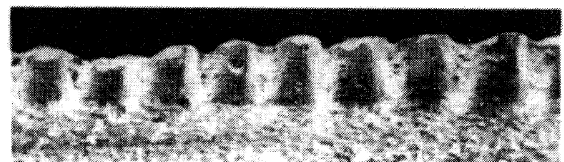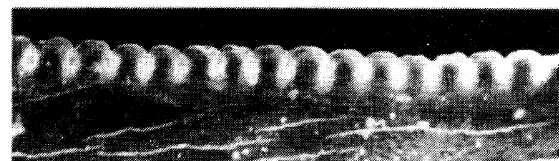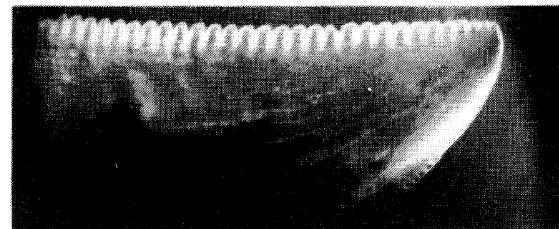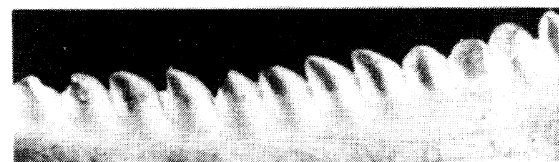
A) *Carcharodon*

B) *Enchodus*

C) *Dimetrodon*

D) *Homotherium*

E) *Varanus*

F) *Megalania*

G) Phytosaur

H) Ziphodont

I) *Saurornitholestes*

J) *Saurornitholestes*

K) *Troodon*

L) Cleveland-Lloyd Quarry Carnosaur

M) Tyrannosaurid

Figure 14   Comparison of tooth serrations of predatory vertebrates. The scale of each SEM photomicrograph is indicated by giving the serration density of the tooth in terms of the number of denticles per 1 millimeter of carina length. A: *Carcharodon* sp. Tooth fore-aft basal length (FABL) indeterminate. Posterior (?) keel, toothtip to left. Serration density = 1–2 denticles/1 mm. B: Yale Peabody Museum 7252 accession number 46, *Enchodus ?ferox*, right dentary tooth. FABL = 10 mm. Posterior keel, toothtip to right. Serration density = 4 denticles/1 mm. *Enchodus* denticles show a tendency to coalesce to form a continuous ridge, as seen at the left and right margins of the photomicrograph. C: U.S. National Museum 407941, *Dimetrodon* sp. FABL = 18 mm. Posterior keel, toothtip to right. Serration density = 2 denticles/1 mm. D: Cast of Los Angeles County Museum 44797 HC, *Homotherium serum*, upper

of non-dinosaurian predators in comparison with theropods, then, are only our impressions based on the teeth available to us.

Many of the smaller varanid teeth (*Varanus varius, V. bengalensis, V. salvator*) seem to have more finely serrate posterior (but not anterior) keels than expected for theropods; teeth of *V. komodoensis, V. dirus*, and *Megalania* have serration basal lengths close to those expected for theropod teeth of comparable size. Teeth of *Mosasaurus* (and some other mosasaurs—Massare, 1987; Nichols, 1988; J. D. Stewart, pers. comm.) are particularly finely serrate. In the *Mosasaurus* teeth we examined, the denticles are more closely packed together than the denticles of theropod teeth; the *Mosasaurus* tooth keel has a flatter, less scalloped margin than the theropod carina. Although mosasaur teeth of this type may have had a cutting function (Massare, 1987), we suspect that this differed from the cutting action of theropod teeth.

The ziphodont teeth that we examined have relatively fine serrations for both the anterior and posterior keels, but ziphodont teeth from Australia (Table 2) have serrations close in size to those expected for theropod teeth. Phytosaur teeth tend to be more finely serrate than theropod teeth, but still greatly overlap the denticle size–tooth size relationship seen in carnivorous dinosaurs.

Some sabercat canines (*Barbourofelis*, some *Hoplophoneus*) have canine teeth with relatively finer serrations than comparably sized theropod lateral teeth (*Smilodon* deciduous sabers lack anterior keel serrations entirely), and others (*Dinictis, Ischyrosmilus, Nimravus, Homotherium*, adult *Smilodon*, some *Hoplophoneus*) have serrations about as coarse or even coarser than those of theropod teeth of similar size. Martin (1980 : 141; 1989) recognized two categories of saber-toothed cats, scimitar-toothed cats with "relatively short, broad canines that usually bear coarse crenulations," and dirk-toothed cats with "long, narrow upper canines with very fine or no crenulations." He suggested that the canines of scimitar-toothed cats ripped prey tissues, while the sabers of dirk-toothed cats had a slicing effect. Martin identified *Dinictis, Nimravus, Homotherium*, and *Ischyrosmilus* as scimitar-tooths, and *Hoplophoneus, Barbourofelis*, and *Smilodon* as dirk-tooths. At least in comparison with theropod teeth of comparable fore-aft dimensions, the relative coarseness/fineness of the denticles of the dirk-tooths does not consistently follow Martin's characterization, but the scimitar-toothed cats do show the expected coarse serrations.

Teeth of *Carcharodon carcharias* tend to be more coarsely serrate than comparably sized theropod teeth, but teeth of *C. megalodon* have teeth with serrations close

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canine tooth. FABL = 28 mm. Posterior keel, toothtip to right. Serration density = 2 denticles/1 mm. Cast courtesy Christopher Shaw. E: Cast of right dentary tooth, *Varanus komodoensis*. FABL = 5 mm. Serration density = 4 denticles/1 mm. Cast courtesy John Ostrom. F: Cast of Queensland Museum F10966, *Megalania prisca* dentary tooth. FABL = 11 mm. Posterior keel, toothtip to right. Serration density = 3 denticles/1 mm. Cast courtesy Ralph Molnar. G: University of Michigan Museum of Paleontology 7269, phytosaur tooth. FABL = 15 mm. Posterior keel, toothtip to left. Serration density = 3-4 denticles/1 mm. H: Yale Peabody Museum 54292, ziphodont crocodile tooth. FABL = 8 mm. Posterior keel, toothtip to right. Serration density = 6 denticles/1 mm. I-K: Small theropod teeth, Judith River Formation, Railroad Grade Cut, Dinosaur Provincial Park, Alberta. I and J: *Saurornitholestes langstoni* (cf. Currie *et al.*, 1990). FABL = 5 mm. J: Posterior keel near tip, toothtip to right. Serration density = 3-4 denticles/1 mm. K: *Troodon formosus*. FABL = 6 mm. Posterior keel, toothtip to left. Serration density = 2 denticles/1 mm. L: Cleveland-Lloyd Quarry 90.1.179, carnosaur (*Allosaurus*?) tooth. FABL indeterminate; only terminal part of tooth crown preserved. Posterior keel, toothtip to right. Serration density = 2 denticles/1 mm. M: Cast of Princeton University 21848, tyrannosaurid tooth. FABL = 23 mm. Posterior keel, toothtip to left. Serration density = 2 denticles/1 mm.
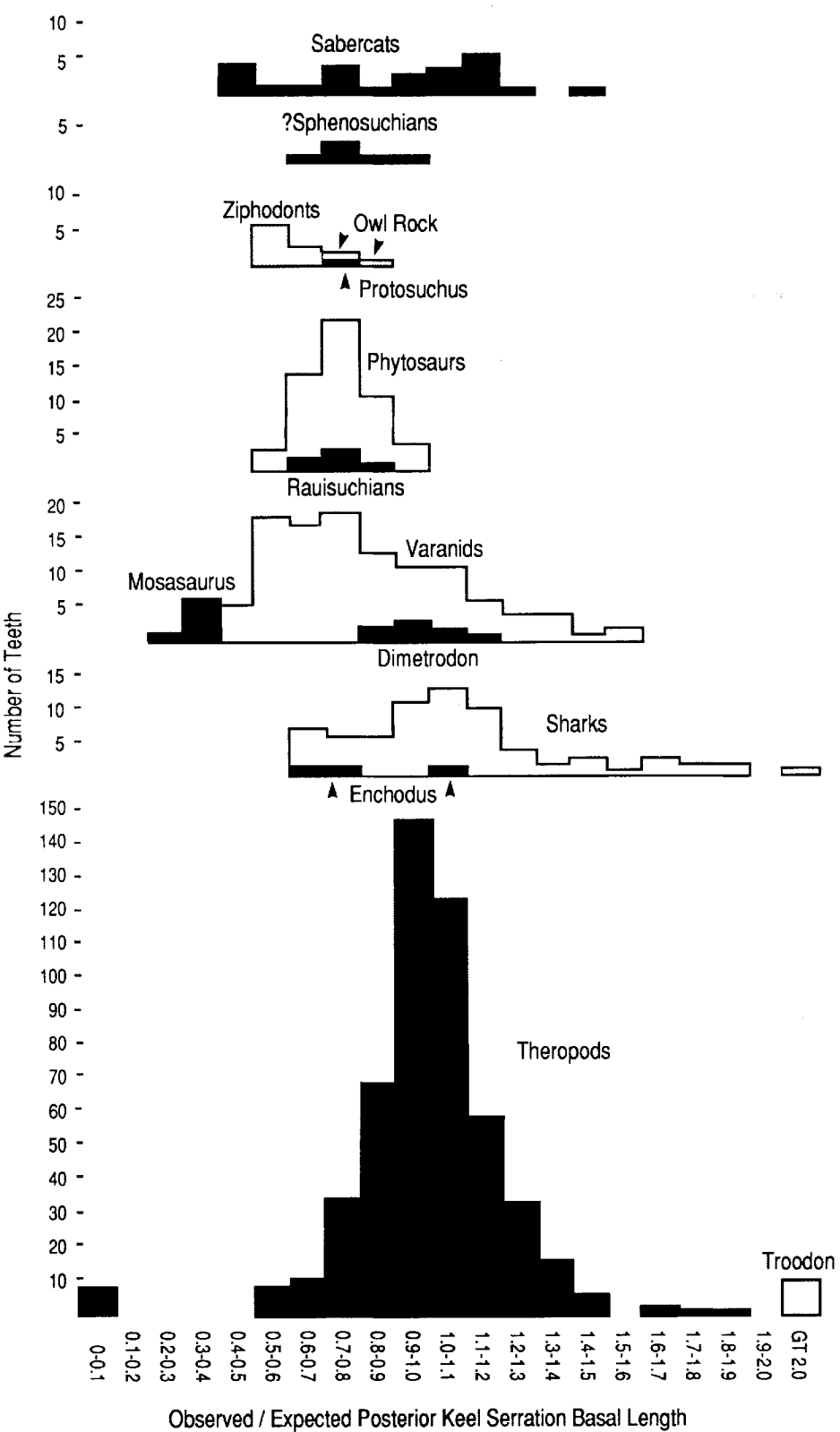
Figure 15 Comparison of basal lengths of posterior keel serrations in theropods and other predators. Serration size is expressed as the ratio of the observed serration basal length to that expected for a theropod tooth of comparable fore-aft basal length, based on the two population linear model of the relationship between tooth size and serration size in carnivorous dinosaurs. Shapes of the distributions should not be interpreted as those taxonomically unbiased samples; the vertical axis represents the number of individual teeth, and not the number of species, showing a particular range of values.

in size to the expectation for theropod teeth. Teeth of *Enchodus* appear to have serrations with basal lengths similar to those of dinosaur teeth of comparable size.

It is very interesting that none of the non-dinosaurian groups departs as markedly from the overall theropod relationship between tooth size and serration density as *Troodon* does. It is intriguing, in this context, that the shape of the denticles of *Troodon* is rather different than that typically seen in carnivorous dinosaurs (Figure 14; Currie *et al.*, 1990).

In most carnivores the serration density is similar for anterior and posterior keels of the same tooth, unlike the condition seen in some small theropods.

A thorough functional explanation of the tooth size–serration size relationship requires a theoretical explanation of what tooth serrations really do, and such an understanding is still rudimentary. Frazzetta (1988) contrasted the effects of smooth-bladed and serrated teeth in a preliminary analysis of the cutting mechanics of compliant substrates. A smooth blade drawn across a compliant surface (like animal hide or muscle) deforms the surface in a direction parallel to the direction in which the blade moves, creating shear stresses that ultimately cut a kerf across the compliant surface. This action may be enhanced by additional friction between bulges in the material of the surface and the two lower faces of the blade, by stretching of the compliant material beneath the blade edge in a direction normal to the substrate surface, and by the generation of compressive stresses in the material ahead of the blade, and tensional stresses behind it. Friction between the blade edge and the substrate depends on the normal force of the blade against the surface and the coefficient of friction. Any drawing force of the blade across the substrate greater than the friction between the blade and the surface is "wasted," because it does not enhance the cutting effect of the blade.

The presence of serrations on a blade reduces the importance of friction generated by the normal force. As the blade is pressed against a compliant surface, the surface is deformed into a reversed image of the serrated edge of the blade. When the blade is then drawn across the surface, bulges of compliant material in the spaces between the serrations are forced against the leading edges of the serrations. As long as the normal force is sufficient to hold the blade against the surface, this results in either cutting or binding of the compliant material; in the latter case, the material may tear some distance away from the serrated edge. In contrast to the action of a smooth blade, all of the drawing force of a serrated blade, up to the rupture of the material, is useful in cutting, increasing the severity of the wound produced.

We differ in our assessment of whether Frazzetta's analysis provides a useful model for discussing the functional significance of smooth-edged as opposed to serrated blades, and an alternative explanation will be presented elsewhere (Abler, in press). In any case, we suspect that the occurrence of serrations on the teeth of predatory vertebrates may reflect other factors than those considered by Frazzetta. Frazzetta notes that for a smooth blade the stress due to friction in draw cutting increases as the area of blade edge decreases; a thin smooth blade cuts more readily than a thicker blade. Given the physical properties of biological hard tissues, it may be difficult to produce a tooth that is thin enough to be as sharp as the best-honed metal knives, but at the same time strong enough to resist stresses transverse to the blade surface (i.e., parallel to tooth basal width) generated by a struggling prey animal. This could be an important consideration in multi-purpose teeth, as in our interpretation of theropod teeth. A serrated edge may allow a tooth to do a comparable amount of damage as a thinner smooth blade, but at the same time be less likely to break.

Because serration size seems to be a linear function of tooth size in theropods

(albeit possibly with different relationships for small as opposed to large teeth), the most straightforward explanation of this relationship would be that it reflects a conservative tooth developmental program. This conclusion is seemingly reinforced by the fact that TCH and BW are both linear (or nearly linear) functions of FABL. The simplest version of this hypothesis would propose that large teeth are merely enlarged, geometrically similar versions of small teeth. We would then predict that theropod teeth of different sizes should have the same total number of serrations, and that the ratio of serration size to overall tooth size should be constant across all tooth sizes.

Such is not the case. Large theropod teeth tend to have more serrations than small theropod teeth (the same is true ontogenetically for *Varanus komodoensis* (Auffenberg, 1981 : 28–29)). Individual serrations are smaller (at least in terms of their basal lengths) relative to tooth size in *Tyrannosaurus* than in *Coelophysis*. While the tooth developmental program in theropods may have been fairly conservative, it was not completely rigid.

The gross similarities in serration form (Figure 14), as well as the rough similarity of denticle sizes at particular tooth sizes, seen among many of the groups of predatory vertebrates considered in our study, suggest that there has been remarkable evolutionary convergence in the development of serrated teeth. Given the physical properties of the enamel that constitutes tooth denticles, along with the properties of the compliant soft tissues (skin, muscle, and sinew) that the serrations serve to, cut, there may be some optimal serration size for cutting such soft tissues.

Each denticle must make a comparatively small contribution to the progress of a serrated tooth as it cuts through the victim's flesh. A ripping function is divided and distributed along the length of the tooth, allowing the action of the tooth to be more like that of a slicing blade than the action of a simple ripping instrument, as would happen if the tooth had only a single denticle.

Little teeth presumably cannot have a few large denticles and still maintain this kind of slicing as opposed to ripping action. With decreasing tooth size, it becomes necessary to have increasingly smaller denticles, and this need can be readily accommodated by the tooth's developmental program. Eventually, however, some minimum denticle size is reached, at which point the action of the "serrated" tooth becomes indistinguishable from that of a smooth-bladed tooth, and the serration-making developmental mechanism shuts down.

A serrated blade has a potential disadvantage, being more likely to bind against the material in which it is embedded than a smooth blade is (Frazzetta, 1988), and this effect is more likely for coarse than fine serrations. Conceivably the relatively smaller denticle size seen in large than in small theropod teeth reflects an attempt to minimize this problem, and to maintain serrations closer to the optimal size, in increasingly larger teeth.

Our hypothesis that the size of theropod denticles represents an attempt to maintain an optimal serration density in the face of changes in overall tooth size is perhaps supported by the fact that the distribution of observed/expected serration basal lengths in our theropod tooth sample is significantly leptokurtic (by the test described by Sokal and Rohlf, 1981: 174–175) for both the anterior and posterior keel, regardless of whether we use the single population linear model or the two population linear model in determining the serration basal lengths expected for teeth of particular FABL. Unless this result is an artifact of the unknown extent to which our theropod sample departs from a taxonomically unbiased sample of flesh-eating dinosaur teeth, it suggests that there has been strong selection to maintain a fairly uniform denticle basal length for teeth of a given FABL.

Evolutionary attempts to maintain an optimal serration size in teeth of different size notwithstanding, in the very largest meat-eating dinosaurs, like *Tyrannosaurus*, binding may have become a real constraint on the cutting action of the serrated teeth, unless the great size of the carnosaur made it able to overcome any binding of its coarsely serrated teeth through brute strength—indeed, it may be misleading to think of the binding of *Tyrannosaurus'* denticles as a disadvantage. Binding or catching may have been the primary function of this reptile's large denticles, with the dinosaur's immense strength simply being part of the creature's overall meat-processing mechanism. Tooth serrations in *Tyrannosaurus* may thus have functioned less in cutting than in holding prey tissues, and causing tears in those tissues some distance away from the serrated tooth carinae themselves. Binding may have been less of a problem for the very large teeth of *Carcharodon megalodon* and the upper canines of *Smilodon* than for the teeth of *Tyrannosaurus*, given the thinner, more blade-like teeth of sharks and sabercats.

The same explanation cannot apply to the much smaller teeth of *Troodon*, but the extreme coarseness of this dinosaur's serrations for the size of its teeth suggests that *Troodon* used its lateral teeth in a manner different from that of other theropods. Although the coarseness of serrations of troodontids suggests that their teeth would have been more susceptible to binding and breakage than those of other small theropods, this may have been counteracted by the smaller size of these teeth relative to the length of the skull. *Troodon* has a relatively large number of small teeth that would not have penetrated as deeply as those of a similar-sized dromaeosaurid.

It seems reasonable to expect that such marked departures from the overall relationship between tooth size and serration size as *Troodon* shows should reflect differences in tooth operation, even if we cannot yet explain those functional differences. More subtle differences in the relative fineness or coarseness of denticles in teeth of particular size may also be worth considering for functional significance, either by themselves or in combination with other features of tooth morphology. Unfortunately, given the relative scarcity of well-preserved theropod material in dinosaur faunas, and the present difficulty of confidently assigning isolated teeth to particular theropod taxa, it is premature to say much about covarying features of theropod teeth that might have systematic or functional significance.

Our understanding of the serration size–tooth size relationship in theropods might be enhanced if we better understood the evolutionary relationships among these dinosaurs, and between dinosaurs and their presumed ornithosuchian ancestors. In particular, did the lineage that ultimately led to theropods continuously retain serrated teeth from the time that such teeth first appeared in more plesiomorphic archosaurs, or did the line of descent at some point include forms with unserrated teeth (perhaps because of small tooth size)? Our interpretation of the denticle size : tooth size relationship might be different depending on whether serrations initially evolved in relatively small or very large forms; our ideas about what the "optimal" size of tooth serrations is (if, indeed, there really is an optimal size) might depend on how the teeth were being used in the forms in which they originally appeared.

Many predator teeth lack serrations (e.g. teeth of sharks of the genus *Odontaspis* and the canine teeth of most carnivorans), and denticle development may vary between teeth of the upper and lower jaws, as in many sharks (Frazzetta, 1988) and, for that matter, some theropods (Currie, 1987). We have already described varying degrees of departure from the theropod tooth size : denticle size relationship in several groups of non-dinosaurian predators. It is clear that the development of denticles is not a function of tooth size alone. Do differences in serration size,

relative to tooth size, reflect differences in the style of attack and/or feeding in the various carnivores, or in the nature of the compliant tissues of the victims against which the teeth were used? Or are these differences simply random variation around the optimal denticle size for teeth of particular size (again, assuming that such an optimum exists)? These questions cannot yet be answered.

Among living carnivores, felids, hyaenids, and varanids have the most theropod-like teeth in terms of the relationships among tooth fore-aft basal length, basal width, and crown height, and of these only varanids have serrated teeth; in addition, varanids, unlike the carnivorans, have theropod-like teeth all along the sides of the jaws. We have seen wear surfaces on varanid teeth that are quite similar to those found on theropod teeth. Lizards like the Komodo dragon may therefore provide the closest modern analogs to the ways in which carnivorous dinosaurs used their teeth to kill and feed (cf. Burden, 1928; Abler, in press; Molnar and Farlow, 1990). Useful insights about the functional morphology of theropod teeth consequently might be obtained through further study of tooth form and wear, and diet and feeding behavior, of varanids (Loop, 1974; Rieppel, 1979; Auffenberg, 1981, 1984; Pianka, 1986; Losos and Greene, 1988), with comparative observations on theropod teeth.

Our study barely begins to consider functional aspects of tooth shape in theropods. Differences in such things as tooth size between upper and lower jaws (cf. Bakker, 1986; Currie, 1987; Paul, 1988), and in different places within a jaw ramus, the degree of tooth curvature in the antero-posterior and labial-lingual directions over the length of the tooth, changes in denticle size along the anterior and posterior keels, the relationship of denticle size to curvature of the tooth, dimensions of denticle size other than the one expressed by serration density, qualitative aspects of denticle shape, inclination of denticles relative to the tooth keel's long axis, the orientation of the anterior and posterior keels with respect to the fore-aft axis of symmetry of the tooth, denticle development in various regions of the jaws, the size and shape of incisiform premaxillary and anterior dentary teeth (not even considered in the present study), the occurrence of tooth wear, and the interaction between tooth shape and cranial kinesis (cf. Rieppel [1979] and Condon [1987] for varanids) or lack thereof, among taxa must all be considered before we will have as complete an understanding as possible of how the jaws of the great hunters worked.

Finally, our finding that the presence of serrated teeth in predatory archosaurs depends at least in part on tooth size means that caution should be exercised should one wish to use this feature in identifying holophyletic groups in these reptiles. Suppose that some archosaurian lineage began as large, big-toothed carnivores that had serrated teeth, and that these big predators gave rise to small-bodied meat-eaters with little, unserrated teeth. If the descendants of these small forms included large-bodied species that once again had big, serrated teeth, we might suppose that the genes responsible for the presence of tooth serrations had been lost in the small-bodied species, and that the presence of tooth denticles in the culminating species was a newly evolved character.

Alternatively, the gene(s) responsible for the making of tooth serrations might instead have been retained, but switched off, during the time that it was housed in small-bodied predators for whom serrated teeth would have been functionally inappropriate. This gene(s) may then have reawakened once it was again part of the DNA of animals whose size and diet made tooth serrations useful. Would the presence of tooth denticles in the final species in the lineage be considered an apomorphy, or merely a revenant plesiomorphy?

Regardless of whether or not tooth serrations disappear and subsequently reappear in this fashion, the striking similarity in denticle form in many predatory

vertebrates (Figure 14) indicates that great caution should be used in invoking the presence and shape of tooth serrations as synapomorphic characters. It is unlikely that the last common ancestor of the many animals whose teeth are shown in Figure 14 had serrated teeth; it is apparently fairly easy to evolve raptorial teeth of this kind. Unless one is willing to entertain such interesting hypotheses as considering *Carcharodon* or *Homotherium* to be the sister group of the Tyrannosauridae, tooth serrations constitute an example of a seemingly complex character that should not be used as the sole criterion for determining the node of a cladogram.

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