



DENTICLE MORPHOMETRICS AND A POSSIBLY OMNIVOROUS FEEDING HABIT FOR THE THEROPOD DINOSAUR *TROODON*

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ABSTRACT: As in many carnivorous vertebrates, the teeth of most theropod dinosaurs are characterized by serrations. Denticle size (or serration coarseness) and its inverse, serration density, scale with relation to absolute tooth size along the same allometric curve for most groups of carnivorous vertebrates. One of the few fossil groups traditionally interpreted as carnivorous that does not follow this same allometric scale is the theropod dinosaur family Troodontidae. Troodontids differ from all other theropods with the exception of therizinosauroids in that their serrations are particularly coarse; that is, their denticles are larger and correspondingly more widely spaced than expected for a plesiomorphic theropod of similar tooth size. Morphometric analysis of the teeth of herbivorous dinosaurs and lizards also show allometric scaling of serration coarseness, with plant-eaters generally having significantly larger denticles than meat-eaters for the same tooth size. The difference in the size of the denticles between herbivores and carnivores may be related to differences in the size and resistance of plant and muscle fibres. *Troodon* and therizinosauroid serration coarseness plot along the herbivorous rather than the carnivorous curve. Although alternative explanations may exist, the denticle morphometrics of *Troodon* may be a reflection of the inclusion of a significant portion of plant matter in its diet compared to that of other theropods. The enlarged brain, grasping manus, and possible stereoscopic vision of the Troodontidae have traditionally been interpreted as predatory adaptations. However, this same suite of characters is found in some herbivorous or omnivorous mammals; and, thus, may reflect a feeding habit in *Troodon* that involved the processing of a significant amount of plant matter.

INTRODUCTION

The species *Troodon formosus* LEIDY, 1856 was established on a single reptilian tooth with a distally pinched root and large serrations, collected from the Judith River Group of Montana. Originally considered lacertilian, it has had a confused systematic history, being classified as a megalosaurid (NOPSICA, 1901; HAY, 1902), a pachycephalosaurid (GILMORE, 1924), the type of L.S. Russell's redefined theropod family Troodontidae (RUSSELL, 1948), a

coelurid (ROMER, 1966), a possible hypsilophodontid (BAIRD, 1981), and correctly, as one of a group of theropod dinosaurs previously referred to as the Saurornithoididae (RUSSELL, 1969; BARSBOLD, 1974; CARPENTER, 1982; CURRIE, 1987).

Part of the confusion as to the taxonomic position of the Troodontidae lies in its characteristic tooth morphology (Fig. 1). As with most other groups of theropods, the teeth of troodontids are serrated. But unlike most theropods, the tooth morphology of

Troodon and other troodontids such as *Saurornithoides* and *Sinornithoides* is characterized by relatively large, apically hooked denticles and a constriction between the root and crown (BARSBOLD, 1974; OSMÓLSKA & BARSBOLD, 1990; RUSSELL & DONG, 1993). Grossly similar morphologies, with a constricted root and large denticles, characterize the teeth of many ornithischians (e.g., basal taxa such as *Lesothosaurus*, thyreophorans, pachycephalosaurs, and basal ornithopods) and primitive sauropodomorphs.

CHANDLER (1990) and FARLOW *et al.* (1991) have demonstrated that in most carnivorous vertebrates with serrated teeth (including theropods, pseudosuchian archosaurs, varanid and mosasaurid squamates, the synapsid *Dimetrodon*, sabretoothed felids, and predatory fish such as *Enchodus* and many sharks), serration coarseness scales with increasing tooth size along the same general trend (Fig. 2). One group traditionally considered to be carnivorous (OSMÓLSKA & BARSBOLD, 1990) that scales along a different trend is the Troodontidae.

Subsequent to these analyses, additional theropod groups have been discovered that possess troodontid-like teeth. The derived coelurosaur group Therizinosauroidea (formerly called Segnosauria) has been found to have teeth of the same general morphology as *Troodon* (RUSSELL & DONG, 1993; CLARK, PERLE & NORELL, 1994), although the crowns of therizinosauroid teeth are less recurved than those of troodontids or most other theropods. Additionally, the tooth morphology of the two most primitive known ornithomimosaurids are similar to that of troodontids in terms of overall shape and basal constriction, although the teeth of the Neocomian (Barremian) *Pelecanimimus polyodon* PÉREZ-MORENO *et al.*, 1994 lack serrations and those of the type and only specimen of the Aptian-Albian *Harpymimus okladnikovii* BARSBOLD & PERLE, 1984 are too weathered to determine precise serration

size (RUSSELL & DONG, 1993). Finally, an isolated tooth from the Upper Jurassic Morrison Formation of Utah, *Koparion douglassi* CHURE, 1994, has been referred to the Troodontidae, although the presence of troodontid-like teeth in therizinosauroids and basal ornithomimosaurids may weaken the validity of this referral.

Previous studies of vertebrate tooth serrations (CHANDLER, 1990; FARLOW *et al.* 1991; ABLER, 1992) have focused on carnivorous taxa. However, some predominantly herbivorous amniotes also possess serrated teeth. In particular, the iguanid squamates, sauropodomorph and ornithischian dinosaurs, and some primitive Tertiary mammal clades include taxa with denticulate teeth. It is the purpose of this study to examine a) the relationship between serration coarseness and tooth size in herbivorous amniotes, b) to compare this relationship between carnivores and herbivores, and c) to determine where troodontid-like teeth plot among these groups.

MATERIALS AND METHODS

In order to examine the allometric relationship between tooth size and serration coarseness in carnivorous and herbivorous vertebrates, measurements were obtained from 600 teeth. This data set included previously collected data of theropods and various non-dinosaurian carnivores (CHANDLER, 1990; FARLOW *et al.*, 1991), and new material, including sharks and extinct and extant herbivorous amniotes. Measurements taken included Maximum Tooth Width (MTW) (mm) and serration coarseness (i.e., the length in mm encompassing five consecutive serrations) measured along the central portion of the mesial or left keel and distal or right keel (Fig. 3). With small teeth, serration coarseness was extrapolated from the length (mm) of two, three, or four serrations.

In order to obtain comparative data from ornithischian and shark teeth, we had to alter somewhat the way we defined our measurements. In such cases, MTW was defined as the distance from the base of the left keel to the base of the right keel when the most convex surface of the tooth crown was oriented towards the viewer. Some shark teeth also required that we modify the manner in which we measured serration coarseness. The keels of some shark teeth have both horizontal and vertical regions connected by intervening mid-keel segments. Whenever possible, our measurements were made along the vertical or mid-keel portions of these teeth.

Measurements of larger teeth were taken with dial calipers while those of smaller specimens were measured under a microscope using an ocular micrometer. Most measurements were made on shed



Fig. 1 - Labial view of maxillary tooth of *Troodon formosus*, modified from CURRIE, RIGBY & SLOAN (1990). **Ant** - Anterior edge. **Post** - Posterior edge. Scale bar is 5 mm.

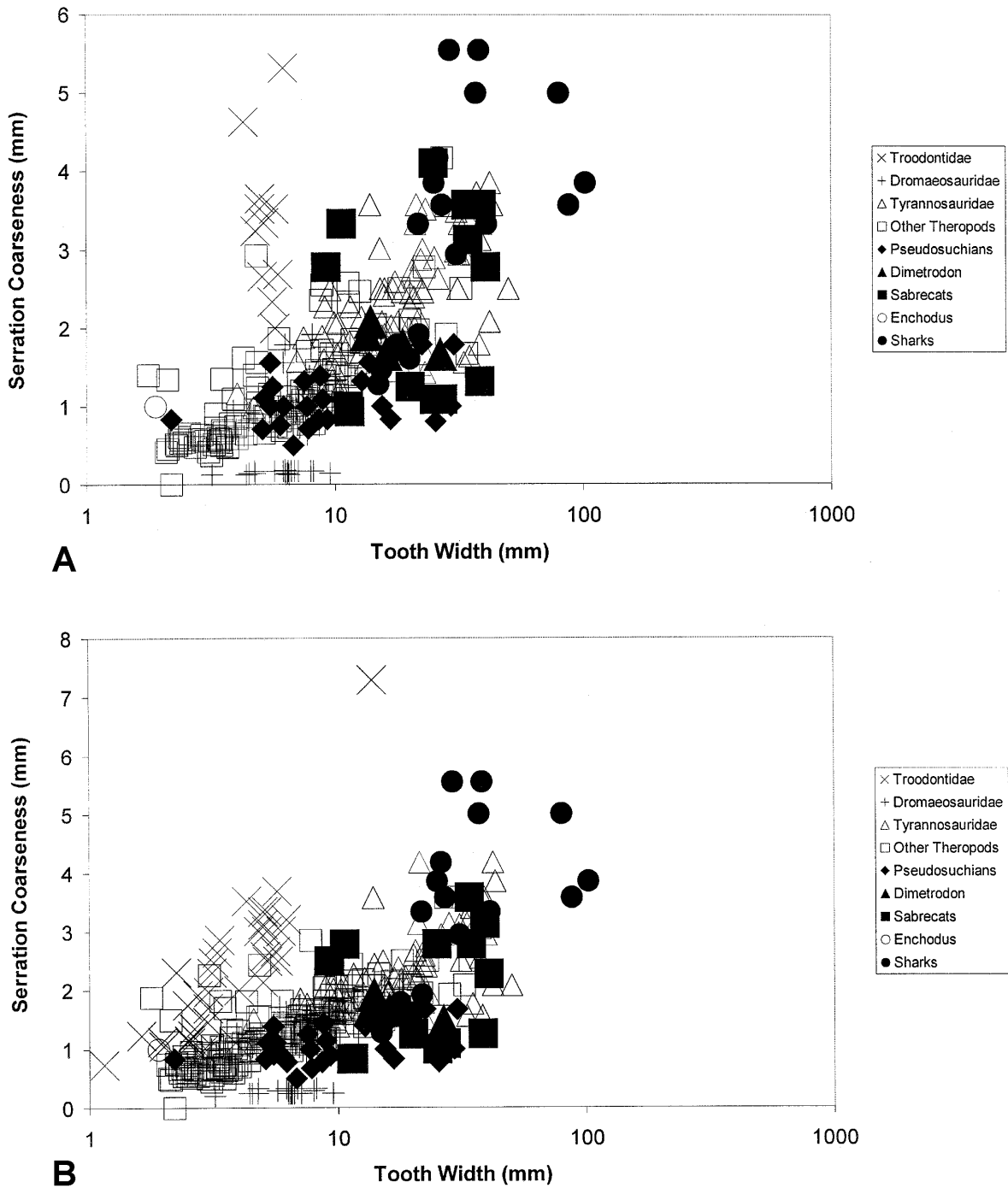


Fig. 2 - Plot of serration coarseness versus tooth width for theropod dinosaurs and other carnivorous vertebrates. **A** - Mesial or left serrations. **B** - Distal or right serrations. Note that *Troodon* plots with greater serration coarseness (i.e., larger serration size) for given tooth width than other theropods.

teeth, but some were obtained from teeth *in situ*. Other measurements were obtained from published illustrations. A representative number of measurements from FARLOW *et al.* (1991), BRINKMAN, CIFELLI & CZAPLEWSKI (1998), and CIFELLI *et al.* (in prep.) were transformed from number of serrations per 5 mm to number of mm per 5 serrations.

RESULTS

After CHANDLER (1990) and FARLOW *et al.* (1991), serration coarseness was plotted against Maximum Tooth Width (MTW) for carnivorous taxa (Fig. 2) and herbivorous taxa (Fig. 4), with troodontid teeth data included on each plot. Several general

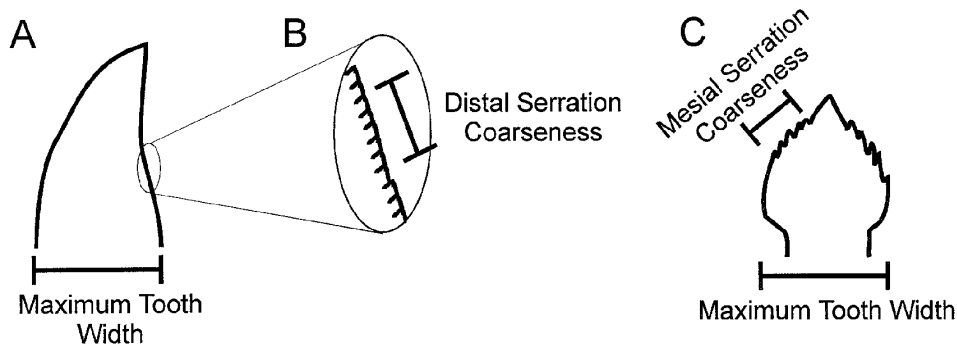


Fig. 3 - Schematic of measurements used in this paper. **A** - Generalized theropod tooth. **B** - Detail of same. **C** - Generalized herbivorous dinosaur tooth. Serration coarseness value is equivalent to the distance encompassing five consecutive serrations/denticles measured along the central portion of the carina (see text for exceptions). Maximum Tooth Width (MTW) is equivalent to the maximum fore-aft width of the tooth.

patterns can be recognized. Many groups demonstrate positive allometric trends with increasing serration coarseness for increasing tooth width. As previously determined, many carnivores (most theropods, pseudosuchian archosaurs, mosasaurid and varanid squamates, the synapsid *Dimetrodon*, sabre-toothed felids, many sharks, and the carnivorous bony fish *Enchodus*) share the same general allometric trend (Fig. 2). Iguanids, mammals, and many herbivorous dinosaur teeth similarly demonstrate positive allometry for serration coarseness but have higher serration coarseness values for a given MTW (Fig. 4). Troodontid teeth plot with serration coarseness values comparable to those of herbivorous dinosaurs of the same tooth width. Additionally, most thyreophoran dinosaurs and some other herbivorous dinosaurs have very high serration coarseness values, ten times that of other herbivores of the same tooth sizes, and thirty times that of a typical carnivore of the same tooth size. The plot of all the data together is presented as Figure 5.

These results suggest that while the allometric scaling observed is related to food habit, there is no simple dichotomy between carnivores and herbivores. In carnivores, most groups scale with proportionately small denticles. Taxa known or interpreted to be herbivorous plot among two distinct regimes: one set comprised of mammals, iguanids, and many herbivorous dinosaurs have serration coarseness values consistently larger than those of carnivores; and a second set of primarily thyreophoran dinosaurs have even larger serration coarseness values.

ABLER (1992) suggested that the serrations on theropod teeth were structures used in severing the muscle fibers of their prey. Perhaps the denticles of herbivore teeth represent structures used to sever plant fibres. If so, then the differences between herbivore and carnivore serration sizes are likely due to

the differences between plant and muscle fibre diameters or consistencies. Additionally, the greater serration coarseness of the thyreophorans may represent structures adapted to processing larger or tougher bundles of tissue fibres, although this will require additional study. Curiously, troodontids and therizinosauroids scale among the predominantly herbivorous rather than the carnivorous groups. Implications of this pattern are discussed below.

DISCUSSION

The serrations of the Troodontidae and the Therizinosauroidea are much larger than those of most theropod dinosaurs of the same tooth size but are similar in size to those of iguanid lizards and sauropodomorph and many ornithischian dinosaurs. There are several possible explanations for this pattern.

It is possible that the larger denticles in troodontids and therizinosauroids represent a reversal to some primitive dental condition in dinosaurs. Similarly proportioned serrations are found both in primitive sauropodomorphs and ornithischians, so it is possible that this tooth form was found in the common ancestor of the Saurischia and Ornithischia. This hypothesis is difficult to test, as the dentition of the immediate sister groups to the Dinosauria (ornithodirans such as *Marasuchus* and *Lagerpeton*; NOVAS, 1996) are currently unknown. However, serrated, blade-like (ziphodont) teeth of the general carnivorous trend are found in most pseudosuchian archosaurs and more primitive archosauriforms (e.g., *Euparkeria*, erythrosuchids), so it is likely that the plesiomorphic theropods, rather than troodontids, represent the basal dinosaurian tooth condition.

It is also possible that the larger denticles of troodontids represent some form of compensation for

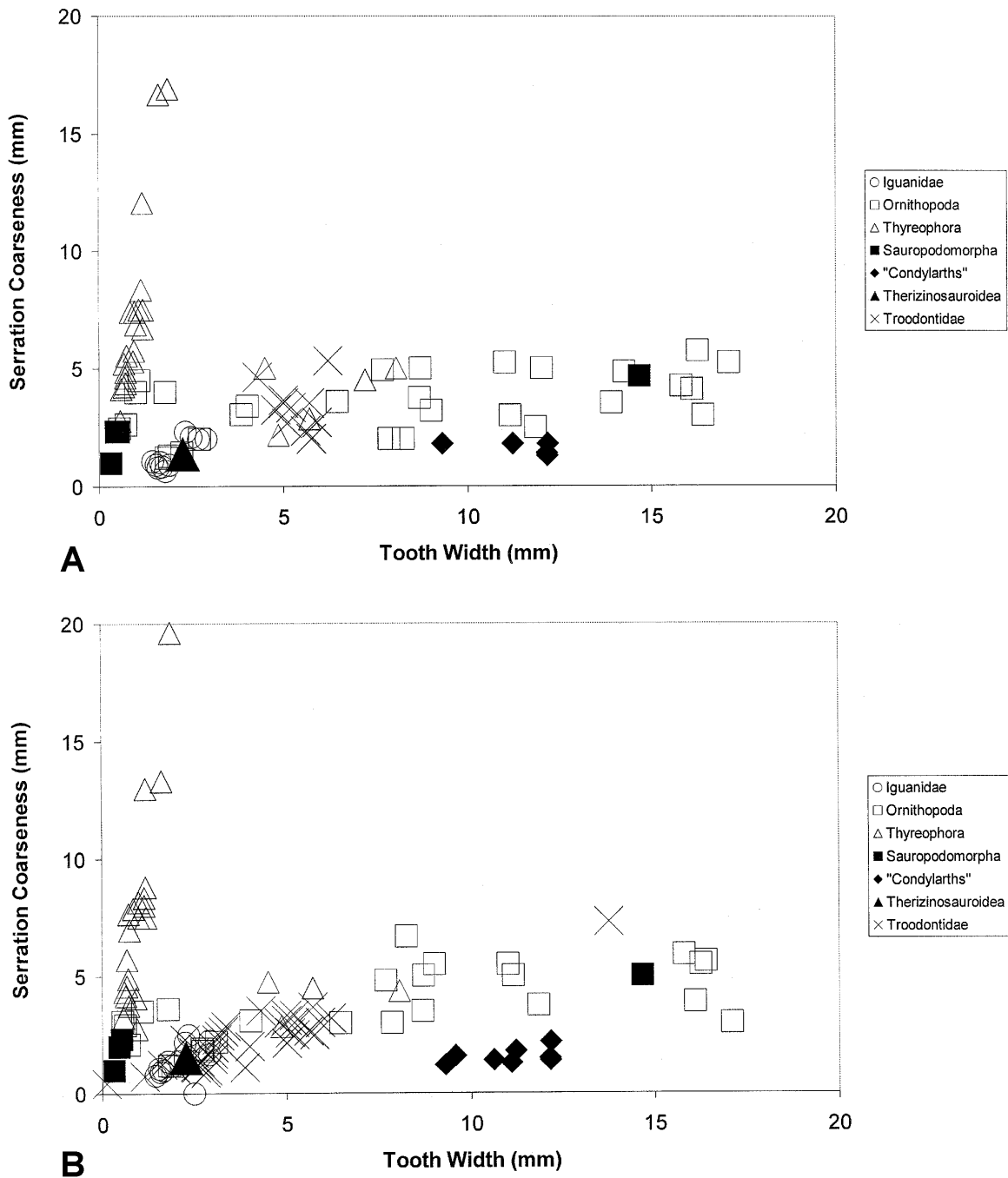


Fig. 4 - Plot of serration coarseness versus tooth width for *Troodon*, therizinosauroids, and herbivorous amniotes. **A** - Mesial or left serrations. **B** - Distal or right serrations. Note that, whereas *Troodon* teeth plotted with greater than expected coarseness for tooth width among carnivorous forms (Fig. 2), teeth of this theropod plots among herbivorous taxa in the present figure.

the generally smaller tooth size in these dinosaurs. While it is true that troodontids have among the smallest teeth in the Theropoda, plesiomorphic carnivorous theropods and varanid lizards of the same tooth size as troodontids do not scale along the herbivore trend.

FARLOW *et al.* (1991) considered that "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". Perhaps the larger size of troodontid denticles was developed to sever larger-sized and/or more resistant structures. Slicing through

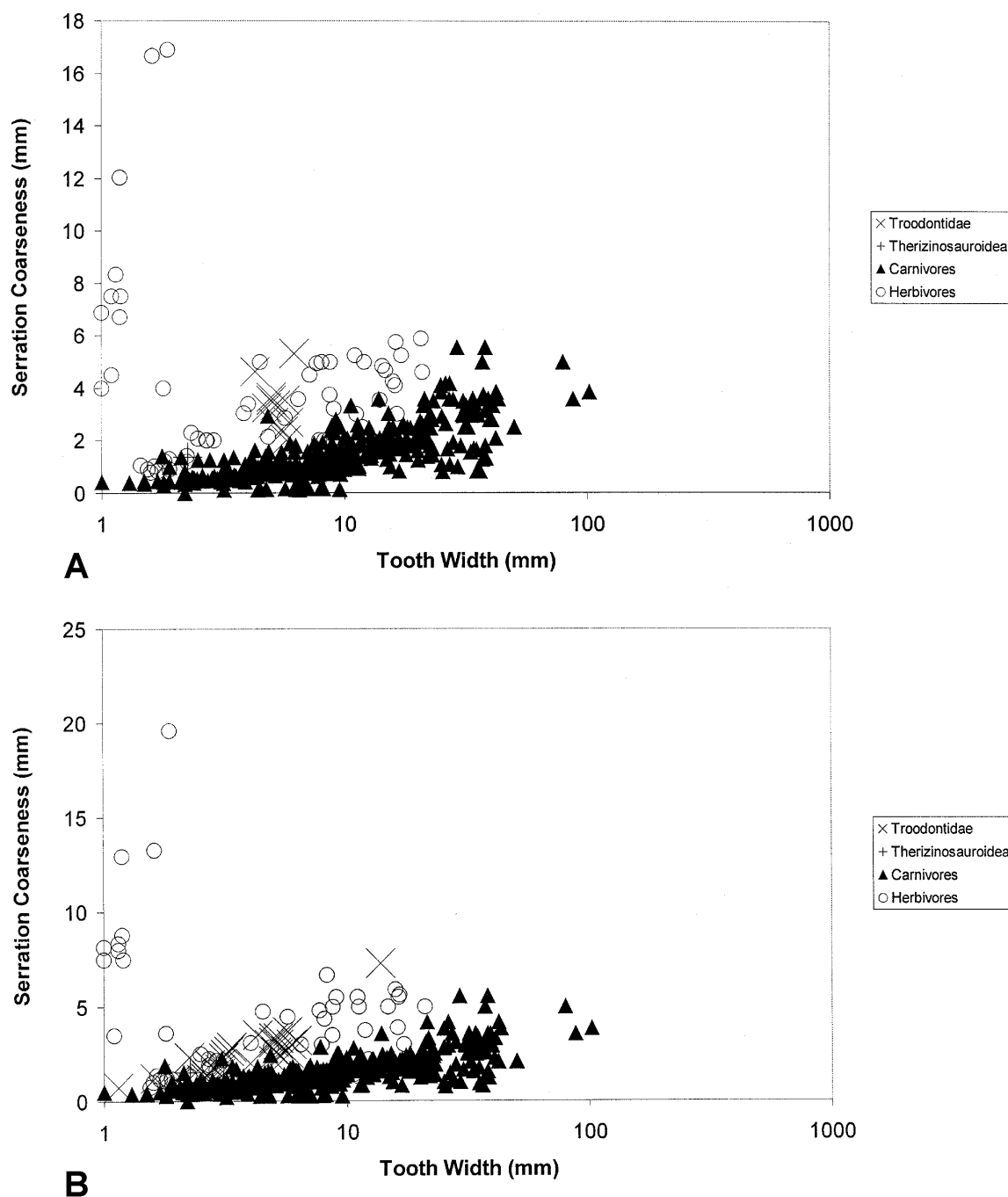


Fig. 5 - Plot of serration coarseness versus tooth width for all teeth examined. **A** - Mesial or left serrations. **B** - Distal or right serrations. Note that *Troodon* plots among herbivorous taxa (primarily sauropodomorph and ornithischian dinosaurs and iguanid lizards) rather than with the majority of known and presumed carnivorous forms.

these larger or tougher bundles of tissues would have subjected the teeth of *Troodon* to substantially greater bending stresses than those inflicted on the teeth of typical theropods. FARLOW *et al.* (1991) found the teeth of *Troodon* to have calculated bending strengths greater than those of most comparably sized theropod teeth and mammalian canines. Whatever the merit of this suggestion, the observa-

tion remains that troodontid teeth scale along the same curve as known herbivores.

Another possible manner in which *Troodon* might have used its teeth differently from other theropods, and other carnivores in general, would be the processing of food other than vertebrate muscle tissue. Potential food items other than meat include eggs

and invertebrates (in the terrestrial environment, primarily arthropods, gastropods, and annelid worms). VARRICCHIO (1997), for example, postulated a primarily insectivorous diet for troodontids.

However, given the morphometric similarities between the teeth of troodontids and those of confirmed or suspected herbivores, perhaps the very large denticles of *Troodon* represent an adaptation towards a diet containing more plant matter than in a more primitive hypercarnivorous theropod. This hypothesis is uncontroversial for therizinosauroids (PAUL, 1984; BARSBOLD & MARYANSKA, 1990; RUSSELL & DONG, 1993) and has been suggested as a possibility for ornithomimosaurids (NICHOLLS & RUSSELL, 1985; KOBAYASHI *et al.* 1999), but goes against the traditional interpretation of *Troodon* being a predatory dinosaur (RUSSELL & SÉGUIN, 1982; OSMÓLSKA & BARSBOLD, 1990). However, troodontids also have other adaptations found in omnivorous or herbivorous vertebrates. For example, the large brain, grasping hands, and possible stereoscopic vision of *Troodon* are often considered predatory adaptations, but among the Mammalia are characteristics of the predominantly herbivorous/omnivorous clade Primates and the omnivorous *Procyon* (North American raccoon).

The phylogenetic position of the Troodontidae is currently unresolved. GAUTHIER (1986), SERENO (1997), and MAKOVICKY & SUES (1998) recovered it as the sister taxon to Dromaeosauridae; similarly, some trees of HOLTZ (1998) support a position where troodontids are the sister taxon to the dromaeosaurid-bird clade. RUSSELL & DONG (1993) found troodontids as the sister taxon to the edentulous oviraptorosaurs within a larger clade also containing Therizinosauroida and Ornithomimosauria: this larger clade would thus contain all known theropods with this tooth morphology. In this scheme, troodontids are deeply nested within a clade of presumably omnivorous and/or herbivorous theropods. Alternatively, the sister group to the Troodontidae may be Ornithomimosauria (PÉREZ-MORENO *et al.*, 1994; HOLTZ, 1994, 1998), a group considered by some to have been omnivores or herbivores (NICHOLLS & RUSSELL, 1985). In this scenario Bullatosauria (=Troodontidae+Ornithomimosauria; HOLTZ, 1994, 1996) represents one of several clades of theropods that developed troodontid-like teeth in response to a diet containing a greater percentage of plants than that of typical theropods.

Five major lines of evidence argue against *Troodon* having been strictly herbivorous. Their lower jaws are similar to those of some advanced, highly predaceous theropods and squamates in having relatively loose mandibular symphyses and movable intramandibular joints. However, the probably herbivorous therizinosauroids also retain these fea-

tures (CLARK, PERLE & NORELL, 1994), which are themselves basal theropod synapomorphies (SERENO, 1997; HOLTZ, 1998). Additionally, troodontids possessed raptorial second pedal digits similar to those of the highly predaceous (CARPENTER, 1998) dromaeosaurids and the extant, omnivorous cariamids (GAUTHIER, 1986). Similarly, the curvature of the manual digits of troodontids conforms to the curvature and narrow cross-section found in the dromaeosaurids, a morphology which has been interpreted as an adaptation for prey acquisition (OSTROM, 1969). The shed teeth of troodontids are sometimes found in close association with isolated skeletal remains and eggs of various ornithopods in the Two Medicine Formation of Montana (HORNER, 1994), suggesting that the theropods may have fed on these forms. Finally, unlike therizinosauroids, the pubes are not opisthopubic, so that the abdominal cavity of *Troodon* was not enlarged relative to those of presumed hypercarnivorous theropods, as found in typical amniotes with a diet based solely or primarily on vegetation (see HOTTON, OLSON & BEERBOWER, 1997 for a discussion of general aspects of herbivory in amniotes). Such morphologic and taphonomic evidence suggests at least some predation and/or scavenging on the part of *Troodon*.

CONCLUSION

Troodontid teeth are found to have larger denticle sizes per tooth width than found in typical theropods and, in fact, scale allometrically with iguanids and many ornithischian dinosaurs. It is almost certainly this difference in serration scaling (as reflected in tooth morphology) that resulted in confusion over the systematic placement of *Troodon* earlier in this century. It is possible that the difference in serration size (or density) between *Troodon* and most other theropods reflects a different diet than in the majority of toothed Theropoda, in particular a diet with a greater contribution of plant material than in a typical "carnivorous" dinosaur.

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