NEW INFORMATION ON THE ANATOMY AND RELATIONSHIPS OF *DROMAEOSAURUS ALBERTENSIS* (DINOSAURIA: THEROPODA)

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ABSTRACT—*Dromaeosaurus albertensis* was one of the first small theropods described that was based on reasonably good cranial material. It was realized from the beginning that this animal was significantly different from other Cretaceous theropods, and the Dromaeosauridae was created for its inclusion. In the intervening years, a number of genera were assigned to this family, which came to assume an important position in discussions on theropod relationships and evolution, and the origin of birds. It is now known that many of the dromaeosaurids are different enough from *Dromaeosaurus* to be included in a distinct subfamily known as the Velociraptorinae. In spite of intensive collecting activity, the holotype of *Dromaeosaurus albertensis* is still the most complete specimen, and it is apparent that this genus is even rarer than other small theropods. Repreparation and restudy of the holotype has produced new anatomical information useful for evaluating the relationships of dromaeosaurids. Contrary to previous reports, the premaxillary teeth are not D-shaped in section, the cranium is not pneumatic, there are interdental plates, and the braincase bones are not pneumatized. Dromaeosaurids form a distinct clade of specialized, successful theropods that are not closely related to other "coelurosaurs" of the Late Cretaceous.

INTRODUCTION

In 1914, a party from the American Museum of Natural History collected a partial skeleton of a small theropod along what is now called Little Sandhill Creek in Dinosaur Provincial Park, Alberta, Canada. Most of the skeleton, including much of the skull roof, had already been destroyed by erosion, and the locality was not marked in any way.

This specimen (AMNH 5356) became the holotype of *Dromaeosaurus albertensis* in a preliminary paper by Matthew and Brown (1922). A proper description of this important animal was not published until 47 years later (Colbert and Russell, 1969). Unfortunately, the skull had been reconstructed for display, and many details were obscured by colored plaster. Only major areas of restoration were noted by Colbert and Russell (1969). In some areas the reconstruction was done so well that it was very difficult to distinguish real bone from plaster and glue.

As one of the few Late Cretaceous small theropods with adequate material, *Dromaeosaurus* has always been important to our understanding of the interrelationships of the Theropoda, and has given its name to both a subfamily (Dromaeosaurinae Matthew and Brown, 1922) and a family (Dromaeosauridae).

In recent years there has been a dramatic increase in the number of papers published on small theropods, and many questions have arisen concerning the dromaeosaurids. Unfortunately, in spite of more intensive collecting programs in the Judith River Group of southern Alberta (Currie, 1987c) and Montana, only a handful of fossils can be referred to *Dromaeosaurus*.

These include an isolated frontal (NMC 12349, Sues, 1978), a partial dentary (Currie, 1987a) and about 30 isolated teeth (Currie et al., 1990). An isolated fourth metatarsal (NMC 12072, Colbert and Russell, 1969), an isolated ungual (NMC 12240, Colbert and Russell, 1969) and several isolated dentaries (UA 12091, UA 12339, Sues, 1977a) were referred incorrectly to *Dromaeosaurus,* and are now known (Currie, 1987b; Paul, 1988a) to be from a more common dromaeosaurid known as *Saurornitholestes langstoni* (Sues, 1978).

Sometime after 1969, AMNH 5356 was damaged, and the largely reconstructed skull roof was separated from the rest of the skull. The parietal fragment is no longer with the rest of the specimen, and its present whereabouts is unknown. However, the damage also exposed features that were not visible for the Colbert and Russell study. The specimen was reprepared, and most of the plaster and remaining sedimentary matrix were removed. CT scans of the braincase proved useful in distinguishing plaster from bone, and in showing internal details of the braincase.

This paper is intended to supplement the anatomical descriptions of Colbert and Russell (1969). As such, the descriptions include only details that were not previously noted, as well as derived characters that are useful for determining the taxonomic status of *Dromaeosaurus.*

There are many errors in the reconstruction of the skull presented by Colbert and Russell (1969), although it continues to be reproduced in other publications (i.e., Ostrom, 1990). Paul (1988b) published a much improved reconstruction, which differs from the present version (Fig. 1) only in minor anatomical details re-

vealed by the present study, and in interpretation of some of the regions not preserved.

Abbreviations — AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; CMN, Canadian Museum of Nature, Ottawa; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MOR, Museum of the Rockies, Bozeman; PIM, Paleontological Institute of Mongolia, Mongolian Academy of Sciences, Ulan Bator; PIN, Paleontological Institute, Moscow; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller; UA, University of Alberta, Edmonton.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
DROMAEOSAURIDAE Matthew and Brown, 1922

DROMAEOSAURUS Matthew and Brown, 1922

Type Species — *Dromaeosaurus albertensis* Matthew and Brown, 1922.

Diagnosis — Fewer maxillary teeth (9) than in any other dromaeosaurid. Anterior carina of maxillary or mandibular tooth close to midline of tooth near the tip, but not far from the tip twists towards the lingual surface. This characteristic twist is not presently known in any other theropod.

Dromaeosaurus differs from velociraptorines in the following features: premaxilla is deeper and thicker; quadratojugal is stouter; top of frontal flatter and margin of supratemporal fossa not as pronounced; postorbital process of frontal more sharply demarcated from the dorsomedial orbital margin; posteromedial process of palatine more slender; anterior and posterior tooth denticles subequal in size.

Type Specimen — AMNH 5356.

Distribution — Campanian, early Maastrichtian, Alberta, Canada.

Description — AMNH 5356 is most of a skull with lower jaws, hyoids, a left first metacarpal, and associated foot bones (Colbert and Russell, 1969). The skull is characterized by a narrow snout, indicated by the shape of the premaxilla, the width of the premaxillary process of the maxilla, the narrowness of the palatine and the palatal process of the pterygoid, the orientation of the jaw symphysis, and the lateromedial curvature of the mandibles. The skull broadens at the nasal-frontal suture, and across the postorbitals, suggesting that *Dromaeosaurus* may have had binocular vision. In lateral aspect, the temporal region is lower than the frontals, and the anteroventrally sloping quadrate pushes the jaw articulation to a level below the jaw margin.

Only the back of the left premaxilla, with two teeth, was preserved (Fig. 2A, B). Differences in the carina of each premaxillary tooth can be used to show that the loose teeth found with the specimen represent no fewer than two more premaxillary tooth positions. The premaxilla probably held four teeth as in velociraptorines and most other theropods. The main body of

the premaxilla is relatively deeper than it is in velociraptorines, and the bone is thicker. The subnarial process is broken, but the base of it is large (9 × 4 mm), oriented posterodorsally, and it would have extended posteriorly to contact the nasal as in *Deinonychus* (Ostrom, 1969), *Utahraptor* (Kirkland et al., 1993), and *Velociraptor* (PIM 100/25). A shallow groove on the lateral surface of the premaxilla (Fig. 2A) passes forward from the subnarial foramen, which opens medially below the anteromedial process of the maxilla. The subnarial foramen is less prominent than it is in *Velociraptor* (PIM 100/25), but more prominent than in *Deinonychus* (YPM 5232) and *Utahraptor* (Kirkland et al., 1993). Because *Dromaeosaurus* is intermediate in size (skull length of 24 cm, compared with 17 cm in the holotype of *Velociraptor mongoliensis* and 32 cm in the Yale Peabody Museum's reconstructed *Deinonychus*), it is likely that this is a size-dependent character. On the medial surface is a distinct suture for the anteromedial process of the maxilla. In contrast with *Allosaurus*, "*Megalosaurus*" *hesperis* (BMNH R332), and other large theropods (Currie and Zhao, 1993a), the premaxilla does not have a medial maxillary process inserting into the anteromedial process of the maxilla. The premaxillary teeth are not D-shaped in cross section (Currie et al., 1990), a characteristic found only in tyrannosaurids. Unlike the premaxillary teeth of tyrannosaurids, those of dromaeosaurids are about the same size as the largest maxillary teeth. The second premaxillary tooth of velociraptorines is the largest in length and diameter (YPM 5232, PIM 100/25), whereas in *Dromaeosaurus* all of the premaxillary teeth are about the same size and basal diameter. The second is the largest of the premaxillary teeth in *Utahraptor* (Kirkland et al., 1993).

There are nine alveoli in the left maxilla (Fig. 2C, D), compared with 15 in *Deinonychus* (Ostrom, 1969), 10 in *Velociraptor* (AMNH 6515) and at least 10 in *Saurornitholestes* (Currie et al, 1990). There is a pronounced anteromedial process (Fig. 2D) on the medial surface of the maxilla, which extends anteriorly beyond the vertical premaxillary-maxillary suture. The lateral surface of this process contacts a triangular sutural surface (Fig. 2B) on the medial side of the premaxilla. The longitudinally striated medial surface of the lamina contacted the opposite maxilla and the vomer as in other theropods where this process is well preserved (Currie and Zhao, 1993a). The longitudinal axes of the teeth are inclined posteroventrally as in velociraptorines (Ostrom, 1969; PIM 100/25).

In contrast with previous reports (Colbert and Russell, 1969; Ostrom, 1990), there are interdental plates (Currie, 1987a), although their presence is obscured by fusion (Fig. 2D, G). They are easier to see in the dentary than they are the premaxilla and maxilla. Microscopic examination of the lingual surface of the dentaries of AMNH 5356 confirms their presence. They can be distinguished from the medial walls by their coarser, pitted texture, which is continuous with the interdental bone that separates the teeth. The best indication of
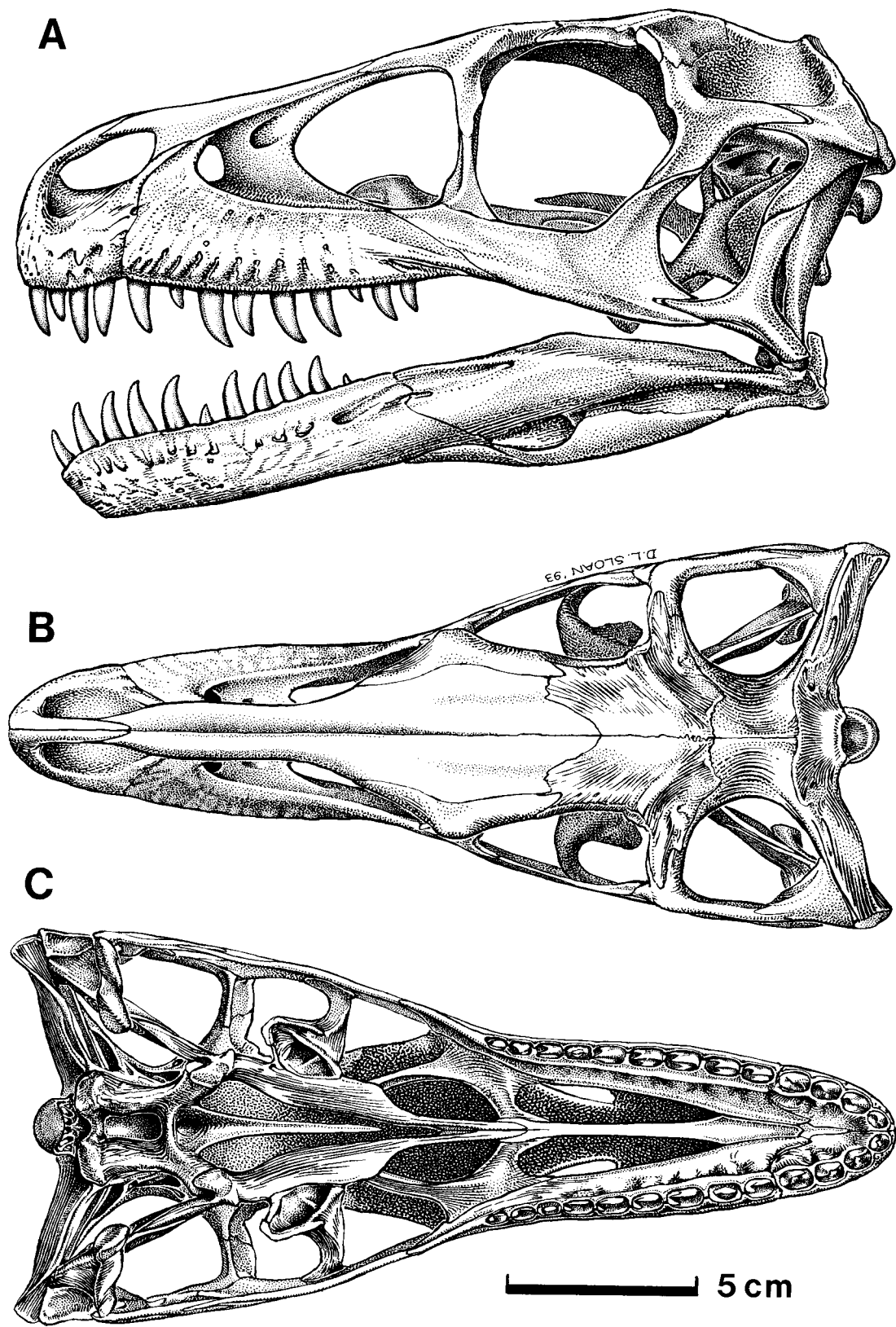
FIGURE 1. Reconstruction of the skull of *Dromaeosaurus albertensis,* based on AMNH 5356, in lateral (**A**), dorsal (**B**), and palatal (**C**) aspects. **D, E, F,** outlines of skull in same views showing areas reconstructed (stippled).

their presence is the fact that the labial and lingual margins of the tooth sockets in the premaxilla, maxilla and dentary are nearly equal in height. In the vast majority of tetrapods, the labial jaw margin is significantly higher than the lingual. Interdental plates developed as a continuation of the interdental bone between individual tooth sockets to provide more support on the lingual side of the teeth. The plates are highest between the sockets, and decrease in height anteriorly and posteriorly. Individual plates meet close to the anteroposterior midpoint of a socket. In most theropods, interdental plates do not fuse together, but they can and do fuse in some genera (including *Allosaurus*, pers. obs.). Even when they fuse, however, there is a space visible at the intersection of two plates and the margin of the dentary, through which passed a branch of the dental artery. These pits have been reduced to foramina in dromaeosaurids. Interdental plates are inset from the real jaw margin, and the dental artery runs longitudinally in a groove along the dorsal surface of this shelf. The dental shelf is not as conspicuous in dromaeosaurids because of the reduced width of the tooth bearing bones, but there is a groove marking the position of the dental artery, and confirming the presence of interdental plates.

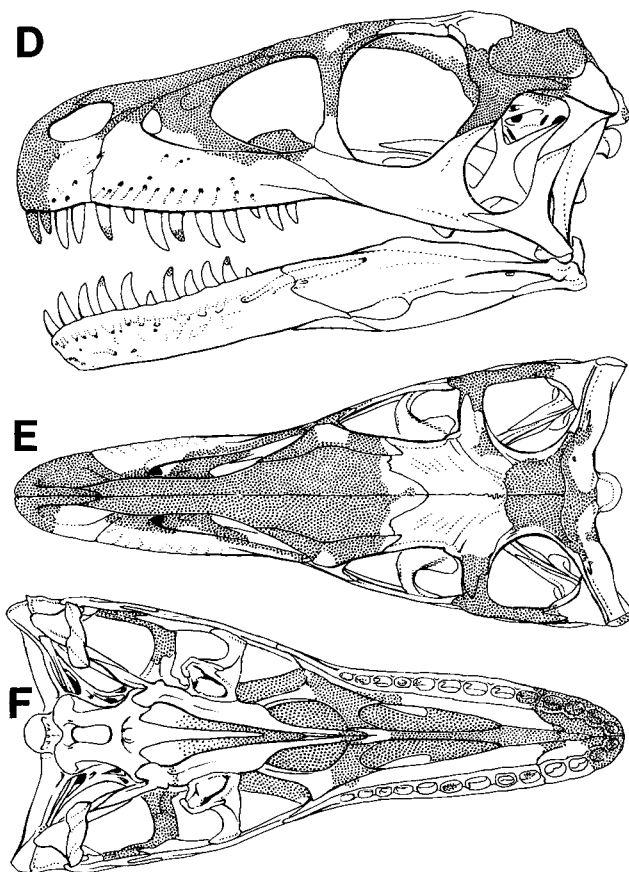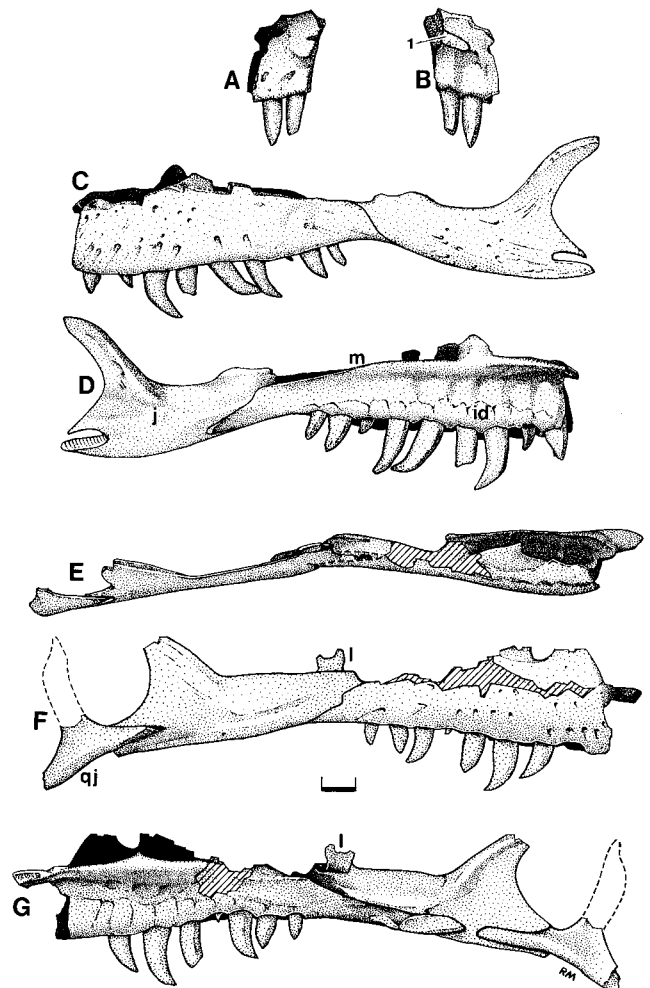Unfortunately, the nasal is not known for *Dro-*

FIGURE 2. *Dromaeosaurus albertensis,* AMNH 5356. Left premaxillary fragment in lateral (A) and medial (B) views; left maxilla and jugal in lateral (C) and medial (D) aspects; right maxilla, jugal and quadratojugal in dorsal (E), lateral (F) and medial (G) views. **amp**, anteromedial process of maxilla; **id**, interdental plate; **j**, jugal; **l**, lacrimal; **m**, maxilla; **qj**, quadratojugal; **1**, sutural surface for anteromedial process of maxilla. Scale = 1 cm.

FIGURE 1. Continued.

maeosaurus. However, given the other similarities with velociraptorines, it is highly likely that the nasal is narrow, and has a sharp demarcation between dorsal and lateral surfaces.

The lacrimal is represented by a fragment (Fig. 2F, G) attached to the right jugal, and by fragments of the dorsolateral protrusion (Fig. 3G, J, K). As in other dromaeosaurids, it was a slender bone that did not contact the maxilla ventrally. The ventral end sat in a shallow groove on the anterodorsal surface of the jugal, the lateral wall of the groove rising higher than the medial. The lacrimal-jugal suture is similar in *Deinonychus* (Ostrom, 1969), although the medial wall of the groove seems to be higher in this genus. Two other fragments are attributed by Colbert and Russell (1969)
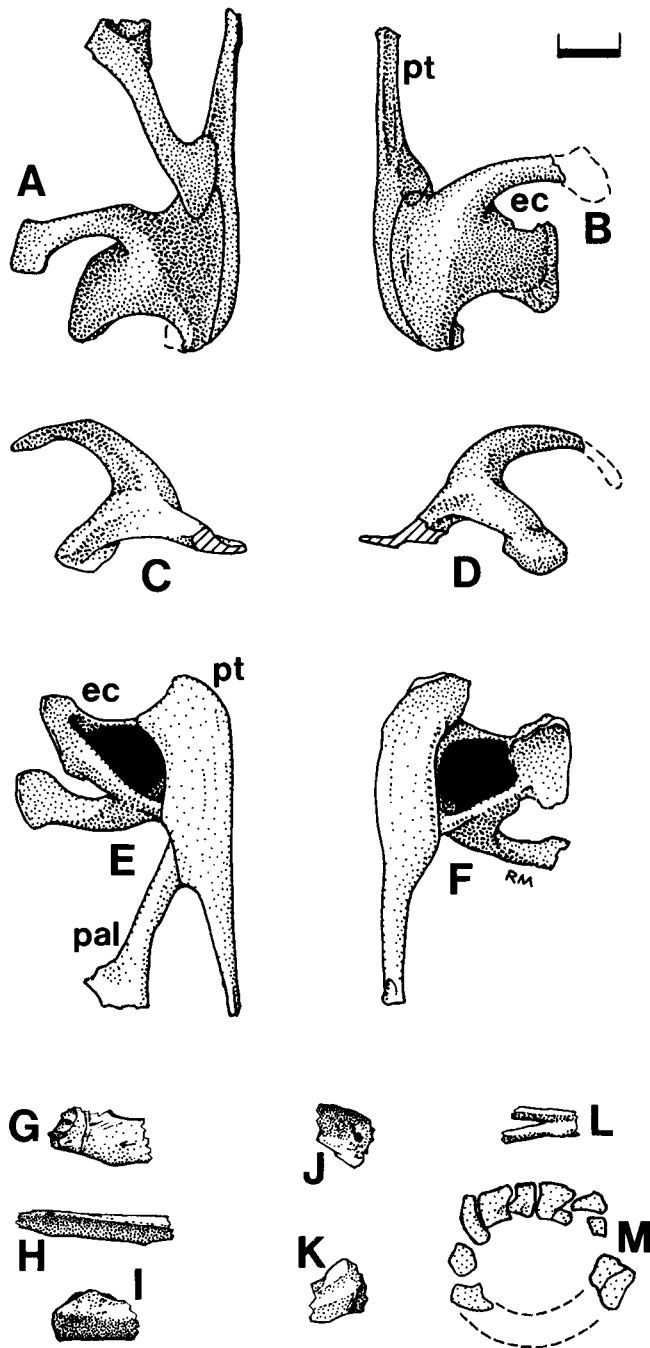
FIGURE 3. *Dromaeosaurus albertensis*, AMNH 5356. Left ectopterygoid, palatine and pterygoid in dorsal (**A**), posterior (**C**) and ventral (**E**) views. Right ectopterygoid and pterygoid in dorsal (**B**), posterior (**D**) and ventral (**F**) views. **G**, fragment of right lacrimal (region anterodorsal to orbit) in dorsal view; **H, I**, unidentified fragments; **J**, fragment of left prefrontal (region anterodorsal to orbit) in dorsal view; **K**, fragment of left lacrimal (region anterodorsal to orbit) in ventral view; **L**, vomer fragment; **M**, scleral ring. **ec**, ectopterygoid; **pal**, palatine; **pt**, pterygoid. Scale = 1 cm.

in the text as pieces of the right and left prefrontals, although their figures show them as lacrimal fragments. Both (Fig. 3G, J) have rugose dorsolateral surfaces, showing that *Dromaeosaurus* had a laterally projecting rugose bump at the anterodorsal corner of the orbit as in *Deinonychus* (Ostrom, 1969) and *Utahraptor* (Kirkland et al., 1993).

No prefrontal has been described for dromaeosaurids. However, the lateromedial thickness of the lacrimal of *Deinonychus* (Ostrom, 1969), its shape in comparison with theropods that have prefrontals, and the presence of a crescent-shaped sutural surface on the medial surface (YPM 5232) suggest that there was a prefrontal between the lacrimal and the frontal. There is no independent prefrontal obvious on the skull roof of *Velociraptor* (PIM 100/25, PIN 3143/8). The prefrontal was probably sutured, or even fused, to the inner surface of the lacrimal and the ventral surface of the frontal.

In general form and structure, the T-shaped quadratojugal (Figs. 2F, G, 4B) is similar to those of velociraptorines. However, it is more robust than in *Deinonychus* (Ostrom, 1969), *Velociraptor* (Barsbold, 1983) or *Saurornitholestes* (RTMP 88.121.39). The posteroventral process broadly overlaps the quadrate laterally, and as in most theropods twists around onto the posterior surface for a limited occipital exposure. The posterodorsal process has a limited contact with the quadrate above the large quadratojugal fenestra, but reached the squamosal. The anterior process fits into a slot in the jugal, where it is overlapped ventrolaterally by the lower prong of the jugal, but overlaps the upper prong dorsomedially. The quadratojugal of oviraptorids (Barsbold et al., 1990) is similar in having a prominent posteroventral quadrate process, although the posterodorsal process has been reduced so that there is no contact with the squamosal and the quadratojugal fenestra has been lost.

The partial right squamosal (Fig. 4) demonstrates a number of dromaeosaurid characters. As in *Deinonychus*, there is a pronounced ventrolateral process sutured to the top of the paroccipital process, and extending conspicuously lateral to the postorbital and quadrate-quadratojugal processes of the bone (Fig. 1B). The postorbital process, although incomplete, was oriented anterodorsally, reflecting the sloping nature of the temporal region. The tapering quadrate-quadratojugal process contacts the anterior edge of the dorsal margin of the quadratojugal (Figs. 1A, 4A), as it no doubt did in *Deinonychus* (unlike the reconstructions in Ostrom, 1969, 1990).

Dromaeosaurid frontals are easily distinguished from those of all other theropods (Currie, 1987b) by the pronounced posterolateral postorbital process, and the clear, sinuous demarcation of the supratemporal fossa. The frontals of *Velociraptor* (PIM 100/25, PIN 3143/8) and *Saurornitholestes* (Currie, 1987b) are indistinguishable from each other, whereas that of *Deinonychus* is presently unknown. The frontal of *Dromaeosaurus* (Fig. 5) is broader anteriorly than a velocirap-
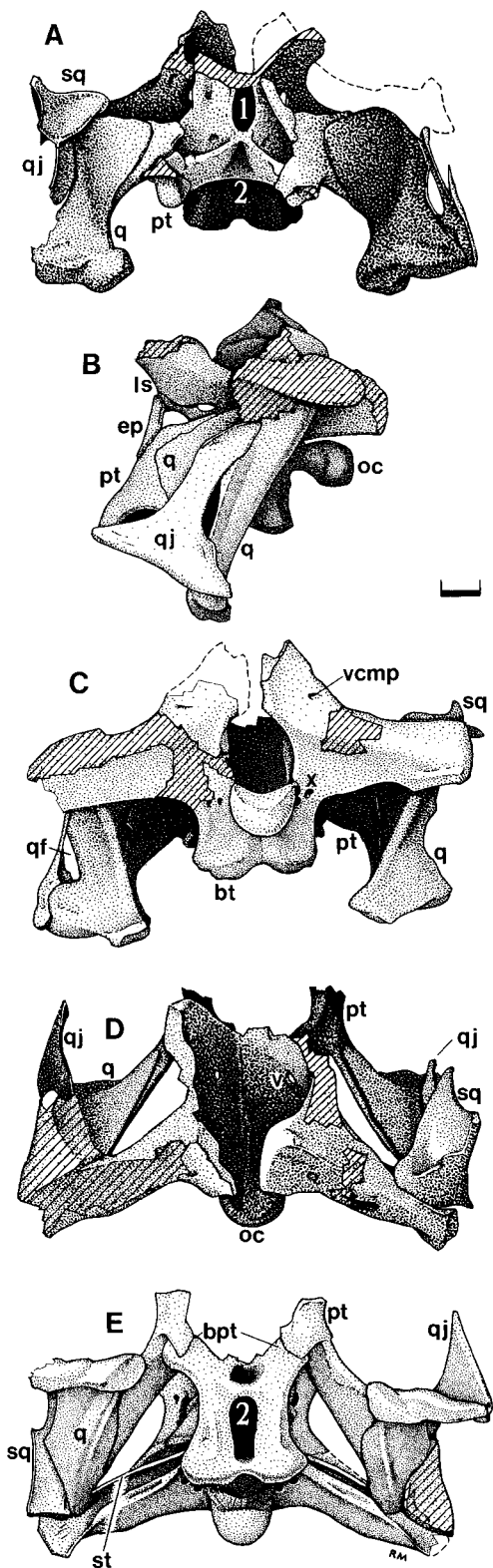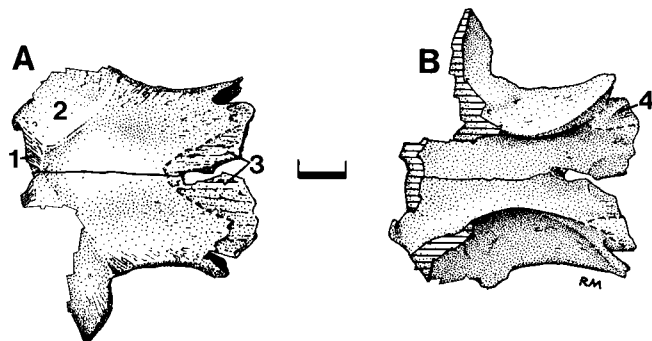
FIGURE 5. *Dromaeosaurus albertensis,* AMNH 5356. Frontals in dorsal (**A**) and ventral (**B**) views. **1**, parietal suture; **2** supratemporal fossa; **3**, nasal suture; **4**, possible prefrontal suture. Scale = 1 cm.

FIGURE 4. *Dromaeosaurus albertensis,* AMNH 5356. Back section of skull, including preserved portion of braincase, in anteroventral (**A**), left lateral (**B**), posterior (**C**), dorsal (**D**) and ventral (**E**) views. **ep**, epipterygoid; **ls**, laterosphenoid; **oc**, occipital condyle; **bpt**, basipterygoid process; **bt**, basal tubera; **oc**, occipital condyle; **pt**, pterygoid; **q**, quadrate; **qf**,

torine frontal, and the medial prong of the nasal overlapped the frontal to a much greater degree. A pronounced slot in the anterolateral margin of the dromaeosaurid frontal housed either the prefrontal, or more likely the lacrimal (Currie, 1987b). The slot is deeper and more pronounced in *Dromaeosaurus* than in *Saurornitholestes.* A triangular region on the ventral surface (Fig. 5B) medial to the slot may be a sutural contact surface for the prefrontal, the coosified prefrontal-lacrimal. The orbital margin is sharp-edged with a vertically striated surface, suggesting the presence of another ossification, possible a palpebral. However, the margin is rugose in velociraptorines as well, and no bone has been reported lateral to the frontal on the orbital margin. A slender bone along the orbital margin of *Troodon* (Currie, 1985) is probably a neomorph (Gauthier, 1987; Russell and Dong, 1993). The postorbital process of the frontal of *Dromaeosaurus* is distinctive from those of velociraptorines in being more sharply demarcated from the dorsomedial orbital margin. The anteromedial margin of the supratemporal fossa is neither as sinuous nor as pronounced as in velociraptorines, and there is no evidence of a deep pit within the temporal fossa such as is often found in the velociraptorine frontal. The parietal overlaps and separates the frontals of *Dromaeosaurus* to a greater degree posteriorly than a velociraptorine parietal would.

Braincase—The braincase of *Dromaeosaurus* (Figs. 4, 6), in spite of a relatively large endocranial capacity, is primitive. As pointed out by Colbert and Russell (1969), the high degree of fusion suggests that this was a mature individual. Most of the supraoccipital was

quadrate fenestra; **qj**, quadratojugal; **sq**, squamosal; **st**, stapes; **vcmp**, posterior canal of middle cerebral vein. Roman numerals represent cranial nerves. **1**, hypophysial fossa; **2**, basisphenoidal recess. Scale = 1 cm.
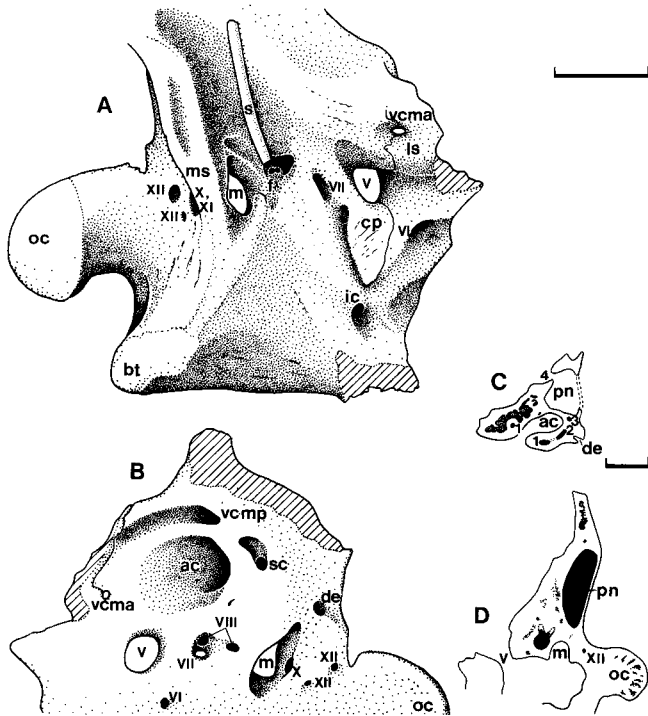
FIGURE 6. *Dromaeosaurus albertensis,* AMNH 5356. Braincase in right posteroventral (**A**) and medial (**B**) views. CT scans (redrawn) through otic capsule and paroccipital process on right side (frontal plane) at level of floccular recess (**C**) and 6 mm lower at level of occipital condyle (**D**). **ac,** fossa auriculae cerebelli; **bt,** basal tubera; **de,** ductus endolymphaticus; **f,** fenestra ovalis and fenestra pseudorotunda; **ic,** internal carotid; **ls,** laterosphenoid; **m,** metotic fissure; **ms,** metotic strut; **oc,** occipital condyle; **pn,** pneumatic space; **s,** stapes; **vcma,** anterior canal of middle cerebral vein; **1,** anterior vertical semicircular canal; **2,** horizontal semicircular canal; **3,** posterior vertical semicircular canal; **4,** pneumatopore. Roman numerals represent cranial nerves. Scale = 1 cm.

destroyed by erosion. Passage of the first four cranial nerves cannot be seen because the orbitosphenoid and ethmoids probably had not ossified, and most of the laterosphenoids were destroyed by erosion. The remaining cranial nerves are discussed in association with the bones they passed through. The impression of vallecula onto the inside of the braincase suggests that the brain filled the cavity completely.

The supraoccipital and epiotic bones are fused indistinguishably as in other theropods (Currie and Zhao, 1993b). The occipital face slopes anterodorsally (Fig. 4B, C), and was not as close to vertical as in most theropods. Dorsolaterally, there is an extensive, triangular suture that would have been covered by the parietal.

The elongate paroccipital process of the combined exoccipital-opisthotic projects posterolaterally (Fig. 4C, D, E), and ends distally in unfinished bone. The distal

end projects significantly beyond the head of the quadrate (Fig. 4E), a derived character correlated with the lateral projection of the squamosal. As pointed out by Colbert and Russell (1969), the distal end of the paroccipital process has a distinct twist so that it faces posterodorsally. This feature is also found in *Velociraptor* (PIM 100/25) and *Archaeopteryx* (London specimen). The exoccipital takes part in the occipital condyle (the suture is still visible on the left side), and did not meet its counterpart on the midline. The exoccipitals approach each other dorsal to the foramen magnum, but would have been separated by the supraoccipital. As in most advanced theropods and birds, the exoccipital-opisthotic sent a metotic strut (Fig. 6A) down the lateral margin of the basal tubera to form the posterior margin of the metotic fissure (jugular foramen). Medially, the tenth and eleventh cranial nerves entered a deep slot in the posteroventral wall of the metotic fissure (Fig. 6B), and turned sharply posteriorly to leave the exoccipital through a foramen (Figs. 4C, 6A) as *Itemirus* (Kurzanov, 1976), allosaurids (McClellan, MS), tyrannosaurids, troodontids (Currie and Zhao, 1993b), *Protoavis,* and birds. The more primitive condition, with the tenth opening laterally, is exemplified by *Syntarsus* (Raath, 1985). Although the vagus foramen has been deflected onto the occiput in dromaeosaurids, the metotic fissure is still widely open laterally behind the fenestra ovalis (Fig. 6A). This contrasts sharply with troodontids, where the inner wall of this chamber, which housed the scala tympani, has been almost completely closed by posterior extension of the opisthotic (Currie and Zhao, 1993b).

The ninth cranial nerve probably left the braincase laterally through the metotic fissure as in *Troodon* (Currie and Zhao, 1993b). Two other openings in the floor of the braincase were for branches of the twelfth cranial nerve (Fig. 6B), and open on the occipital surface of the exoccipital medial to the foramen for the tenth and eleventh (Fig. 6A). The passage for the first branch of the twelfth has a smaller diameter and exits the skull 3 mm below the exit for the second. On the anterior surface of the paroccipital process in the stapedial recess, there is a large, distinctive opening that was incorrectly identified as the "foramen rotundum" by Colbert and Russell (1969). CT scans (Fig. 5C, D) reveal that the opening is a pneumatopore continuous with a large sinus in the proximal half of the paroccipital process. The pneumatopore is posterior to the metotic fissure, and distal to the proximal end of the stapes. There are no air sinuses in the proximal region of the opisthotic-exoccipital complex. The same arrangement is clearly visible in *Itemirus* (PIN 327/699), and the same elongate pneumatopore is present in *Velociraptor* (PIN 3143/8). The pneumatopore and pneumatization of the paroccipital process is found in *Archaeopteryx* and *Protoavis.* Pneumatization of the paroccipital process is from an entirely different position in troodontids, although this may be because of secondary closure of the pneumatopore (Currie and Zhao, 1993b). The paroccipital sinus would have been sup-

plied with air from the middle ear, and the opening is probably a posterior tympanic recess (Currie and Zhao, 1993b).

The basioccipital, which forms most of the kidney-shaped occipital condyle, is relatively stout with large basal tubera. Ventrally it forms the posterior wall of the basisphenoidal recess (Fig. 4E). Two blind posterolateral pits in the roof of the recess were probably bounded posteriorly by the basioccipital. This is also the situation in *Itemirus*. The basisphenoidal recess is well developed in many theropods, ornithomimids (Osmólska et al., 1972), and tyrannosaurs (Bakker et al., 1988), but is closed in troodontids (Currie, 1985).

The basisphenoid-parasphenoid complex is relatively long and low. The cultriform process is a slender bar of bone (Colbert and Russell, 1969), in contrast with the bulbous hollow structure of troodontids. The basipterygoid process is stout (Fig. 4E), and extends ventrally only to the level of the basal tubera. In contrast with *Itemirus*, the lateral surface of the basipterygoid process is not excavated. CT scans show that the interior of the basipterygoid process is solid bone, not pneumatic as it is in troodontids (Currie, 1985). The anterolateral surface of the basisphenoid-parasphenoid is pierced by a foramen for the internal carotid (Fig. 6A), which is relatively small and is not associated with any pneumatic sinuses. The internal carotid was oriented dorsomedially, emerging anteriorly in the pituitary fossa separate from the internal carotid of the other side. The floor of the braincase was coated with plaster when examined by Colbert and Russell for their study (1969), which hid the opening for the sixth cranial nerve posterolateral to the sella turcica, and posteromedial to the opening for the fifth nerve. The foramen identified as the exit for V_1 by Colbert and Russell (1969) is the exit for the sixth, and is in the normal theropod position (Currie and Zhao, 1993b) anterior, ventral and medial to the trigeminal opening (Fig. 6A).

The prootic-laterosphenoid suture is partially visible (Fig. 6A, B). The prootic formed most of the margin for the trigeminal opening, completely enclosed the exit for the seventh, and was the anterior margin of the fenestra ovalis. Lateroventrally, the prootic formed (probably with the basisphenoid) a relatively low crista prootica. On the medial surface, there are three openings (Fig. 6B) in a shallow depression (acoustic fossa) for the seventh and eighth cranial nerves. The dorsal foramen of the anterior pair was for the vestibular branch of the eighth nerve, which turned posterolaterally to emerge from the prootic within the vestibule. The larger, more ventral opening was for the seventh cranial nerve, which exits ventrolaterally. The most posterior of the three openings was for the cochlear branch of the eighth cranial nerve. The same arrangement of the three openings is found in *Itemirus* (PIN 327/699). Medially, the prootic formed the anterior border of the relatively large fossa auriculae cerebelli (floccular recess, subarcuate fossa, recessus interacusticus). The large size of the floccular recess is compa-

rable with *Itemirus, Troodon,* birds and pterosaurs. This has often been considered as a good indicator of balance coordination, but it is also size dependent and is relatively large in small animals.

The preserved portion of the laterosphenoid formed the anterior margin for opening for the fifth cranial nerve (Fig. 6A). Colbert and Russell (1969) identified three separate foramina as exits for three branches of the fifth. This would be very unusual for a vertebrate, although the fifth does emerge from two openings in troodontids, tyrannosaurs and birds. In *Dromaeosaurus*, all three branches of the fifth left the braincase through a single large opening. Immediately outside of the braincase, the ophthalmic branch (V_1) separated and turned anteriorly, following a distinct groove (Fig. 6A) in the lateral wall of the laterosphenoid as in *Itemirus* and most other dinosaurs. The opening dorsal to the exit for the fifth cranial nerve was used by the middle cerebral vein (Fig. 6A), the course of which is marked by a groove (Fig. 6B) on the medial surface of the braincase. As previously mentioned, the third opening identified by Colbert and Russell (1969) for the profundus branch of the fifth is the exit for the sixth nerve.

Palatoquadrate Complex—A fragment of the fused vomers (Fig. 3L) was collected, representing the point where the vomers separate into a pair of thin vertical plates of bone.

Only the posteromedial process of the palatine is known (Fig. 3A, E), expanding posteriorly for contact with the pterygoid and ectopterygoid. This process, separating the palatine fenestra from the subsidiary palatine fenestra (Ostrom, 1969), is slender compared with that of *Deinonychus*. The dorsal surface at the front of the fragment is excavated, but clearly does not include the maxillary margin of the palatine.

The pterygoid is preserved in its entirety (Figs. 3, 4E), and is similar to that of *Deinonychus* (Ostrom, 1969) in all essential characters. The pterygoid does not have a pronounced flange curving anteroventrally from the basipterygoid articulation, a characteristic of large theropods (Currie and Zhao, 1993a), and the "pterygoid flange" is formed mostly by the ectopterygoid. As in *Deinonychus* (Ostrom, 1969), the pterygoid expands laterally into a thin sheet of bone that broadly covers much of the ventral medial surface of the ectopterygoid (Fig. 3E, F). There is a well developed fingerlike extension of the pterygoid that wrapped around the ventral surface of the basipterygoid process (Fig. 4E). The ventral margin of the quadrate process turns outwards to form a narrow shelf (Fig. 4D, E) beneath the pterygoid process of the quadrate.

The ectopterygoid (Fig. 3) is similar to those of *Deinonychus* (Ostrom, 1969) and *Saurornitholestes* (Sues, 1978), but has a broader pterygoid flange. As in other theropods, the ventral surface of the flange is deeply excavated, most likely for a diverticulum of the antorbital air sac (Currie and Zhao, 1993a). In *Saurornitholestes* (RTMP 74.10.5), this excavation is connected by pneumatopores to a conspicuous depression

on the dorsal surface, which is apparently also the situation in *Deinonychus* (Sues, 1978). There is no depression on the dorsal surface of the ectopterygoid of *Dromaeosaurus*. The hooked jugal process expands distally for a firmer contact with the jugal. The medial margin of the ectopterygoid dorsally overlaps the palatine process of the pterygoid.

AMNH 5356 includes the left epipterygoid (Fig. 4B), a relatively short bone extending between the lateral surface of the dorsal margin of the quadrate process of the pterygoid and the laterosphenoid (Colbert and Russell, 1969).

The quadrate is relatively tall (55 mm), and in lateral view its longitudinal axis is inclined anterodistally at an angle of more than 25° from the vertical (Fig. 4B). There is only a single head on the quadrate, which articulates exclusively with the squamosal. A notch in the ventroposterior surface of the quadrate close to the head forms the anteroventral margin of the tympanic opening. As in *Deinonychus* (Ostrom, 1969), the articulation with the squamosal extends from the head down the anterior margin of the anterodorsal lamina, thereby preventing the quadrate from any forward motion. Posterior and lateral movement would have been possible, but this would have been limited because of the position of the stapes and tympanum. The quadrate is broadly exposed laterally above the quadrate fenestra as in *Velociraptor* (PIM 100/25). This is probably a plesiomorphic theropod character because it is present *Eoraptor* (Sereno et al., 1993), ornithomimids (Osmólska et al., 1972), and *Archaeopteryx*. The quadrate is not pneumatic, in contrast with tyrannosaurids, troodontids and most birds.

The Ear—The external acoustic meatus of dromaeosaurids was formed by lateral extensions of the squamosal and paroccipital process. The external acoustic opening would have been oriented anterolaterally, its anterior margins formed by the squamosal and quadratojugal. The distal end of the stapes does not extend laterally beyond its normal terminus below the head of the quadrate.

Both stapes were recovered with the specimen (Colbert and Russell, 1969). Each lies in a long groove in the paroccipital process (Figs. 4E, 6A), and lacks proximal and distal ends, which were probably cartilaginous. The orientation of the groove and the stapes shows that the tympanum was located near the head of the quadrate. The groove itself is deep in some theropods, and was referred to as a posterior tympanic recess in *Syntarsus* (Raath, 1985). There can be no doubt that this region was pneumatic in all theropods, even though most lack the specialized sinuses that invade the bones surrounding the middle ear. As previously mentioned, there is a pneumatopore invading the anterior face of the pneumatized paroccipital process in *Dromaeosaurus*.

The fenestra ovalis and fenestra pseudorotunda are not separated by a bony strut, but form a broadly open region (Fig. 6A) medial to the proximal end of the stapes. The cochlear recess is shallow, in contrast with

the deep vertical pit of *Troodon* (Currie and Zhao, 1993b).

The ductus endolymphaticus left the inner ear chamber on the medial wall of the braincase dorsal and posterior to the metotic fissure (Fig. 6B). The anterior canal of the middle cerebral vein passed through the laterosphenoid-prootic suture anterodorsal to the exit of the fifth nerve, followed a distinct canal posterodorsally around the margin of the otic capsule, and entered the inner ear dorsal to the floccular recess. The posterior canal of the middle cerebral vein exits the otic capsule on the occipital surface of the epioticsupraoccipital complex (Fig. 4C). The characters of the inner ear can be determined from examination of the external features of the surrounding bone, and by CT scan (Fig. 6C, D). The inner wall of the otic capsule has collapsed to show the osseous anterior vertical semicircular canal within the eminentia arcuata (Fig. 6B), looping over the floccular recess in an almost sagittal plane. The posterior vertical semicircular canal loops posterolaterally parallel to the alignment of the floccular recess. The horizontal semicircular canal loops anterolaterally just beneath the floor of the flocculus.

Mandible—Both lower jaws are included with AMNH 5356 (Fig. 7), and demonstrate a number of characteristics peculiar to dromaeosaurids.

The dorsal and ventral margins of the relatively deep but labiolingually narrow dentary are subparallel. Multiple rows of prominent foramina for innervation of the skin and lips by the inferior alveolar nerve pierce the outer surface of the dentary. Like velociraptorines, there is an especially large foramen at the tip of the dentary in *Dromaeosaurus*. The back of the dentary has been broken on both jaws, which has made it difficult to understand its shape and contacts. This is also true for specimens of *Deinonychus* described by Ostrom (1969). Fortunately, well preserved dentaries exist for both *Saurornitholestes* (RTMP 88.121.39) and *Velociraptor* (PIM 100/25), which reveal the significance of the broken pieces at the back of AMNH 5356. Posterior to the dentigerous dorsal margin of the dentary, there is a short process (Fig. 7A) that fits into a slot in the surangular, overlapping the dorsal process of that bone, and in turn being overlapped ventrolaterally by a more ventral process of the same bone. This is a virtually universal characteristic of theropods, being lost in only the highly specialized, toothless oviraptorids. The medial surface of the dentary is marked by a relatively shallow Meckelian canal, which ends anteriorly in a pair of foramina as in *Deinonychus* (Ostrom, 1969) and *Saurornitholestes* (Sues, 1977a). There are eleven alveoli in each dentary compared with 16 in *Deinonychus* (Ostrom, 1969), 15 (RTMP 88.121.39) to 16 (Sues, 1977a) in *Saurornitholestes*, and 14–15 in *Velociraptor* (Sues, 1977b).

Dromaeosaurids were long thought to be lacking interdental plates (Colbert and Russell, 1969; Ostrom, 1969, 1990; Sues, 1977a). The lingual sides of the posterior tooth sockets are further strengthened by the supradentary (intercoronoid). This ossification is al-

ways found dorsal to the lingual jaw margin of the dentary, and lingual to the interdental plates. The supradentary in *Dromaeosaurus* is in this position, lingual to the suspected interdental plates. Finally, close inspection also reveals the diamond-shaped outline of the anterior plates. This has previously been noted in *Dromaeosaurus* (Currie, 1987a), but it can also be seen in *Saurornitholestes* (RTMP 88.121.39) and *Deinonychus* (MCZ 8791).

Although both splenials have been damaged, it is clear that they only extended anteriorly to about the level of the seventh dentary alveolus. The splenial wraps around the ventral surface of the anterior tip of the angular (Sues, 1977b), and has a relatively larger exposure on the lateral surface of the mandible between the dentary and angular than any theropod except other dromaeosaurids and troodontids (Osmólska and Barsbold, 1990). The posterior margin of the splenial is a V-shaped notch (Fig. 7B, E) that defined most of the internal mandibular fenestra as in velociraptorines (Ostrom, 1969; Sues, 1977a; RTMP 88.121.39).

The triangular coronoid (Fig. 7B, E) extends anteriorly between the prearticular and the surangular, and is continuous with a long, slender supradentary (intercoronoid), which covers the medial surface of the interdental plates of the last half dozen mandibular teeth. The latter ossification is also present in *Velociraptor* (Barsbold, 1983).

The angular, surangular and prearticular are indistinguishable from those of velociraptorines, but are also fundamentally the same as in other theropods. The surangular foramen is relatively small compared with tyrannosaurids, but is comparable to those of most other theropods. The external mandibular fenestra is almost certainly bordered by angular, surangular and a posterior slip of the dentary. Colbert and Russell (1969) incorrectly reconstructed it closed anteriorly by the surangular when they interpreted a fragment of bone at the front of the opening as surangular rather than dentary.

The articular, accurately described by Colbert and Russell (1969), has a broad, shallow, shelf-like retroarticular process. There is a vertical, columnar process rising from the posteromedial corner of the retroarticular shelf (Fig. 7). This is present, but not as well developed as in *Deinonychus* (Ostrom, 1969), *Velociraptor* (Sues, 1977b) and *Saurornitholestes* (RTMP 88.121.39). Colbert and Russell speculated that, as in some modern birds, this process served to prevent the jaw from opening too wide and disarticulating.

The teeth of *Dromaeosaurus* have been described elsewhere (Currie et al., 1990), so only the diagnostic characteristics will be reviewed here. There are probably four premaxillary teeth, whereas the maxillary and dentary counts of nine and eleven are certain. The anterior carinae or premaxillary teeth are on the lingual surfaces, and are set back from the anterior margins. They are not D-shaped in cross-section, but are similar to those of *Saurornitholestes*. Denticles on the posterior carina of a premaxillary tooth are longer than, but have smaller basal diameters than, the anterior denticles. The alignment of an anterior carina of a maxillary or mandibular tooth of *Dromaeosaurus* is unique amongst known theropods. The anterior carina is positioned on the lingual surface for most of the height of the crown, but close to the tip it twists onto the anterior midline of the tooth (Currie et al., 1990). The denticles of maxillary and mandibular teeth are relatively broad and chisel-like in appearance, in contrast with the more elongate, sharply hooked denticles of velociraptorines. The basal diameters of anterior denticles (0.33 mm) are slightly greater than the basal diameters of posterior denticles (0.30 mm) in maxillary and mandibular teeth. The number of denticles per 5 mm is about 15 on the anterior and 16 on the posterior carina (average measurements for 16 maxillary and dentary teeth). This contrasts sharply with the condition in velociraptorine maxillary and dentary teeth, where anterior denticles are significantly smaller than posterior denticles (Currie et al., 1990).

DISCUSSION

Dromaeosaurus and its relatives are in many ways rather unspecified theropods for the Late Cretaceous. Contemporary theropods, including oviraptorids, elmisaurids, troodontids, ornithomimids and tyrannosaurids, all show greater specialization in the jaws, braincase, and metatarsus than dromaeosaurids. Nevertheless, dromaeosaurids are highly modified from earlier theropods like *Syntarsus* (Raath, 1985), *Coelophysis,* and *Dilophosaurus* (Welles, 1984).

Within the Dromaeosauridae, *Dromaeosaurus* can be compared with *Deinonychus, Velociraptor,* and *Saurornitholestes,* all of which show greater similarity to each other than to *Dromaeosaurus.* Not enough is presently known about *Utahraptor* to determine whether it is a dromaeosaurine or a velociraptorine, although the relative sizes of the premaxillary teeth suggest it is the latter.

Dromaeosaurids have often been associated with the Troodontidae in the Deinonychosauria, mostly on the basis of similarities in the pes. Although the second digit is specialized as a raised, raptorial claw in troodontids, the proportions and function have developed in different ways from dromaeosaurids (Currie and Peng, 1993). It had been assumed that troodontids possessed a retroverted pubis and elongate caudal prezygapophyses (Russell, 1969), both of which are characteristic of dromaeosaurids. However, several specimens, including the holotype of *Saurornithoides mongoliensis* (AMNH 6516) and two specimens collected recently in China, show that the pubis was not reversed. New specimens from China (Russell and Dong, 1993) and Montana also show that troodontids did not have the elongated bony rods for stiffening the tail. Given the tremendous differences evident in the rest of the skeleton, it is more parsimonious to believe that the specialized raptorial claws of dromaeosaurids and troodontids evolved independently.
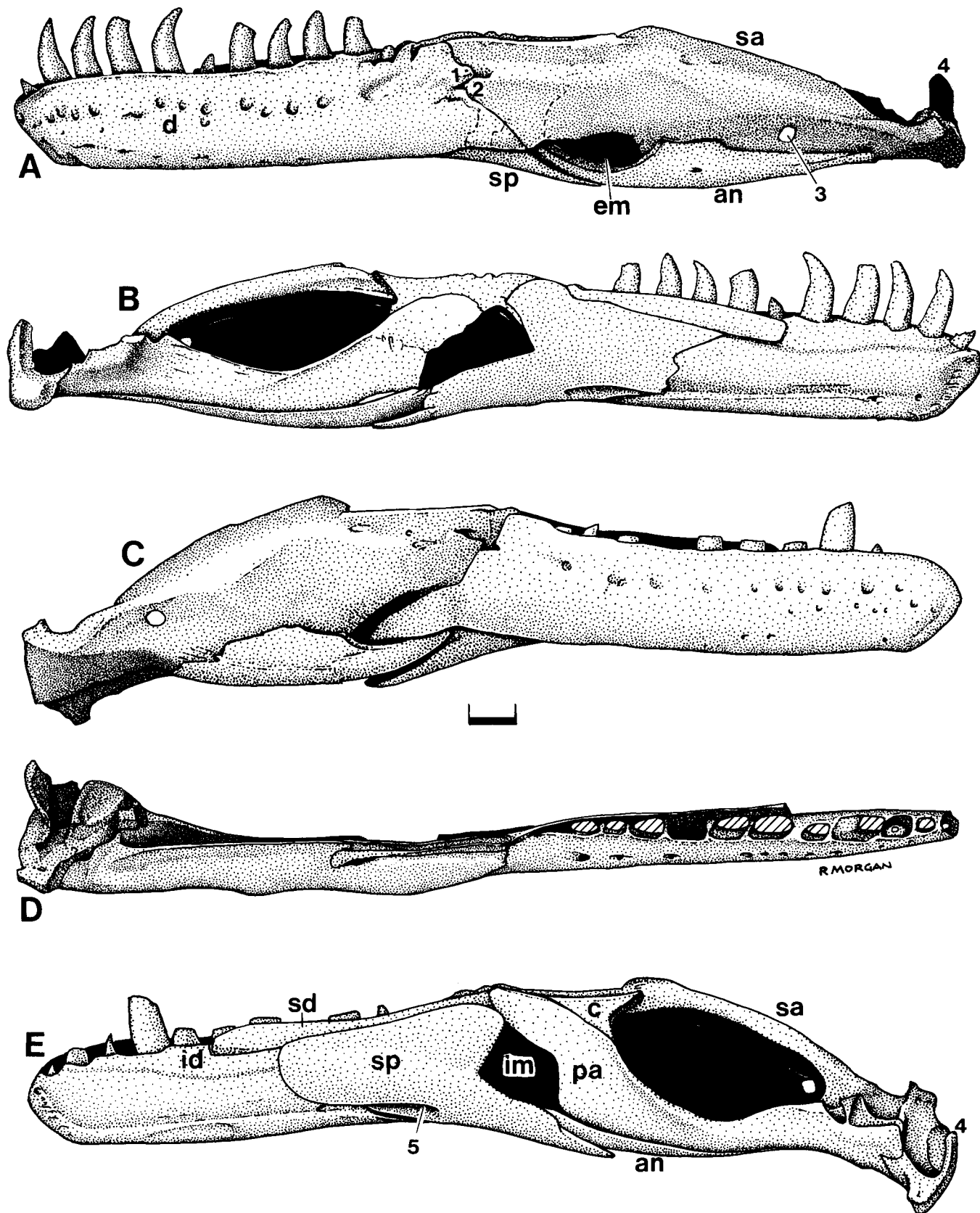
FIGURE 7. *Dromaeosaurus albertensis,* AMNH 5356. Left (**A, B**) and right (**C, D, E**) mandibles in lateral (**A, C**), medial (**B, E**) and dorsal (**D**) views. **an**, angular; **ar**, articular; **c**, coronoid; **d**, dentary; **em**, external mandibular fenestra; **id**, fused

Itemirus is represented by a single specimen, a well preserved braincase from central Asia (Kurzanov, 1976). In size, the degree of ossification and most other characteristics, it is remarkably similar to the braincase of *Dromaeosaurus*. The size, shape and orientation of the pneumatopore that transmitted air from the middle ear into the paroccipital process is the same in *Itemirus* and dromaeosaurids. This could well indicate that *Itemirus* is a dromaeosaurid, but this character is also present in *Protoavis*, where it is referred to as part of the posterior tympanic recess. One character that is distinctly different is the laterally excavated basipterygoid process, possibly for the protractor pterygoideus muscle (Kurzanov, 1976), or perhaps for an anterior extension of the tympanic pneumatic system, as proposed for *Syntarsus* (Raath, 1985). The lateral surface of the braincase is not excavated in *Dromaeosaurus*, and the surface is roughened.

Autapomorphies of the Dromaeosauridae

There are numerous characters that, at present, are known only in dromaeosaurids, and these are presented here as autapomorphies. Unfortunately, although small theropods appear to have been relatively common animals since the late Triassic, few of them are represented by complete skeletons with skulls, and virtually all are poorly known. This character list may change as our knowledge of the cranial anatomy of small theropods improves. The large number of autapomorphies suggests that dromaeosaurids are too specialized to have been ancestral to any of the other Late Cretaceous theropod taxa. And in spite of the fact that dromaeosaurids are often proclaimed to be the most birdlike of the theropods (Paul, 1988b), they lack many of the theropod-avian synapomorphies found in other theropod families, and have too many specializations to be plausible avian ancestors.

(1) The long but shallow premaxillary process excludes the maxilla from the margin of the external naris, and separates the anterior ends of the maxilla and nasal. This appears to have been an accentuation of a character that is widespread, but frequently lost, in theropods. Only ornithomimids show greater posterior extension of the premaxilla. In dromaeosaurids, the posterior margin of the dentigerous margin of the premaxilla is below the posterior margin of the external naris, and the process extends posterodorsally behind this. In ornithomimids (Barsbold and Osmólska, 1990), the main body of the premaxilla is more elongate, and the posterior margin of the ventral edge is well behind the external naris. In most theropods (Currie, 1985), the premaxilla contacts the nasal below the external

naris, but does not separate the nasal and maxilla for any appreciable distance. The great development of this process in dromaeosaurids contrasts with troodontids and *Archaeopteryx*, where the process has been lost (Currie, 1985).

(2) The lacrimal is slender and T-shaped, whereas in most theropods this bone is shaped like an inverted L. The preorbital bar is perpendicular to the ventral margin of the skull.

(3) The frontal process of the postorbital is upturned, which meets a pronounced and posteroventrally inclined postorbital process of the frontal. The frontal has a slot-like sutural contact with the lacrimal, and a sinuous ridge marking the anterior margin of supratemporal fossa. All of these characters contribute to the lowering of the postorbital bar and occiput in relation to the skull roof. The occiput is also lower than the skull roof in *Archaeopteryx* and other birds, but this could be the result of inflation of the avian braincase.

(4) The T-shaped quadratojugal is different than the L-shaped ones of most theropods.

(5) A pronounced ventrolateral process of the squamosal is sutured to the top of the paroccipital process and extends conspicuously lateral to the intertemporal bar and the quadratojugal. The paroccipital process extends noticably lateral to the head of the quadrate. Both of these characters contribute to the formation of an external auditory meatus. *Archaeopteryx* is similar in this region.

(6) The distal end of the paroccipital process is twisted to face posterodorsally. This is also the case in *Archaeopteryx* (London specimen).

(7) A pneumatopore in the anterior surface of paroccipital process opens into a pneumatic sinus within the process. Outside of the Dromaeosauridae, this character is known only in *Itemirus* (Kurzanov, 1976), *Archaeopteryx*, (Walker, 1985) and *Protoavis*. *Itemirus* might be a dromaeosaurid, although there is presently not enough known about this genus to assign it to a theropod family with confidence. In *Protoavis*, most of the periotic bones are pneumatic, and the presence of a paroccipital pneumatopore in the same position as in dromaeosaurs might have been developed independently. It is also conceivable that this is plesiomorphic, but it has not been reported in any of the late Triassic or lower Jurassic theropods that appeared after *Protoavis*, including *Dilophosaurus* (Welles, 1984) and *Syntarsus* (Raath, 1985).

(8) The basipterygoid processes are relatively short, extending ventrally only to the level of the basal tubera. In spite of the relatively unpronounced basal tubera and basipterygoid processes, there is a deep basisphe-

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interdental plates; **im**, internal mandibular fenestra; **mg**, Meckelian groove; **pa**, prearticular; **sa**, surangular; **sd**, supradentary; **sp**, splenial; **1**, intramandibular process of dentary; **2**, intramandibular process of surangular; **3**, posterior surangular foramen; **4**, dorsal process of articular; **5**, anterior mylohyoid foramen. Scale = 1 cm.

noidal recess. Most theropods have deep basisphenoidal recesses (Bakker et al., 1988), although they generally face posteroventrally (rather than ventrally), mostly because the basipterygoid processes tend to be significantly longer and lower in position than the basal tubera. The basipterygoid processes of *Itemirus* are relatively short, but still project ventrally to a level below the basal tubera. The basisphenoidal cavity is closed ventrally in troodontids.

(9) The pterygoid lacks the ventral extension that with the ectopterygoid forms the "pterygoid flange" in theropods as diverse as *Herrerasaurus, Coelophysis, Allosaurus,* and *Sinraptor* (Currie and Zhao, 1993a).

(10) The palatine contacts the ectopterygoid and separates the palatine fenestra from a subsidiary palatine fenestra.

(11) The dentary is relatively tall and labiolingually thin, and the Meckelian groove is shallow. The dorsal and ventral jaw margins are nearly parallel. Most other theropods have dentaries that conspicuously taper anteriorly. The posteroventral region of the dentary is a tapering process that is separated from the ventral margin of the mandible by the splenial. There are two rows of foramina on the lateral surface, one just beneath the alveolar margin, and the second near the ventral margin of the jaw. The upper row of foramina is present in most theropods, but the lower row is not as pronounced in any other non-avian theropods, with the exception of troodontids (Currie, 1987a).

(12) The dromaeosaurid splenial has a relatively large, triangular process exposed on the lateral surface of the mandible between the dentary and angular. Although the splenial is not exposed laterally in *Allosaurus, Coelophysis, Dilophosaurus* (Welles, 1984), oviraptorids (Barsbold et al., 1990), ornithomimids (Osmólska et al., 1972; Barsbold and Osmólska, 1990), or tyrannosaurids, it does have limited lateral exposure in diverse theropods, including *Ceratosaurus, Monolophosaurus* (Zhao and Currie, 1993), and *Proceratosaurus* (BMNH R4860). The lateral exposure of the splenial in other theropods is never as pronounced as in dromaeosaurids with the exception of the troodontid *Saurornithoides junior* (Barsbold, 1974; incorrectly labeled as the angular in Osmólska and Barsbold, 1990).

(13) Relatively large, triangular internal mandibular fenestra (infra-Meckelian fenestra). The posterior margin of the splenial is a V-shaped notch that defined most of the internal mandibular fenestra as in velociraptorines (Ostrom, 1969; Sues, 1977a; RTMP 88.121.39) and some carnosaurs (Currie and Zhao, 1993a; Zhao and Currie, 1993). The internal mandibular fenestra may be widespread in other theropods, including *Allosaurus, Carnotaurus, Ceratosaurus* (Bakker et al., 1988), *Saurornithoides* (Barsbold, 1974) and tyrannosaurids, but is relatively smaller and slit-like. It appears to have been absent in *Dilophosaurus* (Welles, 1984).

(14) Dromaeosaurids have a broad, shallow, shelf-like retroarticular process, with a vertical, columnar process rising from the posteromedial corner. A pro-

cess in this position has not been reported in any other theropods, but is widespread in birds (Colbert and Russell, 1969).

(15) Fusion of interdental plates in the premaxilla, maxilla and dentary to each other and to the margins of the jaws. I know of no non-dromaeosaurid theropods that fuse their interdental plates to the degree seen in the Dromaeosauridae. Interdental plates are not present in troodontids (Currie, 1987a) or hesperornithiforme birds (Martin et al., 1980), but unfused interdental plates are present in *Archaeopteryx* (Wellnhofer, 1993).

(16) A retroverted pubis is known in *Deinonychus* and *Velociraptor,* and is assumed to have been present in all dromaeosaurids. Although no pelvic elements are known for *Dromaeosaurus, Adasaurus mongoliensis* (Barsbold, 1983) has been referred to the Dromaeosaurinae on the basis of pedal similarities (Paul, 1988b). The Mongolian species clearly has a posteroventrally directed pubic shaft (PIM 100/10, 100/22), suggesting that this is found in both dromaeosaurines and velociraptorines. With the exception of segnosaurids, the opisthopubic condition is not found in any other non-avian theropods. Segnosaurids are highly derived saurischians (Barsbold and Maryańska, 1990) that share no other special characters with dromaeosaurids, and there can be little doubt that the pubis was reoriented independently in the two groups. The similarities between the opisthopubic pelves of *Archaeopteryx* and dromaeosaurids is striking. Although this may indicate a relationship, it might also have evolved independently in conjunction with other specializations in the dromaeosaurid hind limb (A. Perle, pers. comm., 1989).

(17) Dromaeosaurids have a specialized (sickle-clawed) pedal digit II. Phalanges II-1 and II-2 are known from AMNH 5356, and are comparable with those of velociraptorines (Colbert and Russell, 1969). Although the second pedal ungual is not known for *Dromaeosaurus* (the specimen identified as such by Colbert and Russell, 1969, is more likely from *Saurornitholestes,* which is a much more common small theropod and has an ungual identical to CMN 12240), the other phalanges of digit II are fundamentally the same as those of velociraptorines, which suggests that the specialized claw was present and raised off the ground. As in the other dromaeosaurids (Paul, 1988b; Currie and Peng, 1993), the lengths of pedal phalanges II-1 and II-2 are almost the same, whereas the troodontids II-1 is at least 50% longer than II-2.

There are additional characteristics presently known only in velociraptorines, but which are probably also in dromaeosaurines. These include the elongation of caudal prezygopophyses in all but the most proximal caudal vertebrae. In *Deinonychus* (Ostrom, 1969), *Velociraptor* (PIM 100/25), *Saurornitholestes* (RTMP 82.26.1, 88.121.39), and *Utahraptor* (Kirkland et al. 1993), the mid-caudal prezygopophyses and chevrons are elongated into long, bony rods that extend anteriorly up to the length of a dozen caudal centra. The

rods overlap, but were capable of independent movement. Their function was obviously to stiffen the tail, although they were thin enough to allow some bending of the distal end of the tail. Two of the preserved dromaeosaurid skeletons (PIM 100/25, RTMP 88.121.39) have articulated tails with gentle curves, even though the bundles of rods are in position. Caudal prezygopophyses are always short in primitive theropods like *Coelophysis* (Colbert, 1989) and *Dilophosaurus* (Welles, 1984). Elongate anterior zygopophyses are found in caudals of *Ornitholestes, Ceratosaurus,* allosaurids, troodontids (MOR 430, IVPP V9612), ornithomimids, and tyrannosaurids, but never exceed the length of a single vertebra.

Dromaeosaurinae: The diagnosis for the subfamily is the same as for *Dromaeosaurus* until more is known about the postcranium of this genus and the crania of other possible dromaeosaurines (such as *Adasaurus*). The anterior carina of a maxillary or mandibular tooth is close to the midline of the tooth near the tip, but not far from the tip it twists towards the lingual surface. This characteristic twist is not presently known in any other theropod.

Dromaeosaurus differs from velociraptorines in the followings features: premaxilla deeper and thicker; quadratojugal stouter; postorbital process of frontal more sharply demarcated from dorsomedial orbital margin; posteromedial process of palatine more slender; no pneumatic depression on dorsal surface of ectopterygoid; premaxillary teeth all about the same length and basal diameter; fewer maxillary (9) and dentary (11) teeth; anterior and posterior tooth serrations subequal in size; vertical, columnar process on posteromedial corner of retroarticular shelf relatively taller.

Velociraptorinae: The denticles on the anterior carinae of velociraptorine maxillary and dentary teeth are significantly smaller than the posterior denticles. The second premaxillary tooth is significantly larger than the third and fourth premaxillary teeth. The nasal is depressed in lateral view (Paul, 1988a); this bone is unknown in *Dromaeosaurus,* so the character may ultimately be found in dromaeosaurines as well. The Velociraptorinae includes *Deinonychus, Saurornitholestes, Velociraptor* and probably *Utahraptor.*

ACKNOWLEDGMENTS

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APPENDIX

CHARACTERS AND TAXON-CHARACTER MATRIX

This list shows the coding and distribution of 27 characters in dromaeosaurids, *Itemirus,* and four outgroups (the carnosaur *Sinraptor, Coelophysis* and *Herrerasaurus*). Characters 1 and 2 are interpreted as autapomorphies of *Dromaeosaurus albertensis,* and Characters 3–5 are considered to be autapomorphies of velociraptorines (*Deinonychus, Saurornitholestes, Velociraptor*). Characters 6–26 are interpreted as dromaeosaurid synapomorphies that unite *Dromaeosaurus*

with velociraptorine genera. All characters are binary (0, plesiomorphic; 1, apomorphic).

Dromaeosaurus albertensis

1. Frontal, postorbital process: smooth transition from orbital margin (0); sharply demarcated from orbital margin (1).

2. Teeth, anterior carina: on anterior margins of maxillary or dentary, or twists gradually onto medial surface (0); sharply twisted distally (1).

Velociraptorinae

3. Frontal, anterior demarcation of supratemporal fossa: straight or slightly sinuous (0); sinusoidal with associated deep pit (1).
4. Teeth, second premaxillary tooth: smaller than or equal in size to third and fourth premaxillary teeth (0); significantly larger than premaxillary teeth 3 and 4 (1).
5. Teeth, maxillary, mandibular: anterior and posterior denticles not significantly different in size (0); anterior denticles, when present, significantly smaller than posterior denticles (1).

Dromaeosauridae

6. Interdental plates: unfused (0); fused (1).
7. Lacrimal: inverted L-shape (0); T-shaped (1).
8. Frontal, lacrimal-prefrontal contacts: sutures on lateral, dorsal and/or ventral surfaces (0); dorsal and ventral sutural surfaces connected by a vertical slot (1).
9. Supratemporal fossa: limited extension onto dorsal surfaces of postorbital and frontal (0); covers most of frontal process of postorbital and extends anteriorly on dorsal surface of frontal to at least level of the posterior orbital margin (1).
10. Postorbital: T-shaped (0); upturned frontal process (1).
11. Quadratojugal: L-shaped (0); Y- or T-shaped (1).
12. Quadratojugal fenestra: small foramen-like opening (0); widely open (1).
13. External auditory meatus: does not extend beyond level of intertemporal bar of postorbital and squamosal (0); ventrolateral process of squamosal and lateral extension of paroccipital process beyond head of quadrate (1).

14. Paroccipital process: occipital surface of distal end oriented more posteriorly than dorsally (0); conspicuous twist in the distal end orients distal surface more dorsally than proximal region (1).
15. Opisthotic-exoccipital: no periotic pneumatopore or pneumatized paroccipital process (0); periotic pneumatopore enters hollow paroccipital process (1).
16. Pterygoid flange: includes major contribution from pterygoid (0); is formed mostly by ectopterygoid (1).
17. Palatine: does not contact ectopterygoid (0); contacts ectopterygoid (1).
18. Palatine, subsidiary palatine fenestra: not present (0); present (1).
19. Dentary: thick when compared to height, deep Meckelian groove, pronounced dental shelf (0); thin and high with shallow Meckelian groove and dental shelf (1).
20. Dentary, lateral view: tapers conspicuously anteriorly (0); upper and ventral margins subparallel (1).
21. Splenial: limited or no exposure of splenial on lateral surface of mandible (0); conspicuous triangular process on external surface of mandible between dentary and angular (1).
22. Internal mandibular fenestra: absent or small and slit-like (0); triangular and relatively large (1).
23. Vertical columnar process on retroarticular process: absent (0); present (1).
24. Ossified caudal rods extending lengths of prezygapophyses and chevrons: absent (0); present (1).
25. Orientation of proximal portion of pubis and pubic peduncle of ilium: anteroventral (0); posteroventral (1).
26. Foot: second toe weight supporting in function (0); second toe held off ground (functionally didactylous foot) (1).

Theropoda

27. Intra-mandibular joint: absent (0); present (1).

Taxon	Character					
	5	10	15	20	25	27
Dromaeosaurus	11000	11111	11111	11111	111??	11
Velociraptorinae	00111	11111	11111	11111	11111	11
Itemirus	?????	?????	????1	?????	?????	??
Sinraptor	00000	00010	00000	00000	01000	01
Coelophysis	00000	00000	00000	00000	0?000	01
Herrerasaurus	00000	00000	00000	000?0	0?000	01

Character state abbreviations: 0 = plesiomorphic state; 1 = autapomorphic state; ? = not preserved/unknown.