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4. A New Dromaeosaurid from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada

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Abstract

The discovery of a new dromaeosaurid in the Horseshoe Canyon Formation (uppermost Campanian–lowermost Maastrichtian, Upper Cretaceous) increases the known diversity of this interesting group of theropods, considered by many as the closest non-avian theropod relatives of *Archaeopteryx* and other more derived birds. The new animal, known from a partial skull, is relatively small. It differs from the contemporary *Bambiraptor, Saurornitholestes,* and *Velociraptor* in having a short, deep face. The teeth are more strongly inclined toward the throat than they are in most other dromaeosaurids, and are all almost the same size. Phylogenetic analysis suggests that the new dromaeosaurid may represent an independent lineage having origins back in the early Cretaceous.

Introduction

Dromaeosaurids are an important group of theropods that have been strongly implicated as being the closest known relatives of birds. *Dromaeosaurus* (Matthew and Brown 1922), *Velociraptor* (Osborn 1924), and *Deinonychus* (Ostrom 1969) have formed the core of our understanding of the Dromaeosauridae. Although little material is

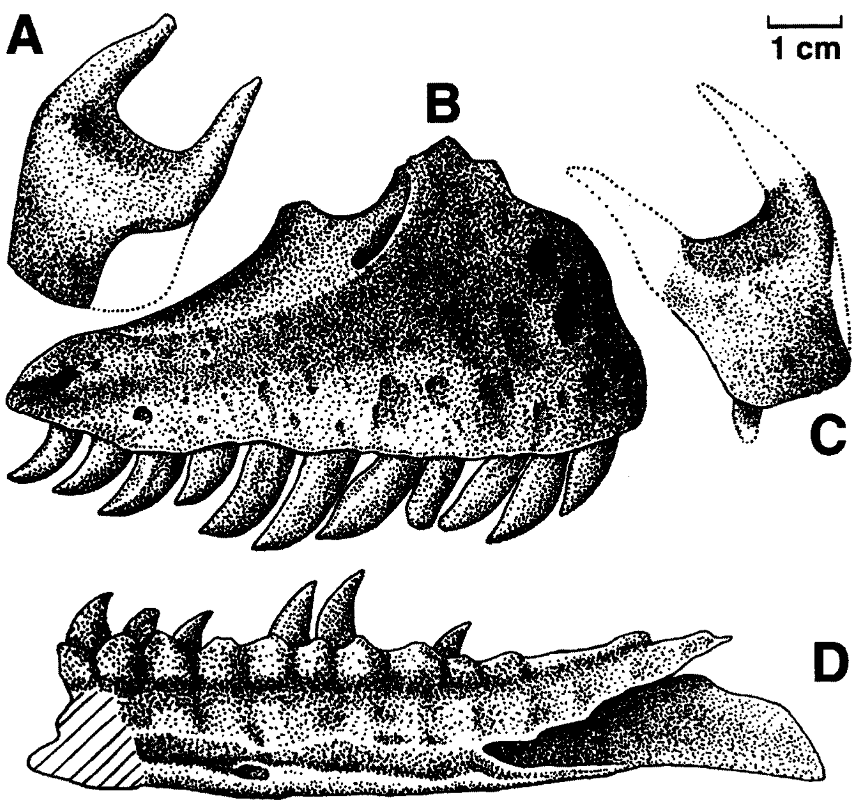

Figure 4.1. Atrociraptor marshalli *(TMP 95.166.1, holotype). A, left premaxilla, lateral view; B, right maxilla, lateral aspect; C, right premaxilla, lateral aspect; D, left dentary, medial view.*

known for *Dromaeosaurus* other than the holotype (Currie 1995), a great deal of new information is available for *Deinonychus* (Maxwell and Ostrom 1995; Brinkman et al. 1998) and *Velociraptor* (Barsbold and Osmólska 1999; Norell and Makovicky 1997, 1999; Norell et al. 1997). Two skeletons of velociraptorines have been collected by the Museum of the Rockies and the Royal Tyrrell Museum of Palaeontology (Varricchio and Currie 1991), and are being described by the authors of this paper. The known diversity of the group has been increased by the description of many new Cretaceous forms, including the giants *Utahraptor* (Kirkland et al. 1993) and *Achillobator* (Perle et al. 1999), the diminutive *Bambiraptor* (Burnham et al. 2000), and the feathered *Sinornithosaurus* (Xu et al. 1999). Other dromaeosaurid species, such as *Adasaurus* (Barsbold 1983) and *Hulsanpes perlei* (Osmólska 1982), are distinctive but incompletely known. A suspected dromaeosaur from Japan (Azuma and Currie 1995) has turned out to be a carnosaur (Azuma and Currie 2000). *Megaraptor* was also compared to dromaeosaurids because of its sickle-like claw (Novas 1998; Calvo et al. 2002), although it was always clear that it is not related.

In 1995, a partial skull of a dromaeosaurid was discovered close to the Royal Tyrrell Museum of Palaeontology in beds of the Horseshoe Canyon Formation. Fragments of jaws and teeth on the hillside led to the discovery of TMP 95.166.1 (fig. 4.1). The specimen was in a relatively hard, isolated block of sandstone capping softer, medium-grained sands. Preparation revealed the right maxilla (exposed in lateral view) and the medial surface of the right dentary. Although the

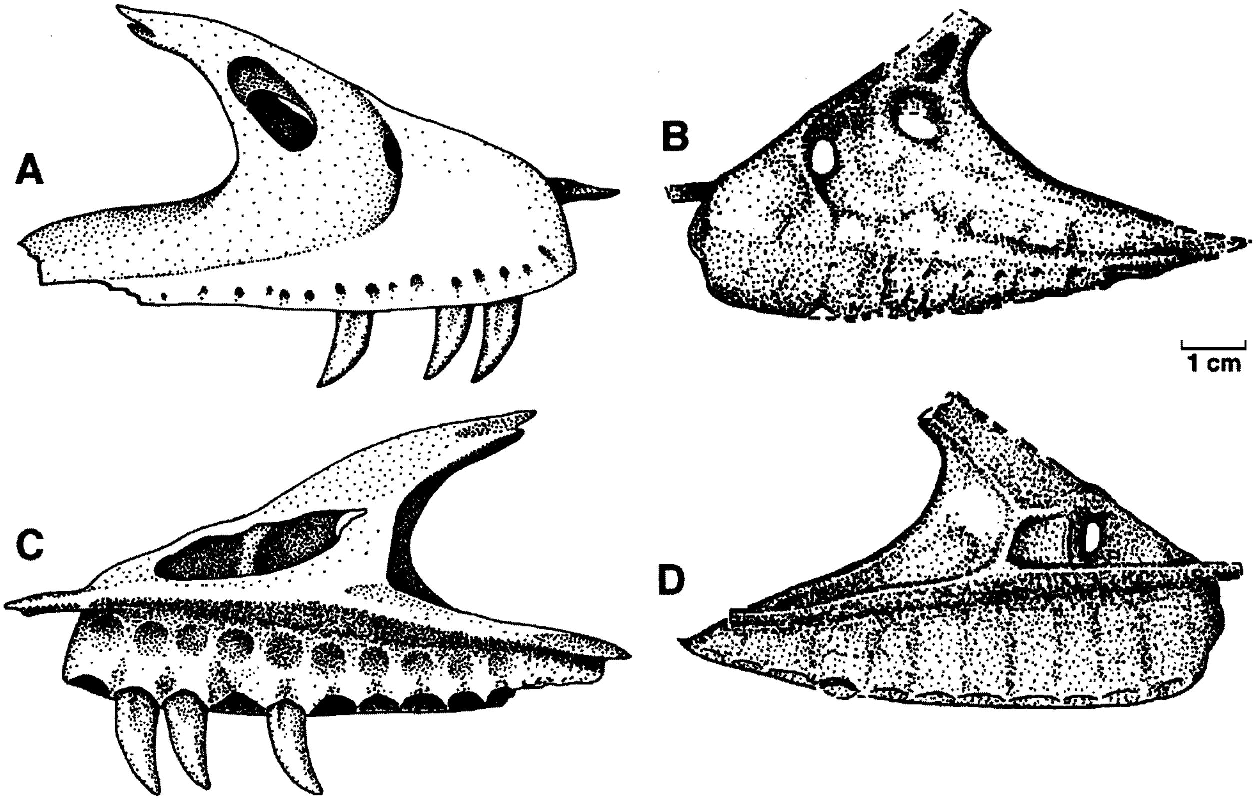

Figure 4.2. Maxillae of Saurornitholestes langstoni *(TMP 94.12.844) (A, C) and cf.* Bambiraptor feinbergi *(MOR 553S—7.30.91.274) (B, D) in lateral (A, B) and medial (C, D) views.*

teeth are clearly velociraptorine, the distinct osteology of the specimen immediately showed that it represents a new taxon.

In order to establish the identity of the new specimen, it is necessary to compare it with other dromaeosaurids known from the region. Most of the maxilla of *Dromaeosaurus albertensis* is known (Currie 1995), but this bone has not been described for *Saurornitholestes langstoni* (Sues 1978). Although the holotype of *Bambiraptor feinbergi* (Burnham et al. 2000) includes both maxillae, it represents a juvenile individual and introduces potential allometric complications into comparative analysis. Two velociraptorine maxillae recovered from Campanian beds of Alberta and Montana will therefore also be described in this paper. TMP 94.12.844 (figs. 4.2A, 4.2C) is an isolated right maxilla from the Dinosaur Park Formation (Campanian) of Dinosaur Provincial Park, Alberta. It lacks the posterior end of the jugal process, and only three of the teeth remain in position. The specimen can be identified as *Saurornitholestes langstoni,* the only known velociraptorine dromaeosaurid from the Park, on the basis of tooth denticulation, which is the same as that of the holotype. MOR 553S-7.30.91.274 (figs. 4.2B, 4.2D) is an isolated, left maxilla found in the Two Medicine Formation (Campanian) of Montana (South Quarry at Jack's Birthday Site near Cutbank, Montana). It is nearly complete, and lacks only a portion of the dorsal process for the lacrimal contact. Identification is more problematic in this case. In overall morphology, it closely matches *Bambiraptor feinbergi,* which is from the same formation 100 kilometers farther south. It is identified as cf. *Bambiraptor feinbergi* in this paper because of this similarity, and because it comes from the same formation. However, it is also morphologically similar to *Saurornitholestes,* the remains of which are found in a different but contemporaneous formation only 300 kilometers to the north.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, U.S.; CEU, College of Eastern Utah Prehistoric Museum, Price, Utah, U.S.; GIN, Institute of Geology, Ulaan Baatar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MNUFR, Mongolia National University, Ulaan Baatar, Mongolia; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; YPM, Yale Peabody Museum, New Haven, Connecticut, U.S.

Taxonomy

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
Dromaeosauridae Matthew and Brown, 1922
Velociraptorinae Barsbold, 1983
Atrociraptor marshalli, new genus, new species

Etymology: "Atroci" is a Latin word meaning savage, whereas "raptor" is Latin for robber. The species is named after Wayne Marshall of East Coulee, Alberta, who discovered the type specimen.

Holotype: TMP 95.166.1, a partial skull that includes premaxillae, the right maxilla, the right dentary, portions of the left dentary, teeth, and numerous bone fragments.

Locality and age: The holotype was recovered from strata about 5 m above the Daly Coal Seam #7 (Gibson 1977) in the Horseshoe Canyon Formation (upper Campanian or lower Maastrichtian, Upper Cretaceous) at UTM 12U 372,125 E, 5,708,055 N, which is about 5 km west of the Royal Tyrrell Museum of Palaeontology in Drumheller, Alberta.

Diagnosis: Small velociraptorine, dromaeosaurid theropod that differs from *Saurornitholestes* and *Velociraptor* in having a shorter, deeper face. Subnarial body of premaxilla is taller than its anteroposterior length as in *Deinonychus* and possibly *Dromaeosaurus.* Internarial and maxillary processes of premaxilla subparallel and oriented more dorsally than posteriorly. Larger maxillary fenestra than in any other velociraptorines. Maxillary fenestra is directly above the promaxillary fenestra, rather than well behind it as in all other dromaeosaurids. Maxillary teeth more strongly inclined toward the throat than in all other dromaeosaurids except *Bambiraptor* and *Deinonychus.* Maxillary dentition is essentially isodont.

Description of *Atrociraptor marshalli*

TMP 95.166.1 (fig. 4.1) consists of a pair of premaxillae, a right maxilla, two dentaries (only one of which is reasonably complete), and associated teeth and bone fragments from other parts of the same skull.

TABLE 4.1
Numbers of premaxillary, maxillary, and dentary tooth positions in dromaeosaurids

Species, Specimen No.*	Premax	Max	Dent
Achillobator, MNUFR 15	?	11	?
Atrociraptor, TMP 95.166.1	4	11	14†
Bambiraptor, AMNH 001	4	12	13
Bambiraptor, MOR 553S-7.30.91.274	-	12	-
Deinonychus, YPM 5232	4	15	16
Dromaeosaurus, AMNH 5356	4	9	11†
Dromaeosaurid, GIN 100/22	4	11	13
Saurornitholestes, TMP 88.121.39, TMP 94.12.844	4	12	15
Sinornithosaurus, IVPP V12811	4	11	12
Utahraptor, CEU 184v.400	4	?	?
Velociraptor, AMNH 6515	4	10	14
Velociraptor, GIN 100/25	4	11	?

*All counts taken directly from specimens.
† = estimate.

Although the premaxillae are free from matrix, the maxilla (exposed in lateral view) and the right dentary (lingual aspect exposed) have been left in the hard block of sandstone that they were found in.

There are four teeth in each relatively deep premaxilla, which is the same number in all other dromaeosaurids (table 4.1). Like *Deinonychus* (Kirkland et al. 1993), the subnarial body is taller than it is anteroposteriorly long (figs. 4.1A, 4.1C), whereas this relationship is the opposite in *Bambiraptor* (AMNH 001), *Saurornitholestes* (TMP 94.12.844), and *Velociraptor* (Barsbold and Osmólska 1999). In *Utahraptor,* the height is slightly greater than its anteroposterior length (Kirkland et al. 1993). As in other dromaeosaurids (Currie 1995; Barsbold and Osmólska 1999), there is an elongate subnarial extension that wedges between the nasal and maxilla. Because of the depth of the snout, however, the subparallel internarial and subnarial processes are oriented more dorsally than posteriorly, in contrast with other dromaeosaurids in which the reverse is true. The shallow lateral depression marking the anteroventral limit of the narial opening is nested between the bases of the internarial and subnarial processes (figs. 4.1A, 4.1C), whereas it extends more anteriorly in *Velociraptor* (Barsbold and Osmólska 1999). As in *Dromaeosaurus* (Currie 1995), there is no posteromedial maxillary process, but the anteromedial process of the maxilla contacts a smooth triangular facet on the posteromedial surface of the premaxilla.

The sizes of the right alveoli show that the second premaxillary tooth was the largest of the four as in other velociraptorines (Currie

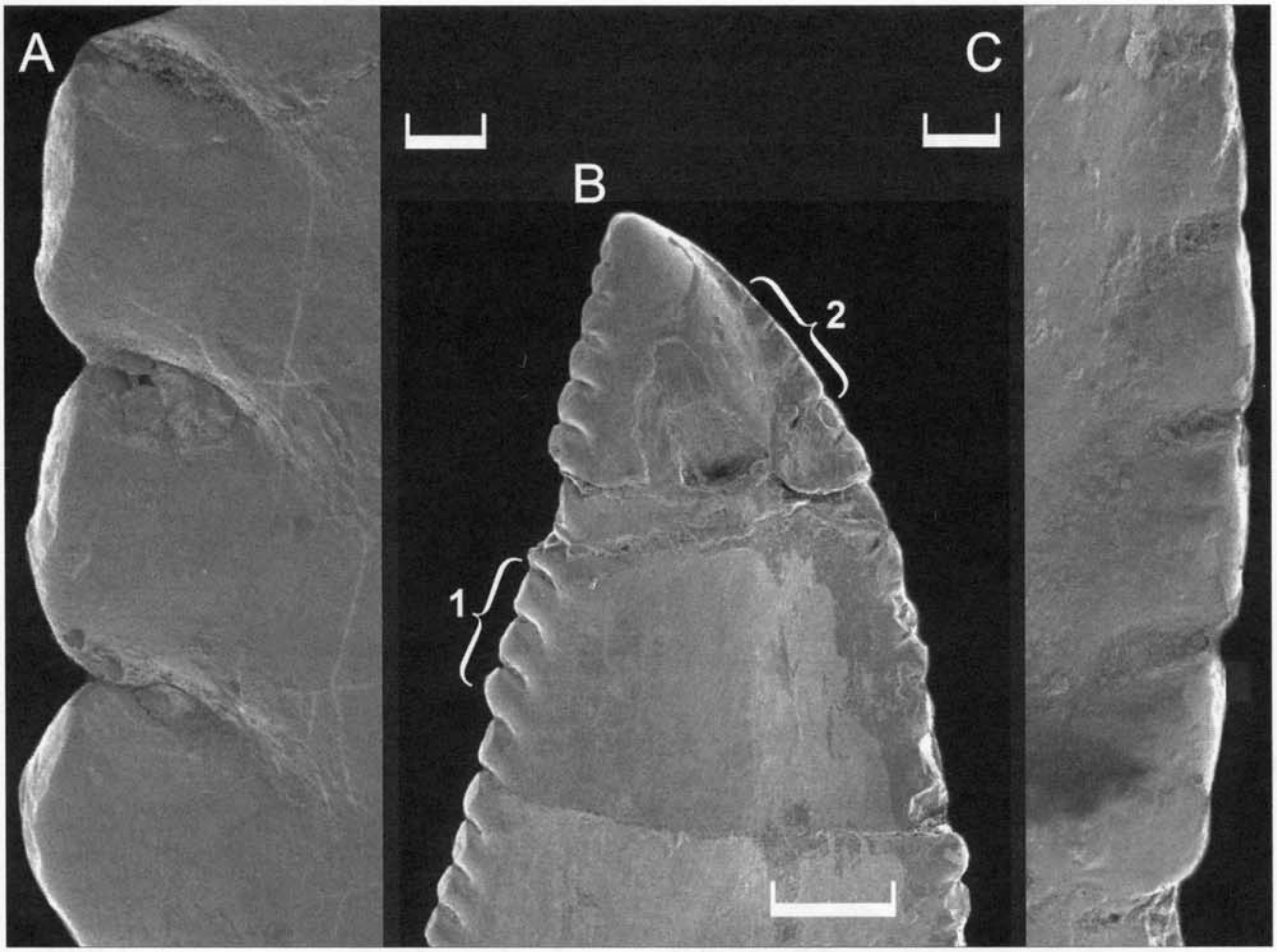

Figure 4.3. *Scanning electron microscope photographs of isolated first right premaxillary tooth of* Atrociraptor marshalli *(TMP 95.166.1). A, enlargement of the posterior denticles labeled "1" in B. C, enlargement of anterior serrations labeled "2" in B. Scale bars for A and C are 100 µm, and that for B is 1 mm.*

1995). The first premaxillary tooth of the right side is complete, as is the second premaxillary tooth of the left side. Both were found adjacent to the articulated premaxilla and maxilla, and had clearly fallen out of their sockets before burial and fossilization. In the right premaxilla, two functional premaxillary teeth remain in their sockets (second and fourth positions). The crown of the right third premaxillary tooth was broken and lost sometime after the specimen was exposed. The first alveolus of the left premaxilla still contains a germ tooth.

Like the teeth of *Saurornitholestes* (Currie et al. 1990), the anterior carina is on the posteromedial edge of the tooth, but is more anterior in position than the posterior carina. In cross section, the tooth is more J-shaped than D-shaped. The denticles on the premaxillary teeth have almost the same basal diameters on both anterior and posterior carinae (figs. 4.3, 4.4A; table 4.2), although the posterior denticles are taller. There are 2.3–3.0 denticles per millimeter (this figure is usually quoted as number of denticles per five millimeters in theropods with larger teeth, and multiplication gives a range of 11.5 to 15 denticles per five millimeters in *Atrociraptor*).

The maxilla (fig. 4.1B) is 92 mm long as preserved, but lacks part of the short, slender postalveolar process that articulates with the jugal. The maxillary tooth row is 85 mm long. The posterodorsal lacrimal-

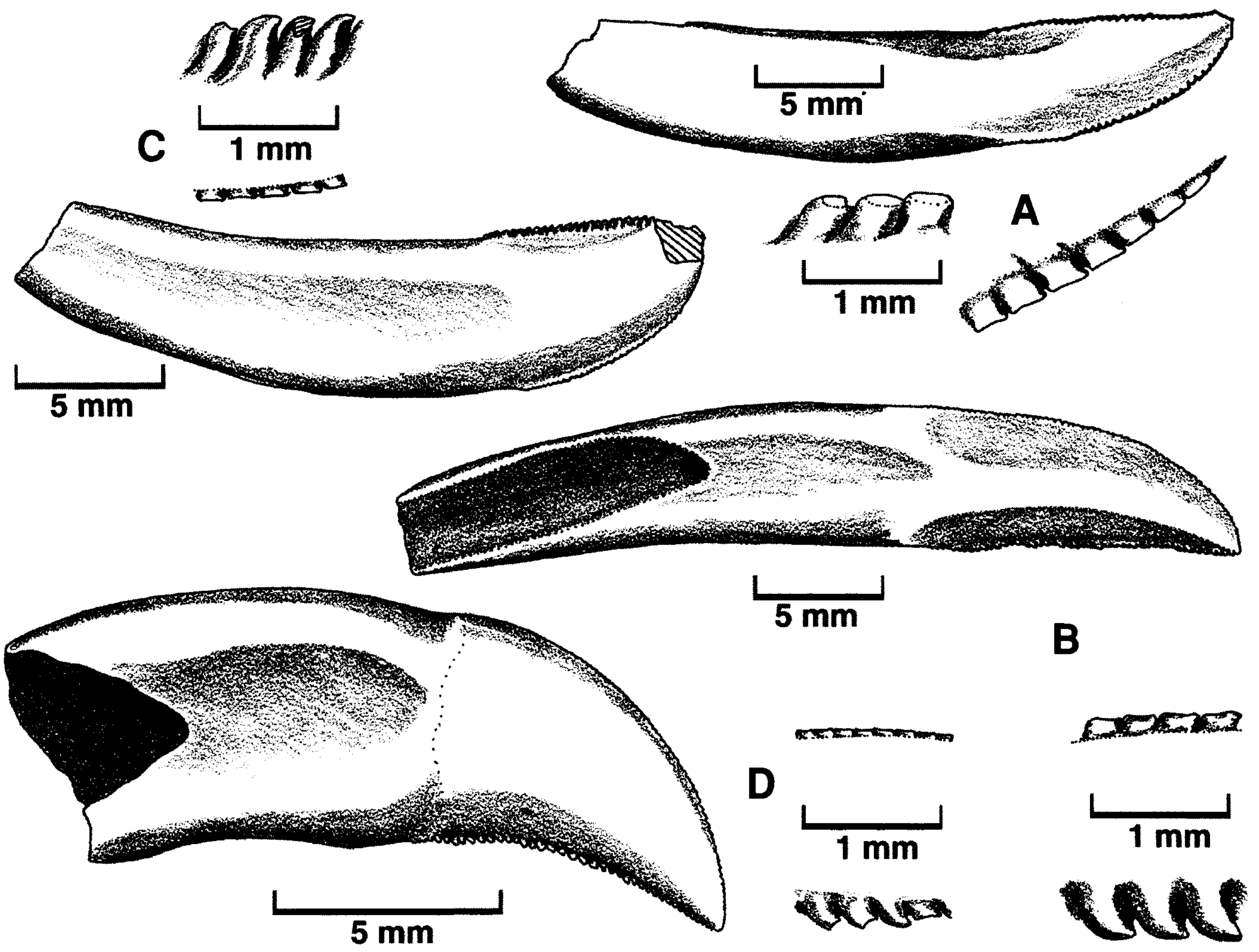

Figure 4.4. Isolated teeth of Atrociraptor marshalli *(TMP 95.166.1) with enlargements of anterior and posterior denticles. A, premaxillary tooth with enlargements of anterior and posterior denticles; B, maxillary tooth with enlargements of anterior and posterior serrations in the upper righthand corner; C, anterior dentary tooth with enlargements of posterior and anterior denticles; D, dentary tooth with anterior and posterior serrations enlarged above.*

nasal process was destroyed by erosion, and the maxilla as preserved is 45 mm high. The lower margin of a relatively large, round maxillary fenestra is evident. The promaxillary fenestra is tucked under the anterior margin of the antorbital fossa directly under the maxillary fenestra. In other velociraptorines where both features are known (fig. 4.5), the promaxillary fenestra is also at a lower level than the maxillary fenestra, but is also well anterior to it.

The roughly triangular maxilla is relatively deeper than other dromaeosaurid maxillae. The distance between the lower edge of the maxillary fenestra and the dentigerous margin is 32 mm, which when divided by the length of the maxillary tooth row gives a ratio of 0.38. The same ratio is 0.33 in *Bambiraptor* (MOR 553S-7.30.91.274) and 0.33 in *Deinonychus,* but both of these animals have relatively small maxillary fenestrae (figs. 4.5A, 4.5B, 4.5F). In other dromaeosaurids, the ratio is 0.31 in *Dromaeosaurus* (AMNH 5356), 0.28 in *Saurornitholestes* (TMP 94.12.844), and 0.19 in *Velociraptor* (GIN 100/25). Generally in dromaeosaurids, the height between the maxillary fenestra

TABLE 4.2
Teeth of *Atrociraptor* and *Saurornitholestes* (TMP 74.10.5, TMP 88.121.39)

	Tooth Position	TL	Crown	FABL	BW	ANT	POST
PM-1	L	xx	xx	4.5	xx	2.5	3
PM-2	R	xx	xx	6.5	4	xx	xx
PM-3?	L	26.5	10	5.0	3.5	2.7	2.3
PM-3	R	xx	xx	5.5	4	xx	xx
PM-4	R	xx	xx	5.5	4	4	3
Mx-1	R	xx	11.5	5.5	xx	xx	4
Mx-2	R	xx	13.5	6.3	xx	xx	4
Mx-3	R	xx	11.8	6.5	xx	xx	3.6
Mx-4	R	xx	11+	5.9	xx	xx	4
Mx-5	R	xx	13.0	6.1	xx	6	4
Mx-6	R	xx	15.3	6.6	xx	5	4
Mx-7	R	xx	11.9	5.5	xx	6	4
Mx-8	R	xx	7.8e	5.6	xx	7	4
Mx-9	R	xx	10.5	5.6	xx	5.5	4
Mx-10	R	xx	7.7	5.1	xx	xx	4.2
Mx-11	R	xx	7.0	4.4	xx	8	4.5
Mx-ant	L	32	12	5.5	3.5	3.5	3
D-1a	L	xx	xx	4.5	xx	xx	xx
D-2a	L	xx	xx	5.1	xx	xx	xx
D-3	L	xx	xx	5.2	3.0	xx	xx
D-4	L	xx	xx	4.5	2.6	5	4
D-4	R	xx	xx	4.9	xx	xx	xx
D-5	R	xx	xx	5.1	xx	xx	xx
D-6	R	xx	5.7e	3.2e	xx	6	5
D-7	R	xx	xx	xx	xx	xx	xx
D-8	R	xx	11.3	5.5	xx	5.2	4
D-9	R	xx	11.8	5.7	xx	xx	3.5
D-10	R	xx	xx	xx	xx	xx	xx
D-11	R	xx	xx	5.0	xx	xx	xx
D-ant	L	23+	7.5+	5.2	2.8	5	4
D-post	R	16	7	5.2	2.6	8	4
74.10.1	Max	xx	9.2	4.5	2.1	5	4
74.10.1	Dent	xx	8.9	3.9	xx	7	5
88.121.39	Dent	xx	9	5.1	2.3	6	4

a = anteroposterior alveolar length; ANT = lowest number of denticles per 1 mm along the anterior carina; BW = labial-lingual base width of crown; CROWN = height of the crown, measured from the tip to the proximal end of the posterior carina or to the edge of the enamel layer; e = erupting tooth; FABL = fore-aft base length, which is anteroposterior length of tooth at the base of the crown; POST = lowest number of denticles per 1 mm along the posterior carina; TL = total length of crown and root; xx, unknown; + = tip of tooth lost to wear.

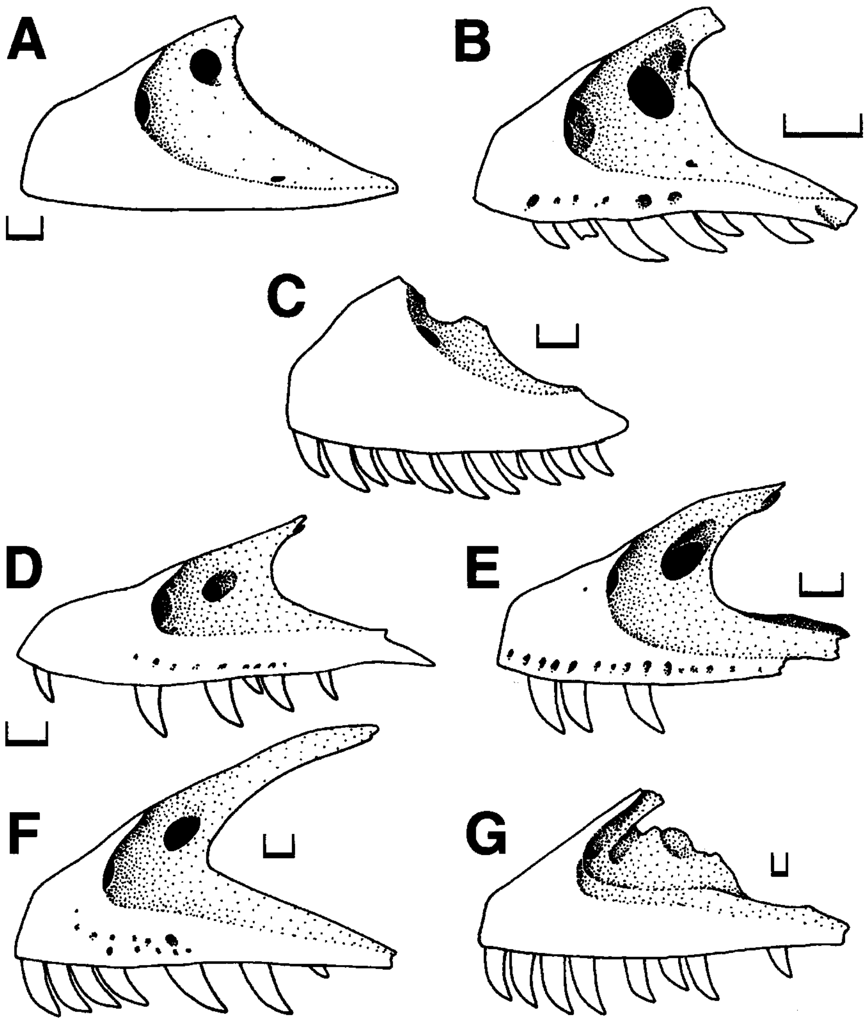

Figure 4.5. Left lateral views of dromaeosaurid maxillae:
A, cf. Bambiraptor feinbergi *(MOR 553S—7.30.91.274);*
B, Bambiraptor feinbergi *(AMNH 001);*
C, Atrociraptor marshalli *(TMP 95.166.1), reversed image of right maxilla;*
D, Velociraptor mongoliensis *(GIN 100/25);*
E, Saurornitholestes langstoni *(TMP 94.12.844), reversed image of right maxilla;*
F, Deinonychus antirrhopus *(YPM 5232);*
G, Achillobator giganticus *(MNUFR 15).*

and the dentigerous margin is less than twice (1.5 in *Bambiraptor,* 1.6 in *Deinonychus,* 1.6 in *Dromaeosaurus,* and 1.8 in *Saurornitholestes*) the height of the largest tooth, whereas in *Atrociraptor* it is more than twice (2.2) as high. If we assume that the teeth have the same relative heights in all of these animals, this would suggest that the short, deep appearance of the maxilla of *Atrociraptor* could be attributed to an increase in snout depth rather than to an abbreviation of the snout.

The anterior margin of the maxilla contacted the premaxilla in a tall butt joint that is notched at mid-height by a conspicuous subnarial foramen (fig. 4.1B). The maxilla is excluded from the narial border by the elongate, thin maxillary process of the premaxilla as in other dromaeosaurids. The margin of the antorbital fossa is restricted to the posterior 52 percent of the preserved length of the maxilla, whereas in *Velociraptor,* it occupies two-thirds of the total length (Barsbold and Osmólska 1999). Compared to most other dromaeosaurids, the antorbital fenestra was relatively small (fig. 4.7), the maxillary portion of it making up less than 43 percent of the maxillary length. The distance between the anterior margin of the antorbital fenestra and the anterior margin of the antorbital fossa is only 19 mm, which shows that the

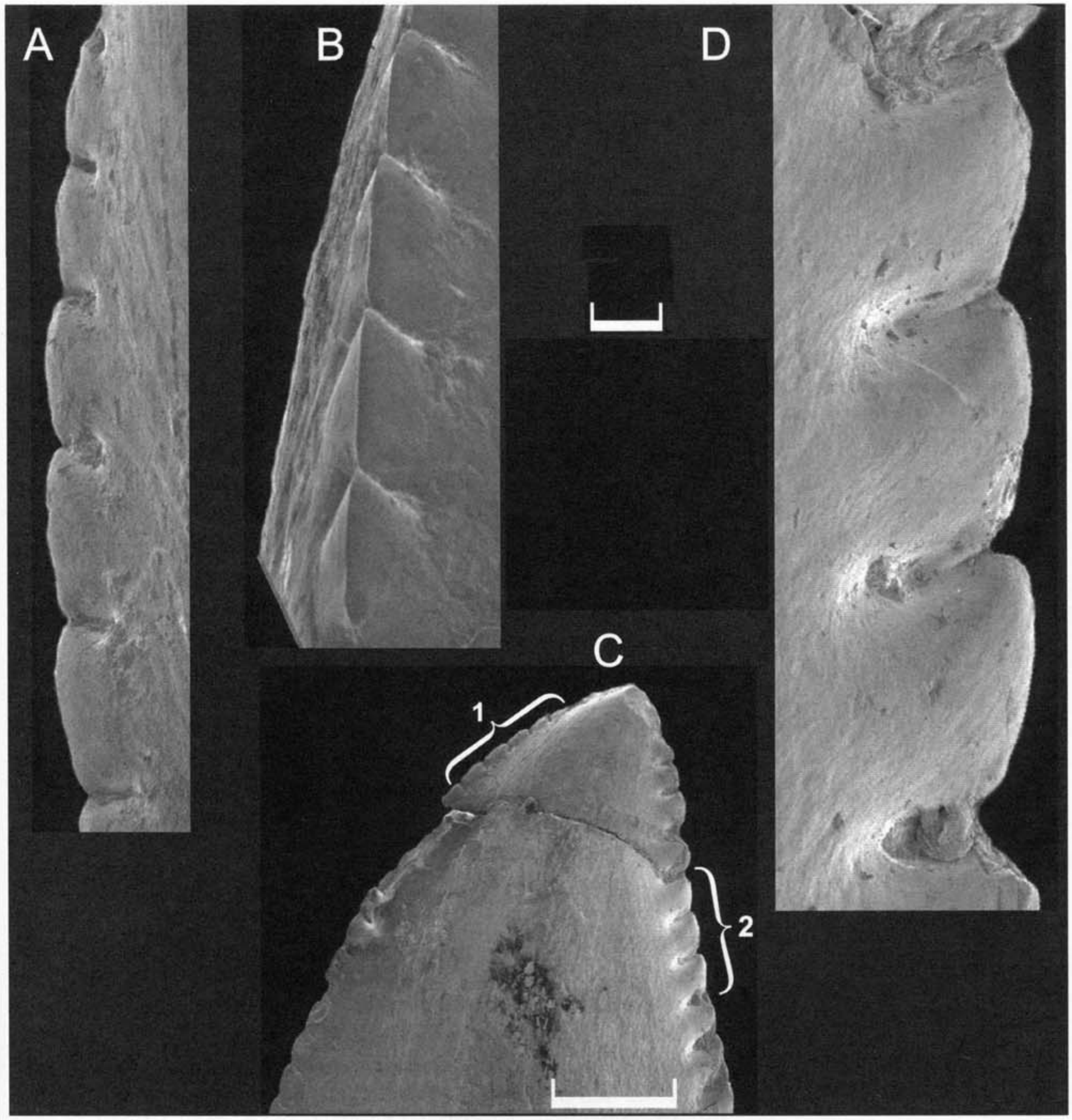

Figure 4.6. Scanning electron microscope photographs of isolated left maxillary tooth of Atrociraptor marshalli *(TMP 95.166.1). A, enlargement of the anterior denticles (5th to 9th from the tip) labeled "1" in C. B, enlargement of 7th to 10th anterior serrations from the tip of the tooth, mostly covered by region "1" in C. D, enlargement of posterior serrations labeled "2" in C. Scale bar for A, B and D is 100 µm, and that for C is 1 mm.*

fossa is also relatively smaller than other dromaeosaurids. The preserved ventral margin of the maxillary fenestra shows that this rounded opening was relatively large, with a diameter of about one centimeter.

There is a shallow posterior trough on the lateral surface at the back of the maxilla. Its anterior end is above the last maxillary tooth. Anterodorsal to this depression, the well-defined margin of the antorbital fossa slopes forward and upwards at a higher angle than in other dromaeosaurids. Most of the external surface of the maxilla is sculptured, and there is a row of neurovascular foramina just above the alveolar margin.

The ventral margin of the maxilla is strongly convex in lateral view. There are eleven closely packed teeth in their alveoli, with no gaps between the teeth. The number of tooth positions compares well with most other dromaeosaurids (table 4.1). All of the labiolingually narrow, bladelike maxillary teeth have a conspicuous posteroventral inclination (fig. 4.1B). The only dromaeosaurids that have a similar inclination are *Bambiraptor* (AMNH 001) and *Deinonýchus* (YPM 5232). Because of the inclination of the teeth, the enamel at the base of the crown is also inclined. In contrast, the edge of the enamel is almost perpendicular to the longitudinal axis of the tooth in *Saurornitholestes, Dromaeosaurus,* and other genera where the teeth have more vertical orientations.

The maxillary dentition is almost isodont with no gaps left by shed teeth, which is unusual for a dromaeosaurid (fig. 4.5). The teeth vary relatively little in overall height, whereas in the anterior part of the tooth row of *Velociraptor* every second tooth is conspicuously longer than its neighbors (Barsbold and Osmólska 1999). The maxillary teeth (figs. 4.4B, 4.6; table 4.2) all have larger denticles (3–4.5 per mm) on the posterior carinae than they do on the anterior carinae (5–8 per mm). Posterior denticles have relatively straight, elongate shafts with distally hooked tips, and are much taller than the anterior denticles (figs. 4.4b, 4.6). As in other velociraptorines, and in contrast with *Dromaeosaurus* (Currie et al. 1990), the anterior and posterior carinae lie on the midlines of maxillary teeth. The maxillary teeth are closely comparable in terms of tooth shape, carina position, denticle size, and denticle shape with those of *Bambiraptor* (Burnham et al. 2000), *Deinonychus* (Ostrom 1969), *Saurornitholestes* (Currie et al. 1990), and *Velociraptor* (Barsbold and Osmólska 1999).

The dentary of *Atrociraptor* (fig. 4.1D) is comparable with those of other dromaeosaurids. Dorsal and ventral margins are almost parallel, although the height decreases somewhat toward the back of the dentigerous region. The external surface of the fragmentary left dentary has two rows of nutritive foramina. Below the external intramandibular process for the surangular (Currie and Zhao 1993), the posterior margin of the dentary slopes posteroventrally. There is no accommodation in that margin for the external mandibular fenestra, which suggests that this opening was small and low in position as in other dromaeosaurids. As in other velociraptorines, the dentary is thin labiolingually, the Meckelian canal is shallow, the dental shelf is narrow, and the interdental plates are fused to each other and to the margin of the dentary. The dental shelf splits posterior to the last alveolus to accept the anterior end of the surangular. The medial fork extends more posteriorly than the lateral one. The posteroventral edge of the dentary was excluded from the ventral margin of the jaw by a lateral extension of the splenial, which is a feature characteristic of dromaeosaurids and troodontids (Currie 1995). In addition to the shallow Meckelian groove, there is a shallow groove along the bases of the interdental plates for the dental artery. The exact number of tooth positions is unknown. Six teeth are positioned in ten alveoli in the right dentary, and six teeth and alveoli can be seen in the fragment of the left. The left

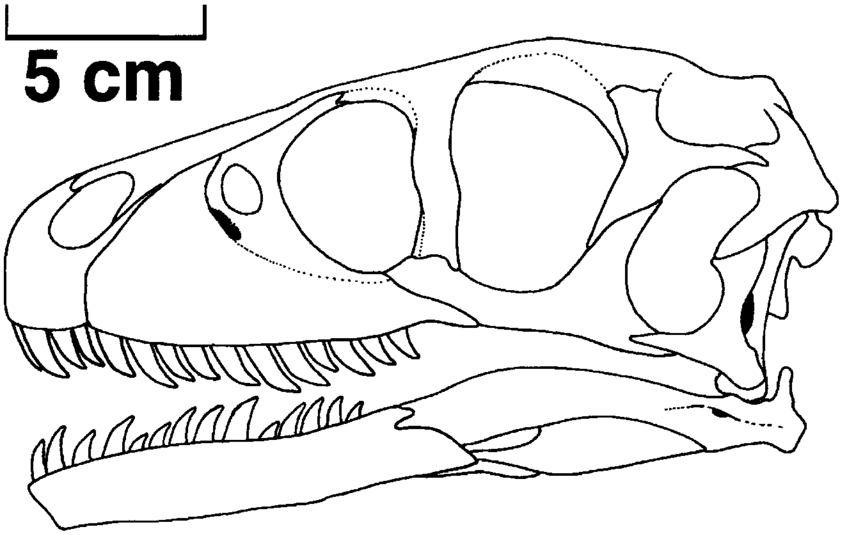

Figure 4.7. Reconstruction of the skull of Atrociraptor marshalli *with missing parts restored from* Dromaeosaurus *and* Velociraptor.

dentary fragment, which includes the symphysis, overlaps the right dentary, which lacks the anterior part. Based on the evidence from both dentaries, there would have been twelve or thirteen dentary teeth (fig. 4.7).

The dentary teeth seem to be generally smaller than the maxillary teeth (fig. 4.1), and are not as strongly inclined posteriorly. They are all labiolingually narrow, and are as bladelike as the maxillary teeth. The anterior denticles (5–8 per mm) are smaller (figs. 4.4C, 4.4D; table 4.2) and more numerous than the posterior denticles (3.5–5 per mm).

Two Isolated Velociraptorine Maxillae

The best maxilla of *Saurornitholestes langstoni* is TMP 94.12.844 (figs. 4.2A, 4.2C), which is 96.5 mm long as preserved, has a tooth row length of 82.5 mm, and has a maximum height of 47 mm. MOR 553S-7.30.91.274 (figs. 4.2B, 4.2D), identified as cf. *Bambiraptor feinbergi* in this paper, has a total length along the lateral margin of 91 mm, and the total preserved height is 46 mm. The two maxillae are similar enough to be described together, although differences will be noted.

Similar to other velociraptorine maxillae, the lateral surface above the tooth row is marked by irregular, short, and subvertical grooves terminating in ventrally opening neuro-vascular foramina. The margin that defines the anterior limit of the antorbital fenestra in each of the specimens forms a broadly open arc, much broader than in *Deinonychus* or *Velociraptor,* but apparently not as broad as in *Atrociraptor.* The margin of the antorbital fossa is well defined everywhere except above the sixth and seventh tooth sockets. Posteriorly it is at the posteroventral edge of the antorbital fenestra close to the alveolar margin, but anteriorly curves progressively more dorsally until it is vertical between the fourth and fifth alveoli in TMP 94.12.844, and between the third and fourth alveoli in MOR 553S-7.30.91.274. The fossa covers 70–75 percent of the total length of the maxilla. The distance between the front of the antorbital fenestra and the back of the maxilla is 43 mm (or 47 percent of the total length) in MOR 553S-7.30.91.274, but is only 38 percent of the total length in TMP 94.12.844. Relative to each other, the promaxillary and maxillary fenestrae are positioned much like those of *Bambiraptor, Deinonychus,* and *Velociraptor* (fig. 4.5). This region is incomplete in *Achillobator,* although the presence of two posterodorsally oriented channels suggests that the arrangement was similar. The subcircular promaxillary fenestra is tucked under the anterior margin of the antorbital fossa, and its lower edge is aligned with the bottom of the antorbital fenestra and the anteromedial process of the maxilla. The maxillary fenestra is positioned at a higher level in the base of the posterodorsal lacrimal-nasal process, slightly anterior to the margin of the antorbital fenestra. The maxillary fenestra is oval in TMP 94.12.844, and more rounded in MOR 553S-7.30.91.274. Like *Bambiraptor,* the maxillary fenestra is nested within a shallow depression, and opens anteroventrally into the more medial sinus system. In contrast, the maxillary fenestra of *Velociraptor* is relatively smaller, and is positioned well anterior to the antorbital fenestra.

The posterodorsal nasal-lacrimal process of the maxilla passes between the nasal bone and the antorbital fenestra, and bifurcates distally into dorsal and ventromedial prongs (figs. 4.2A, 4.2C) to embrace the anteroventral process of the lacrimal. The dorsal process wedges between the front of the lacrimal and the nasal, and the ventromedial fork is overlapped laterally by the lacrimal.

The ventral portion of the maxilla/premaxilla contact slopes anterodorsally and has a small triangular anterior projection that is medially concave.

On the lingual side, a medially directed horizontal ledge, roughly 10 mm wide, extends along the entire length of the maxilla. It angles slightly anterodorsally until it is 15 mm above the alveolar margin. Continuing forward from this ledge is a well-developed anteromedial process, the anterior end of which extends well anterior to the main premaxillary-maxillary contact in TMP 94.12.844 (figs. 4.2A, 4.2C), but is broken in MOR 553S-7.30.91.274. Its medial margin is grooved for contact with the vomer and the opposing maxilla. Sutures on the medial surface of the ledge show that the secondary palate extended posteriorly to at least the level of the maxillary fenestra. Dorsomedial to the last three alveoli, the inner surface of the ledge is also scarred for the palatine suture.

The sinus above the medial ledge is divided into chambers (figs. 4.2C, 4.2D) that connect with the antorbital, maxillary, and promaxillary fenestrae. A thin sheet of bone (postantral strut of Witmer 1997) extends dorsally from the medial ridge to the dorsomedial surface of the dorsoposterior nasal-lacrimal process of the maxilla. The sheet encloses a chamber (the maxillary antrum) medial to the maxillary fenestra, and ventrally forms the medial border of the passage between the sinus system and the antorbital fenestra. This sheet formed a partition that completely separated a posterior space opening into the antorbital fenestra, from the two anterior chambers and their associated fenestrae. Extending downward and then across the top of the medial ledge, a bar on the medial side of the maxilla weakly defines the anterior promaxillary recess, which connects to the promaxillary fenestra directly in front of the bar. The maxillary sinus system is basically the same as those of *Deinonychus* (Ostrom 1969), *Velociraptor* (Barsbold and Osmólska 1999), and other theropods (Witmer 1997).

As is typical of dromaeosaurids, the interdental plates are fused to the maxilla and each other in TMP 94.12.844 (fig. 4.2C) and MOR 553S-7.30.91.274 (fig. 4.2D). They can only be distinguished from the maxilla because of subtle textural differences in the surfaces, the interdental plates being more highly vascularized.

Twelve alveoli are present, although only three of the teeth remained in the sockets of TMP 94.12.844, and only the tip of the replacement tooth in the fourth alveolus was preserved in MOR 553S-7.30.91.274. In both specimens, the denticles of the anterior carina are slightly smaller in basal lengths than those of the posterior carina. The anterior carina lies wholly on the midline and shows none of the twisting of the carina onto the lingual side as in *Dromaeosaurus*.

Phylogenetic Analysis

A data matrix (Appendix 4.1) was assembled for the best-known dromaeosaurid genera, plus various outgroup taxa. The purpose of the analysis was not to determine the relationships of dromaeosaurids to other theropods or birds, but it was simply to see what could be learned about the position of *Atrociraptor* within the Dromaeosauridae. For this reason, the analysis was limited to cranial characters.

The phylogenetic analysis was performed using the beta version of PAUP 4.0 (Swofford 2001). The analysis included 42 characters, twelve of which could be coded for *Atrociraptor.* All of the characters were parsimony-informative. *Coelophysis* and *Allosaurus* were used as successively proximal outgroups, and Troodontidae were included in the analysis because of their purported relationship with dromaeosaurids. The Branch-and-Bound search method produced a single most parsimonious tree (tree length = 61, C.I. = 0.80, R.I. = 0.82, R.C. = 0.66) under an Acctran transformation. *Atrociraptor* sorted most strongly with *Deinonychus* (fig. 4.8), and secondarily with *Bambiraptor.*

Discussion

Atrociraptor can be identified as a dromaeosaurid, and distinguished from contemporary tyrannosaurids and troodontids by the collective evidence of its relatively small size, the sizes and positions of the antorbital and maxillary fenestrae, the presence of a subnarial-maxillary process on the premaxilla that extends posteriorly to wedge between the maxilla and nasal, the subparallel dorsal and ventral margins of the dentary, a labiolingually thin dentary, fusion of the interdental plates, and by its bladelike teeth. *Atrociraptor* is easily distinguishable from previously described dromaeosaurids by its short, deep snout (fig. 4.7).

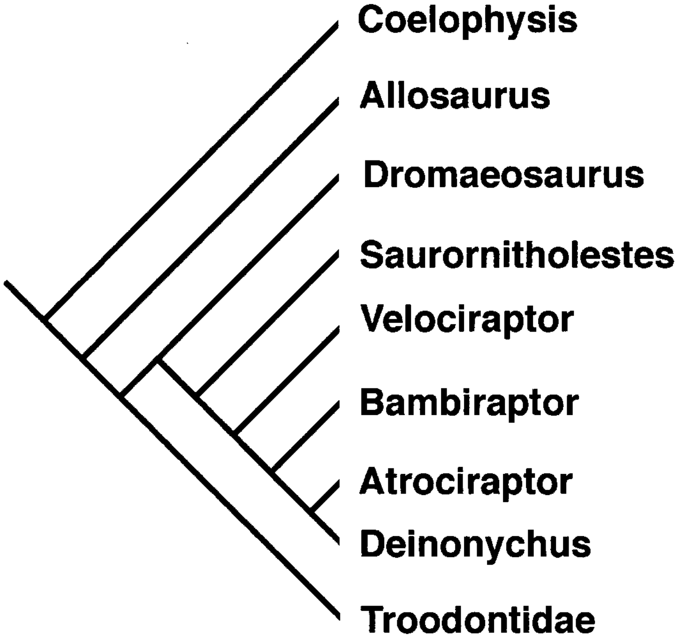

Figure 4.8. Most parsimonious tree generated in restricted analysis of phylogenetic relationships of Atrociraptor.

Atrociraptor can also be identified as a member of the Velociraptorinae because denticles on the anterior carinae are significantly smaller than posterior serrations in maxillary and most dentary teeth. Furthermore, the largest premaxillary tooth in *Atrociraptor* is in the second alveolus, as in other velociraptorines but not *Dromaeosaurus* (Currie 1995).

Atrociraptor is similar to *Deinonychus* in having maxillary teeth that are inclined sharply posteroventrally. The maxillary fenestra is relatively larger and more circular in *Atrociraptor.* The posterodorsal nasal-lacrimal process of the maxilla rises more steeply in *Atrociraptor* than it does in *Deinonychus,* but the process is relatively shorter and the anterior margin of the antorbital fenestra forms a more open curve. Whereas *Deinonychus* has 15 maxillary teeth, *Atrociraptor* has only 11.

Two other Early Cretaceous dromaeosaurids have been described, but both *Achillobator* (Perle et al. 1999) and *Utahraptor* (Kirkland et al. 1993) are fundamentally different than *Atrociraptor* because of allometric differences related to their much larger sizes.

Saurornitholestes is known from the middle Campanian beds of Dinosaur Provincial Park in southern Alberta (Sues 1978). Cranial material recovered with the type specimen includes a pair of frontals and teeth. TMP 94.12.844 can be assigned to *Saurornitholestes langstoni,* because it was found close (less than 5 kilometers) to the locality from which the holotype was recovered, comes from the same formation (Dinosaur Park Formation), and has teeth that are indistinguishable from the holotype. Other skull bones, including a premaxilla (TMP 86.36.117), frontals (Currie 1987b), several dentaries (Sues 1977; Currie 1987b), and hundreds of teeth (Currie et al. 1990), have been assigned to this genus on the basis of their recovery from the same region and formation. The subnarial body of the premaxilla of

Saurornitholestes is longer anteroposteriorly than it is high, thereby distinguishing it from *Atrociraptor.* The maxilla of *Saurornitholestes* is relatively longer and lower, the ventral rim of the antorbital fossa is almost horizontal for most of its length, the maxillary fenestra is higher in position but smaller, the alveolar margin is only shallowly convex, and the teeth are more heterodont. The dentary is similar in most respects, although the height does not increase anteriorly. The teeth are almost indistinguishable, although the enamel begins beneath the crown at almost the same level anteriorly and posteriorly. This character can be correlated with the differences in the angles that the teeth erupt from the jaws.

The diminutive holotype of *Bambiraptor* is based on an immature skeleton from Campanian strata of western Montana. Isolated bones from the same site show that larger individuals of this taxon would have been close to the same size as *Atrociraptor. Atrociraptor* can be distinguished from *Bambiraptor* (and other velociraptorines) by its deeper maxilla, by the more limited incursion of the antorbital fossa onto the maxilla anterior to the antorbital fenestra, by the sizes and relationships of the promaxillary and maxillary fenestrae, and by its isodont dentition.

An isolated maxilla from Montana MOR 553S-7.30.91.274 is morphologically similar to *Bambiraptor feinbergi* and comes from the same formation (Two Medicine Formation). For these reasons, it has been identified in this paper as cf. *Bambiraptor feinbergi.* Burnham et al. (2000) reported that *Bambiraptor* had only 10 maxillary teeth, which is significantly lower than the tooth count in MOR 553S-7.30.91.274. However, reexamination of the holotype of *Bambiraptor* (AMNH 0001) revealed that there are in fact 12 tooth positions (one tooth had broken postmortem through the posterior wall of its socket and now occupies two sockets, and two more posterior alveoli were difficult to see because of their tiny size and the fact that they were still filled with matrix). The teeth of *Bambiraptor* slope strongly backward like those of *Atrociraptor* and *Deinonychus,* whereas the bases of the maxillary teeth of *Saurornitholestes, Achillobator,* and *Velociraptor* are perpendicular to the jaw margin. Unfortunately, it is difficult to determine how strongly the teeth sloped in MOR 553S-7.30.91.274, which has lost all its functional teeth. There are other differences between *Bambiraptor* and *Saurornitholestes* in the sizes and shapes of the maxillary and promaxillary fenestrae, but these differences are not so great that they could not be accounted for by ontogenetic or individual variation. In short, it is not possible at this time to distinguish these genera on the basis of maxillae alone, and MOR 553S-7.30.91.274 could conceivably turn out to be *Saurornitholestes.* This conundrum is irrelevant to the diagnosis of *Atrociraptor* because MOR 553S-7.30.91.274 is different from the maxilla of *Atrociraptor* in the same ways that both *Saurornitholestes* and *Bambiraptor* are.

Velociraptor is closely related to *Saurornitholestes,* and the two are considered to be congeneric by some authors (Paul 1988a,b). It is not surprising then that *Velociraptor* shows the same differences as *Atrociraptor.*

Hulsanpes (Osmólska 1982) is a dromaeosaurid, but lacks cranial material and therefore cannot be compared with *Atrociraptor. Adasaurus* is known from several undescribed partial skulls and skeletons (GIN 100/20, 100/22, 100/23) from the Nemegt Formation at Büügiin Tsav (Barsbold 1983). As in *Atrociraptor,* there are 4 premaxillary, 11 maxillary, and 13 dentary teeth (GIN 100/23) in *Adasaurus*, although the teeth have anterior denticles that are the same size (20 denticles per 5 mm) as the posterior ones.

The phylogenetic analysis suggests that *Atrociraptor* is very closely related to *Deinonychus* from the early Cretaceous Cloverly Formation of Montana. The relationship may change, however, if more material is found. Perhaps most surprising about this analysis is that both taxa seem to be more derived than other dromaeosaurids, even though *Deinonychus* is one of the earliest known dromaeosaurids.

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APPENDIX 4.1
Morphological characters used in this chapter. 0 represents the primitive state.

1. Articular, vertical columnar process on retroarticular process: 0, absent; 1, present (Currie 1995).
2. Basipterygoid process: 0, moderately long; 1, very short.
3. Braincase, endocranial cavity: 0, typical size; 1, enlarged, but temporal musculature extends onto frontals.
4. Braincase, trigeminal nerve, separation of ophthalmic branch: 0, no; 1, incipient; 2, complete (Bakker et al. 1988).
5. Dentary: 0, thick when compared to height, deep Meckelian groove; 1, thin and high with shallow MG and dental shelf (Currie 1995).
6. Dentary, lateral view: 0, tapers conspicuously anteriorly; 1, upper and ventral margins sub-parallel (Currie 1995).
7. Ectopterygoid, ventral recess: 0, absent; 1, present and comma-shaped; 2, present and sub-circular.
8. Exoccipital-opisthotic, paroccipital process: 0, no pneumatization; 1, pneumatized in proximal part.
9. Exoccipital-opisthotic, paroccipital process: 0, occipital surface of distal end oriented more posteriorly than dorsally; 1, conspicuous twist in the distal end oriented more dorsally than proximal end (Currie 1995).
10. External auditory meatus: 0, does not extend beyond level of inter-

temporal bar of postorbital and squamosal; 1, ventrolateral process of squamosal and lateral extension of paroccipital process beyond head of quadrate (Currie 1995).

11. Frontal: 0, anterior margin of supratemporal fossa straight or slightly sinuous; 1, sinusoidal with deep pit (Currie 1995).
12. Frontal, anterior part: 0, relatively broad and square with obtuse or W-shaped suture with nasals; 1, triangular, distinct acute angle.
13. Frontal, lacrimal-prefrontal contacts: 0, sutures on lateral, dorsal and/or ventral surfaces; 1, dorsal and ventral sutural surfaces connected by a vertical slot (Currie 1995).
14. Frontal, supratemporal fossa: 0, limited extension onto dorsal surfaces of frontal and postorbital; 1, covers most of frontal process of the postorbital and extends anteriorly onto dorsal surface of frontal (Currie 1995).
15. Interdental plates: 0, present and separate; 1, fused together; 2, absent (Currie 1987a).
16. Jugal: 0, does not participate in margin of antorbital fenestra; 1, participates in antorbital fenestra.
17. Jugal, pneumatic: 0, no; 1, yes.
18. Lacrimal shape in lateral view: 0, L-shaped; 1, T-shaped (Currie 1995).
19. Lacrimal, dorsal ramus: 0, dorsoventrally thick; 1, pinched and narrow; 2, absent.
20. Maxilla, anterior ramus size: 0, absent; 1, shorter anteroposteriorly than dorsoventrally; 2, as long or longer anteroposteriorly.
21. Maxilla, palatal shelf: 0, narrow; 1, wide and forms part of secondary bony palate (Makovicky and Sues 1998).
22. Maxilla: 0, no maxillary fenestra; 1, maxillary fenestra occupies less than half of the depressed area between the anterior margins of the antorbital fossa and the antorbital fenestra; 2, maxillary fenestra large and takes up most of the space between the anterior margins of the antorbital fossa and fenestra.
23. Orbit, length: 0, subequal to or longer than antorbital fenestra length; 1, shorter than antorbital fenestra length.
24. Orbit, margin: 0, smooth; 1, raised rim.
25. Palatine, recesses: 0, absent; 1, present.
26. Palatine, subsidiary fenestra between pterygoid and palatine: 0, absent; 1, present (Sues 1997).
27. Parietal, dorsal surface: 0, flat with ridge bordering supratemporal fossa; 1, parietals with sagittal crest (Russell and Dong 1993).
28. Prefrontal: 0, well-exposed dorsally; 1, reduced or absent.
29. Premaxilla, palatal shelf: 0, absent; 1, broad (Sues 1997).
30. Premaxilla, subnarial depth: 0, shallow; 1, higher than long.
31. Premaxilla, subnarial-maxillary process: 0, distal end separated from maxilla by nasal; 1, distal end separates nasal and maxilla; 2, no subnarial contact between premaxilla and nasal (Currie 1995).
32. Pterygoid flange: 0, includes major contribution from pterygoid; 1, is formed mostly by ectopterygoid.
33. Quadratojugal: 0, L-shaped; 1, Y- or T-shaped (Currie 1995).
34. Quadratojugal-Squamosal (qj-sq) contact: 0, tip of dorsal ramus of quadratojugal contacts tip of lateroventral ramus of squamosal; 1, dorsal ramus of qj does not contact squamosal; 2, broad contact between dorsal ramus of qj and lateroventral ramus of sq.
35. Splenial, forms notched anterior margin of internal mandibular fenestra: 0, absent; 1, present.

36. Splenial: 0, limited or no exposure of splenial on lateral surface of mandible; 1, conspicuous triangular process on external surface of mandible between dentary and angular (Currie 1995).
37. Surangular, horizontal shelf on lateral surface anterior and ventral to the jaw articulation; 0, absent or faint; 1, prominent and lateral; 2, prominent and pendant.
38. Teeth, maxillary, mandibular: 0, anterior and posterior denticles not significantly different in size; 1, anterior denticles, when present, significantly smaller than posterior denticles (Ostrom 1969).
39. Teeth, maxillary: 0, 13 to 15; 1, 11 or 12; 2, 8 to 10; 3, 16 or more; 4, none.
40. Teeth, maxillary: 0, almost perpendicular to jaw margin; 1, teeth inclined strongly posteroventrally (new).
41. Teeth, maxillary: 0, tooth height highly variable with gaps evident for replacement; 1, almost isodont dentition with no replacement gaps and with no more than a 30% difference in height between adjacent teeth (new).
42. Teeth, premaxillary tooth #1, size compared with crowns of premaxillary teeth 2 and 3: 0, slightly smaller or same size; 1, much smaller (Currie 1995).

APPENDIX 4.2

Data matrix used for phylogenetic analysis.
0 = primitive state; 1, 2, 3 = derived character states; ? = missing data.

Allosaurus	01020 01000 00000 01001 00100 00000 20021 02000 00
Atrociraptor	????? 1???? ????1 ????1 ??1?? ???11 1???? 1?111 1?
Bambiraptor	10101 1??11 11111 10111 1101? ?1?10 1110? 11111 01
Coelophysis	00000 01000 000?0 00000 00100 00000 20010 00000 0?
Deinonychus	1???1 11?11 1??11 11111 1101? 1?111 11101 11101 01
Dromaeosaurus	11101 12111 00111 10110 1?001 1?11? 11121 11020 00
Saurornitholestes	1?1?1 12??1 11111 1???2 1101? ???10 11121 11110 01
Troodontidae	00120 02100 01002 10100 12011 111?0 ??020 10030 10
Velociraptor	1?1?1 12111 11111 11112 1101? 111?0 11101 11110 01

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