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## The Small Cretaceous Dinosaur *Dromaeosaurus*

BY EDWIN H. COLBERT<sup>1</sup> AND DALE A. RUSSELL<sup>2</sup>

### INTRODUCTION

*Dromaeosaurus albertensis* was described by Matthew and Brown in 1922, the type being a partial skull with lower jaws, some hyoids, and an assortment of foot bones. The specimen had been collected by Barnum Brown in 1914, at "Sand Creek," on the south bank of the Red Deer River, Alberta, several miles below Steepleville. The fossil was found in beds then designated as belonging to the Belly River Formation, but which are now designated as being within the Oldman Formation of the Belly River Series.

The original description, obviously a preliminary announcement, was brief and illustrated by a sketchy figure showing an outline restoration of the skull and mandible in lateral view. Little has been published about *Dromaeosaurus* since (although it frequently is cited in the literature), although the type fossil is of particular interest because of its small size. This genus is one of the few known, small, toothed theropods from the Upper Cretaceous of Alberta, and it has elicited certain questions that have not as yet been satisfactorily answered. What are the relationships of *Dromaeosaurus*? What ontogenetic stage is represented by the type of *Dromaeosaurus albertensis*? Is this a fully adult individual? The

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<sup>1</sup> Curator, Department of Vertebrate Paleontology, the American Museum of Natural History; and Columbia University, New York.

<sup>2</sup> Curator of Fossil Vertebrates, National Museum of Natural Sciences, Ottawa, Ontario.

present paper is devoted to a new study of the type of *Dromaeosaurus albertensis*, not only for the purpose of presenting an adequate description of the fossil, but also to provide answers, so far as possible, to the several questions that have been raised concerning it.

Matthew and Brown, in their original description, created a separate subfamily, the Dromaeosaurinae, for the reception of the genus, this being "provisionally referred" by them to the family Deinodontidae (= Tyrannosauridae). This allocation of the genus was accepted by Hay (1930), and he included, in addition to the type, three species described by Cope and one by Marsh, all questionably within the genus *Dromaeosaurus*. These were *Laelaps cristatus* Cope, *L. explanatus* Cope, and *L. laevifrons* Cope, all from the Judith River Formation of Montana, and *Coelurus gracilis* Marsh, from the Potomac beds of Maryland.

In 1928 Nopcsa included *Dromaeosaurus* within the Megalosauridae.

In 1930 L. S. Russell designated *Dromaeosaurus* as a deinodontid.

Other authors who have treated the taxonomic allocation of the genus have considered it as a coelurosaurian, and have generally placed it in the Compsognathidae or an equivalent family, as follows: Huene (1932, 1956), Coelurosauria, Compsognathidae; Romer (1956, 1966), Coelurosauria, Coeluridae (including Compsognathidae); Rozhdestvensky and Tatarinov (1964), Coeluroidea, Compsognathidae.

#### ACKNOWLEDGMENTS

We wish to acknowledge the helpful advice and assistance received from Dr. John H. Ostrom, of Yale University, whose studies of the faunas of the Cloverly and related formations in western North America have revealed dinosaurs that seem to be closely related to *Dromaeosaurus*. We are also deeply indebted to Dr. Walter Bock, of Columbia University, for helpful suggestions and criticisms with regard to the mechanics of the skull and jaw musculature in this dinosaur. Figures 2, 4, and 6 were drawn by Mr. Michael Insinna, of the Department of Vertebrate Paleontology, the American Museum of Natural History, under the direction of the authors. Figures 12, 14, and 15 were made by Mr. Chester Tarka, of the Department of Vertebrate Paleontology, the American Museum of Natural History. Figures 7, 8, 10, and 13 were drawn by the junior author. Figures 1, 3, 5, and 9 were made in the Division of Photography of the American Museum of Natural History.

#### ABBREVIATIONS

A.M.N.H., the American Museum of Natural History

N.M.C., National Museum of Natural Sciences, Ottawa  
Y.P.M., Peabody Museum of Natural History, Yale University

## DESCRIPTION

### *DROMAEOSAURUS* MATTHEW AND BROWN, 1922

*Dromaeosaurus* MATTHEW AND BROWN, 1922, p. 383. Type, *Dromaeosaurus albertensis* Matthew and Brown.

### *Dromaeosaurus albertensis* Matthew and Brown

*Dromaeosaurus albertensis* MATTHEW AND BROWN, 1922, pp. 383-385.

Type: A.M.N.H. No. 5356, a partial skull with lower jaws, hyoids, and associated foot bones.

The skull consists of the following bones: posterior part of left premaxilla, containing two teeth in place, and in addition two other premaxillary teeth; two right premaxillary teeth; alveolar border of the left maxilla complete with nine teeth, and portions of the alveolar border of the right maxilla with seven posterior teeth; both jugals; both quadratojugals; both quadrates; both pterygoids; both ectopterygoids; left epipterygoid; both laterosphenoids; basioccipital; basisphenoid; parasphenoid; exoccipitals; both opisthotics; right prootic and fragment of left prootic; right squamosal, incomplete; frontals; parietals, incomplete; fragments of left and right prefrontals; fragment of a left postorbital; both stapes, the left one incomplete; two hyoid bones; some sclerotic plates on the right side.

Both mandibular rami are complete, with all bones present. Ten teeth are preserved in the left ramus; seven teeth are preserved in whole or in part in the right ramus. There are alveoli for 11 teeth in each dentary.

The available bones of the pes are: the distal ends of the first three metatarsals, five phalanges, and fragments from the ends of two other phalanges.

**HORIZON AND LOCALITY:** From the Oldman Formation, Belly River Series, Upper Cretaceous. Brown's field records indicate that the specimen was discovered on the right bank of the Red Deer River, 12 miles downstream from Steeveville, Alberta, at a level 150 feet above the river. This was Brown's general locality designation for all the specimens he collected in the Little Sandhill Creek (Sand Creek) badlands, situated about 7 miles southeast of Steeveville. The type of *Centrosaurus* ("Monoclonius") *nasicornis* (A.M.N.H. No. 5351) was collected during the same year from this area of badlands, also at a level "150 feet above the



FIG. 1. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, skull and lower jaws, lateral view. Portions restored are cross hatched. The bone shown in the parietal region is a portion of the lateral wall of the braincase erroneously placed in this position.  $\times 2/3$ .

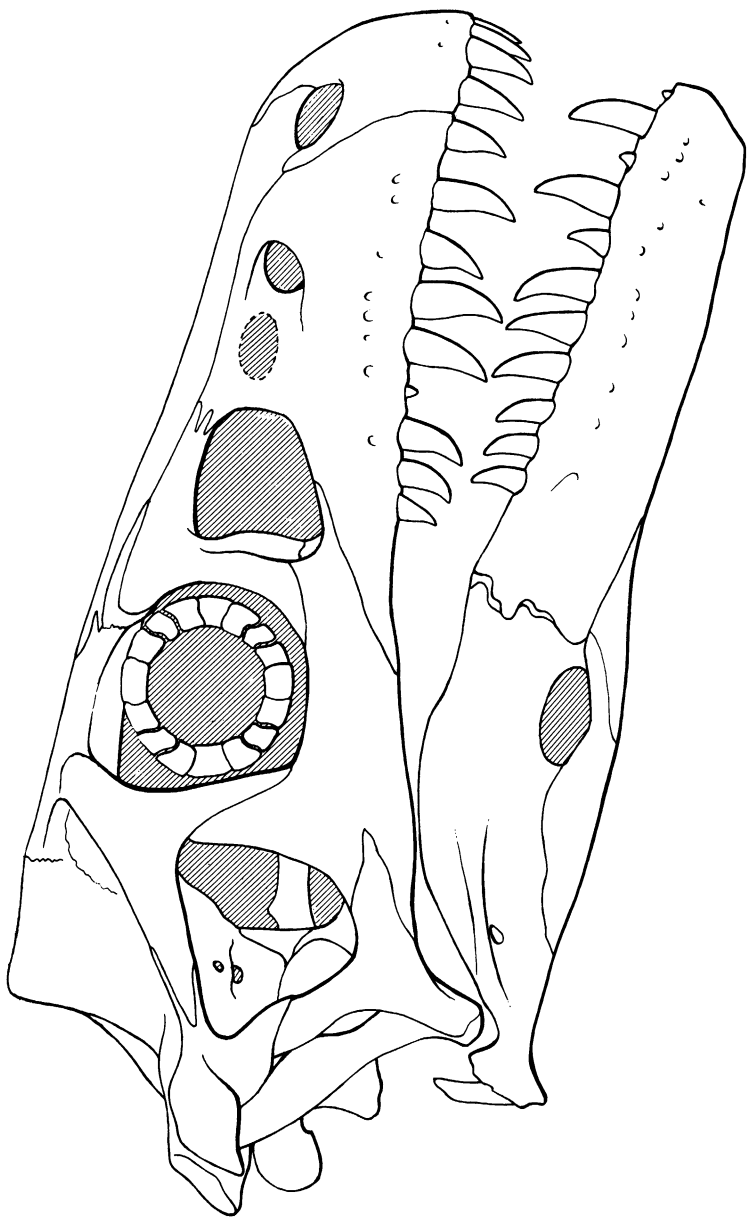


FIG. 2. *Dromaeosaurus albertensis* Matthew and Brown, reconstruction of skull and lower jaws in lateral view.  $\times 2/3$ .

river." Sternberg (1950) relocated the quarry of the latter specimen at an elevation of 2261.5 feet above sea level, or at about the base of the upper third of the dinosaur-bearing section of the Oldman Formation in this region. Presumably the type of *Dromaeosaurus albertensis* was found at about this level.

### THE SKULL

Although the skull of *Dromaeosaurus* was probably fossilized entire, the dorsal and anterior regions were evidently disassociated and partly destroyed through erosion. The premaxillae, except for a fragment from the left side, the nasals, dorsal portions of the maxillae, prefrontals, essentially all of both postorbitals and parietals, the left squamosal, and all of the anterior portion of the palate have been lost. Parts of other elements were also damaged, especially the lacrimals and the left side of the braincase. Fortunately the remainder of the skull and both mandibular rami are sufficiently well preserved to provide an adequate impression of the cranial morphology.

The skull of *Dromaeosaurus* is small, measuring only about 236 mm. from the restored anterior end of the premaxilla to the apex of the occipital condyle, and 109 mm. across the lateral surfaces of the quadratejugs. The temporal region is rather deep, in contrast to known conditions in most of the smaller carnivorous saurischians, but not nearly so compressed anteroposteriorly as in the large carnosaur. The orbit is large, exceeding the first antorbital fenestra in size, and is approximately equidimensional. In dorsal aspect the skull tapers gradually from its widest point in the temporal region into an elongated, abruptly terminated muzzle. The mandible is deeper than usual in the smaller carnivorous saurischians. The alveolar margins of the jaws are lined with compressed, trenchant teeth, bearing witness to the raptorial habits of *Dromaeosaurus*.

**EXTERNAL CRANIAL ELEMENTS:** Only the posterior portion of the left premaxilla is preserved. Near the alveolar border the premaxillo-maxillary contact is vertical, but as the suture rises it curves posteriorly to pass beneath the base of a rather broad ala from the premaxilla bounding the external naris posteroventrally. There are two teeth present in the alveolar margin of the fragment and four additional premaxillary teeth, evidently found in association with the skull. These teeth indicate, as is shown below, that there were four teeth in each premaxilla. The teeth are as large as those in the maxilla, but differ in that the anterior, serrated cutting edge shows considerable posteromedial displacement so that each tooth presents a rounded surface anterolaterally.

This last character, so marked in the premaxillary teeth of *Dromaeosaurus*, approaches the condition typical of the premaxillary teeth in the large Cretaceous carnososaurs. The extreme result of this displacement of the anterior serrated cutting edge in the premaxillary teeth is that each tooth shows a D-shaped cross section, with the serrated edges occupying more or less the posterior buccal and lingual corners of the tooth, and with the posterior face of the tooth between them somewhat flattened.

There are six supposed premaxillary teeth preserved in the type of *Dromaeosaurus*, two of them in place as the posterior teeth in the left premaxilla. Of the four other teeth, all originally loose, two are obviously from the left side and two from the right. Because the serrated cutting edges on the backs of two of these teeth are closer together than in any of the other premaxillary teeth, it can be assumed that they are the first teeth in the premaxillary series on each side. The remaining loose tooth of the left side, which shows serrated edges somewhat more separated each from the other than is the case in the two teeth just mentioned, may be placed as a second premaxillary tooth, to be matched by the other right premaxillary tooth that is preserved. In the third and fourth premaxillary teeth of the left side, preserved in their alveoli, the serrated crests are still farther apart, and approach the characteristic anterior and posterior positions that typify the position of these crests in the maxillary teeth.

The inferior borders of two antorbital fenestrae are indicated in the maxillae. Quite probably a third fenestra was situated in the bar of bone separating these fenestrae, in a more elevated position, as in *Velociraptor* and *Deinonychus* (see Osborn, 1924; Ostrom, 1969, and in press). A sharp flexure in the surface of the bone links the anteroventral margins of both lower antorbital fenestrae. Below the flexure the surface of the alveolar border deepens anteriorly and is marked with numerous small, ventrally opening, U-shaped concavities, containing the exits of the terminal branches of the maxillary division of the fifth nerve. Nine teeth are present in the left maxilla. Seven of the original nine teeth are preserved in the right maxilla; the first two are absent. They are compressed, slightly recurved, and bear serrate edges. The anterior row of serrations, starting at the tip of the tooth, curves proximolingually, so that near the alveolus the serrations occupy a lingual position behind the anterior border of the tooth. The serrations are of equal size on both edges of the tooth. There are approximately 16 serrations per 5 mm. The dentigenous portion of the maxilla ends in front of the antorbital ramus of the lacrimal, although the teeth in this region are not greatly reduced. It is not possible to trace the jugal



FIG. 3. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, skull, dorsal view. Portions restored are cross hatched. The bone shown in the parietal region is a portion of the lateral wall of the braincase erroneously placed in this position.  $\times 2/3$ .



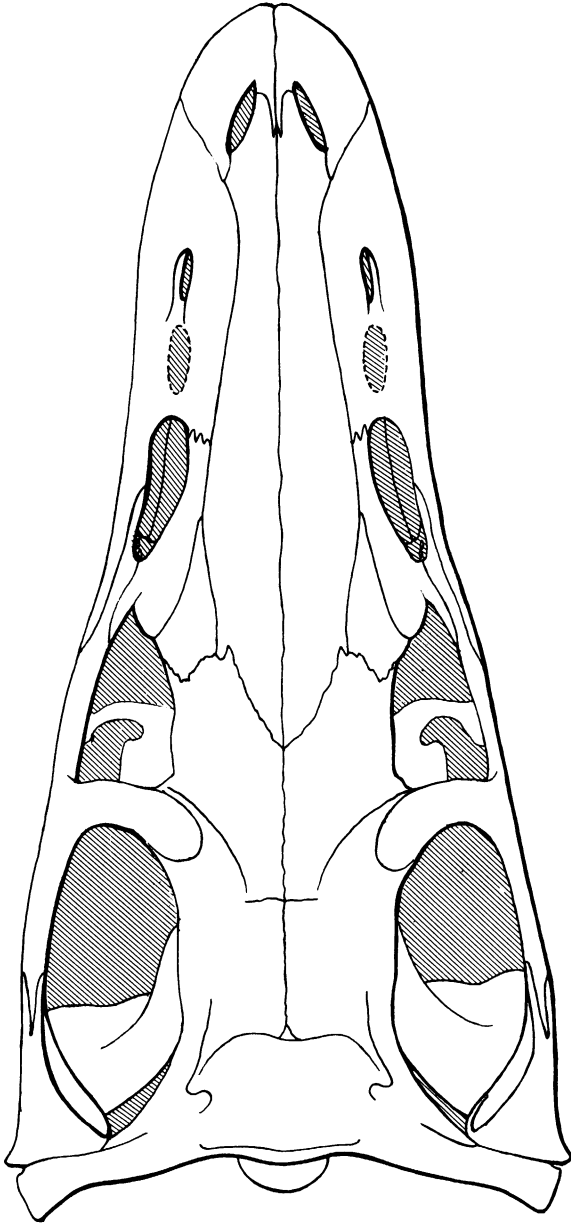


FIG. 4. *Dromaeosaurus albertensis* Matthew and Brown, reconstruction of skull in dorsal view.  $\times 2/3$ .

contact, and the posterior limit of the subjugal process of the maxilla is conjectural. There is no suggestion of interdental plates on the medial surface of the alveolar margin, a condition that is most unusual. A lamina of bone projects dorsomedially, above the alveolar margin. It becomes much broader anteriorly, giving this part of the maxilla a robust appearance in dorsal aspect. The anterior ends of the laminae of each side are not preserved, and it is impossible to ascertain whether or not they met on the midline. If they did, the contact was probably not very extensive. A process rises abruptly from the dorsal edge of each lamina and sends a thin ala of bone posterolaterally, in front of the posterior fenestra, to become confluent with the lateral surface of the maxilla. The oral cavity, situated between the alveolar margin and the medially directed lamina, about equals the height of the crowns of the marginal teeth in depth.

Because of the presence of fine, digitate structures along the anterior edges, as well as their gross bilateral symmetry, the anterior borders of the frontals as preserved are taken to represent the natural limit of the bones (see also Matthew and Brown, 1922, p. 384). They are extensively overlapped medially by a broad, V-shaped tongue from the nasals, from which the presumed prefrontal contacts extended laterally and somewhat posteriorly to the respective orbital rims. The frontals are broad between the orbits, and the roughened orbital margins parallel each other and the cranial midline. Behind the orbits each frontal makes an abrupt turn laterally to form a pedunculate base for the postorbital. Matthew and Brown (*ibid.*) suggested that the prefrontals and postorbitals excluded the frontals from the orbital rims, but, as the prefrontals were apparently limited to the anterodorsal corner of the orbits, and the postorbitals similarly lacked a supraorbital extension, it seems more likely that the roughened rims of the frontals were finished in cartilage. The anterodorsal limit of the supratemporal fenestra is indicated by a ridge curving posteromedially from the posterodorsal corner of each orbit, to approach within 5 mm. of the midline of the skull at the frontoparietal contact. The posterior edge of the frontal is marked by small, nearly vertical ridges and grooves, indicating that a flexible mesokinetic hinge passed transversely through this region. The frontals are separated by a median suture throughout their entire length and are slightly basined dorsally between this suture and the orbital rims. It is not possible to find the laterosphenoid contacts.

There appears to be a small fragment of the right temporal region, showing two sutures. We suggest that this fragment is composed of a small part of the parietal, where it meets the frontal and the latero-

sphenoid. A scar on the proximodorsal surface of the paroccipital process indicates that a small ventrolateral tongue from the parietal covered this region of the process.

The jugal has the triradiate structure typical of most carnivorous saurischians. Its relationships with the maxilla and lacrimal anteriorly are uncertain, owing to the absence of definable sutures. The suborbital and postorbital regions of the jugal are broad, and the bone receives a wide tongue of the quadratojugal within its posterior ramus. The base of the antorbital ramus of the lacrimal is broad and slightly anteriorly inclined. The lunate crest from the jugal rises vertically across the center of its lateral surface. The posterior portion of a slight dorsal rugosity or "horn" has been mounted in plaster on each side of the skull, but other areas of the lacrimal were not preserved. Altogether the arrangement of the jugal, base of the lacrimal, and frontal indicates that the orbital fenestra could not have differed greatly from its shape as restored here.

The quadratojugal is a Y-shaped element, with one broad ala extending forward beneath the lateral temporal fenestra to end in a deep notch within the jugal. The dorsal ramus is very slightly dilated distally and terminates in a posterodorsally inclined, laterally everted lip. A heavier, medially recurved process of the quadratojugal buttresses the lateral edge of the quadratic condyle. A loosely defined, elongate quadrate foramen is contained between the lateral edge of the quadrate shaft and the posterior branches of the quadratojugal. The foramen opens posterolaterally.

The right squamosal abuts against the anterodorsal portion of the paroccipital process. The triangular dorsal surface of the bone narrows anteriorly, but is broken off before it passes beyond the suspensorial region. Indications are, however, that the supratemporal arcade rose toward the posterodorsal corner of the orbit at an angle of about 35 degrees to the longitudinal axis of the skull. The squamosal contains an extensive hollow beneath the external edge of the dorsal surface of the bone, and this looks down on the posterolateral flank of the quadrate. The medial surface of the squamosal is also hollowed to form a small part of the area of origin of the adductor muscle mass passing between the quadratojugal and pterygoid wing of the quadrate to insert on the mandible. Between these two excavations the squamosal sends a long tongue anteroventrally, which passes over the dorsal edge of the quadratojugal and projects slightly into the lateral temporal fenestra. The proximal head of the quadrate fits into a cotylus on the squamosal between this tongue and the paroccipital process.

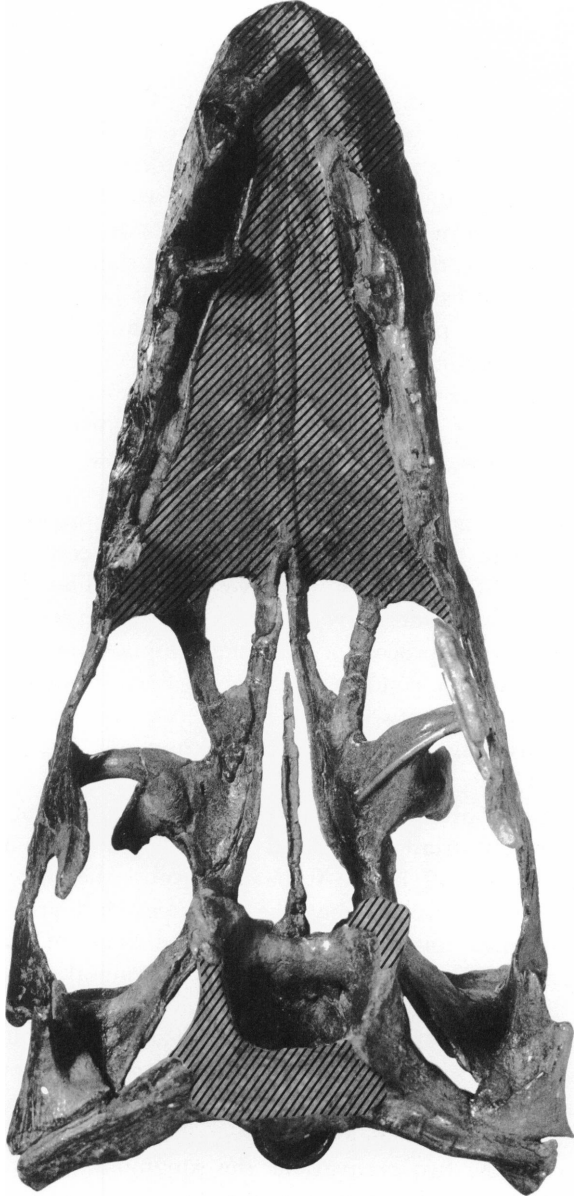


FIG. 5. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, skull with the dorsal roof removed, showing in dorsal view the restored palate, the bones of the palatal and basicranial regions in part, and the floor and walls of the braincase. Portions restored are cross hatched.  $\times 2/3$ .

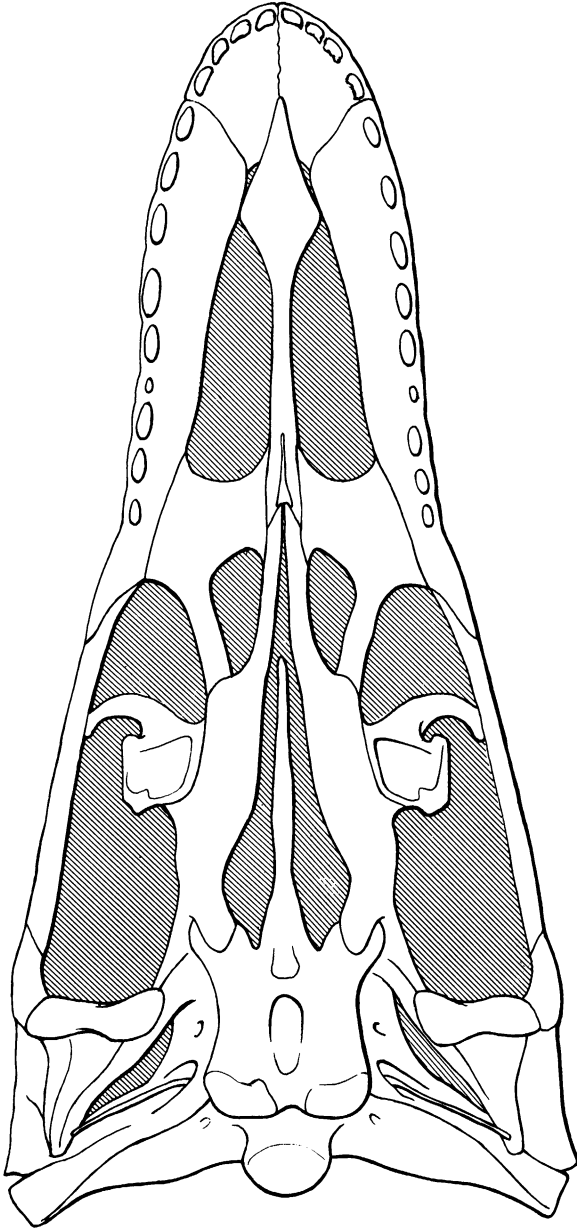


FIG. 6. *Dromaeosaurus albertensis* Matthew and Brown, reconstruction of skull in palatal view.  $\times 2/3$ .

The quadrate is unusually elongate. The posterior and lateral surfaces of the quadrate shaft are smoothly continuous and broadly exposed behind the quadratojugal and squamosal in lateral view. The antero-lateral edge of the shaft is rounded and gently emarginate along the quadrate foramen, above which it thins and extends slightly anterolaterally to touch the quadratojugal. The shaft becomes gradually more slender dorsally but expands into a small condyle at its proximal end, which fits into a cotylus in the squamosal. Elsewhere the quadrate shaft and squamosal do not form a firm contact. A straight, sharp, vertical flexure links the medial mandibular condyle of the quadrate with the squamosal articulation and separates the deep, anteromedially curving pterygoid flange from the main body of the bone. The shaft of the quadrate has a marked anteroventral inclination and ends in a broad, transversely oriented, mandibular articulation which projects well below the alveolar margin of the upper jaw. The lateral condyle and the somewhat larger medial condyle of this articulation are each traversed by a sinuous, oblique, anteromedially trending crest.

**PALATAL ELEMENTS:** The palate of *Dromaeosaurus*, as preserved, does not differ fundamentally from that of *Ceratosaurus* or the tyrannosaurids. A vertical wing of the pterygoid overlaps the medial surface of the quadrate flange almost to its postero-internal border, the dorsal edge of this wing descending anteriorly to a point above the basiptyergoid process of the basisphenoid. In front of this process the greatest transverse dimension of the pterygoid changes from a vertical to a horizontal direction. A posteriorly facing socket of the pterygoid embraces the basiptyergoid process, its ventral surface being extended posteriorly as a sort of shelf beneath this process. The palatal surface of the pterygoid is elongated, and from this portion of the bone a slender, flattened process projects toward the internarial region. The process is unexpanded vertically, in contrast to conditions in the tyrannosaurids.

The left epiptyergoid is present on the dorsal edge of the quadratic wing of the pterygoid, midway between the basiptyergoid process and the posterior termination of the wing. A vertical groove on the ventrolateral surface of the bone seems to divide its base into a broad lip overlapping the dorsal rim of the pterygoid internally, and a narrower, more anteriorly placed external lip. The epiptyergoid narrows dorsally and is in contact with the laterosphenoid above and anterior to the exit of the profundus branch of the fifth cranial nerve, a relationship essentially similar to that seen in *Ceratosaurus* (Gilmore, 1920, p. 85, fig. 54) and *Plateosaurus* (Huene, 1926a, p. 17, pl. 1, fig. 10), in which the contacts with adjacent cranial elements are probably also the same.

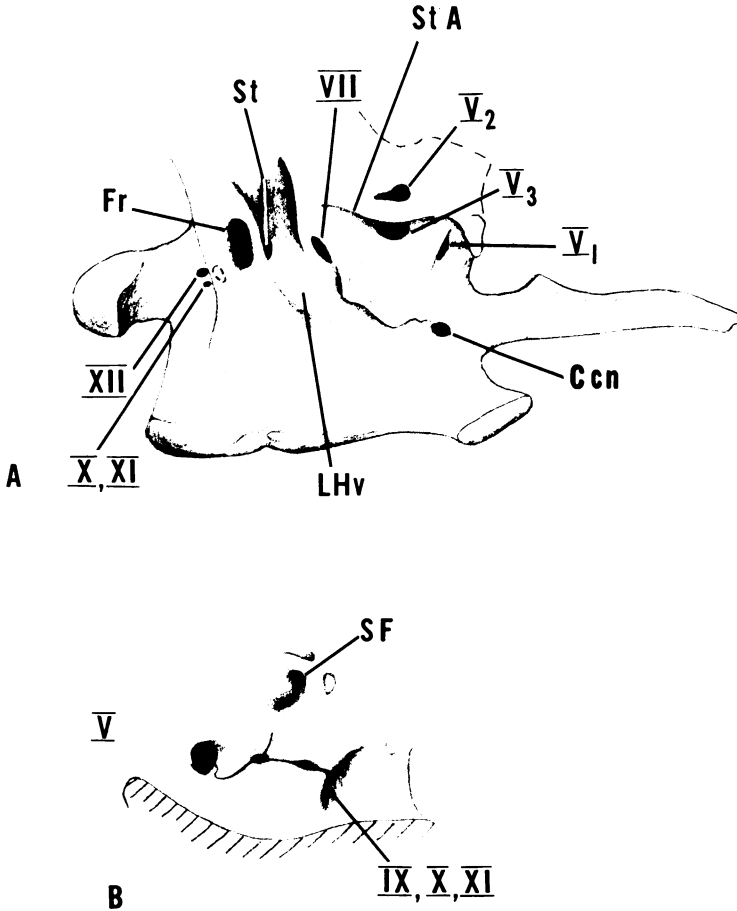


FIG. 7. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type. A. Right lateral view of the braincase. B. Internal view of a portion of the right wall of the braincase. Approximately  $\times 1$ .

Abbreviations: Ccn, carotid canal; Fr, foramen rotundum; LHv, course of lateral head vein; SF, subarcuate fossa; St, stapes; StA, course of stapedial artery; V, V<sub>1</sub>, V<sub>2</sub>, V<sub>3</sub>, foramina for the branches of the fifth cranial nerve; VII, foramen for the seventh cranial nerve; IX, X, XI, XII, foramina for the ninth to twelfth cranial nerves.

A powerful jugular ramus of the ectopterygoid arises from a flattened fan-shaped base sutured to the dorsal surface of the pterygoid. It curves anterolaterally, then lateroventrally to abut in a somewhat expanded articulation against the jugal, medial to the base of the postorbital process. A strong, anteroposteriorly expanded process descends vertically from the ventrolateral edge of the ectopterygoid, beneath the jugular

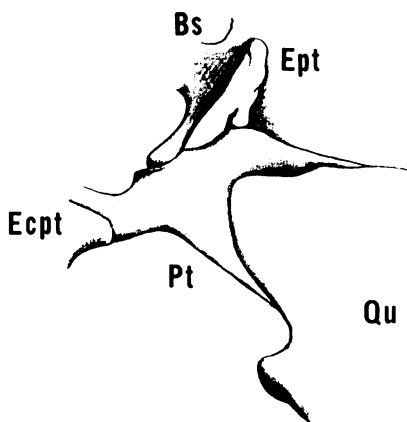


FIG. 8. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, left lateral view, showing the left epipterygoid articulating with the dorsal edge of the pterygoid. The articulations of this latter bone with the ectopterygoid (left) and pterygoid ramus of the quadrate (right) are shown. Approximately  $\times 1$ .

*Abbreviations:* Bs, basisphenoid; Ecpt, ectopterygoid; Ept, epipterygoid; Pt, pterygoid; Qu, quadrate.

ramus. Possibly a thin, strap-shaped extension of the pterygoid bordered this process posteriorly and posterodorsally as it descends, as is the case in tyrannosaurids, but this area is indistinct. The ventral process, slightly expanded distally, is especially noteworthy because its ventral surface is deeply excavated, forming a large ventral hollow, or pocket, similar to, but relatively much larger than, that seen in the ectopterygoid of tyrannosaurids (Osborn, 1912, fig. 6).

A straight, slender process of the palatine projects posteromedially from the maxilla. It expands over the anterior part of the dorsal surface of the pterygoid, entering a deep notch in the anterior base of the ectopterygoid, and divides the suborbital space into a larger lateral and a smaller medial vacuity. The main bodies of the palatines are not preserved, but they probably met the vomers and vomerine processes of the pterygoids near the midline of the skull, as in the tyrannosaurids.

**BRAINCASE:** The anterior and dorsal regions of the braincase of *Dromaeosaurus* are either incompletely preserved or missing entirely, and some of the more minute cranial foramina cannot be found. There are very few clearly discernible sutures within the entire structure, bearing witness to the maturity of the animal when it died. The braincase, however, has not been distorted and is on the whole quite well preserved. Most significantly, it seems to represent a morphology atypical



of the larger saurischian dinosaurs.

The basioccipital is ordinary in appearance. The articulating surface of the occipital condyle is wider than deep and caps a distinct, somewhat ventrally inclined neck which separates it from the occipital face of the skull. The basal tubera are well developed, transversely oriented, and connected medially by a short ridge of bone. In contrast to conditions in the tyrannosaurids, there are no sinuses developed in their posterior surfaces.

The longitudinal axis of the basisphenoid-parasphenoid rostrum parallels that of the skull. Well-developed basiptyergoid processes project anterolaterally and somewhat ventrally from the basisphenoid behind the pituitary fossa. The basisphenoid and base of the parasphenoid rostrum are strongly vaulted along the ventral midline, the vault being bridged by a transverse crest of bone between the bases of the basiptyergoid processes, and posteriorly terminated against the crest of bone linking the basal tubera of the basioccipital. The latter structures are sheathed anterodorsally by a rounded tongue of the basisphenoid from each side of the vault. The parasphenoid rostrum is long and slender, extending anteriorly to a point between the suborbital fenestrae of the palate. Its slightly dilated dorsal margin bears a median longitudinal sulcus, which is accentuated posteriorly by small triangular laminae rising from the dorsolateral edges of the rostrum in front of the pituitary fossa.

The lateral surface of the basisphenoid is smooth and shallowly sulcate longitudinally, and approximately rectangular in outline. There are no visible sutures with adjoining elements of the braincase. The foramen for the internal carotid artery (carotid canal) enters the anterodorsal region of the basisphenoid just below and behind the pituitary fossa (sella turcica). A broad shallow channel is discernible extending posterodorsally from the foramen over the dorsolateral portion of the basisphenoid to the vicinity of the internal auditory meatus in the opisthotic. This channel is partly protected dorsolaterally by a flange (otosphenoidal crest), probably from the laterosphenoid. The channel surely conducted the internal carotid artery to the carotid canal. It is probable that the channel also contained the lateral head vein, and may even have transmitted the palatine ramus of the facial (seventh) nerve beneath the otosphenoidal crest to the roof of the mouth.

In internal aspect the basisphenoid forms the floor of the anterior medullary cavity and, as preserved on the right braincase wall, extends dorsolaterally to form the ventral margin of the foramen for the undivided stem of the trigeminal (fifth) nerve. From this point the basi-



FIG. 9. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, basicranial portion of the skull in ventral view. The two stapes are in position.  $\times 1$ .

sphenoid-prootic suture rises posteriorly to a small foramen situated at the base of the internal prootic-opisthotic suture, which may have enclosed the roots of the facial nerve, as well as those of the acoustic (eighth) nerve. It is not possible to find the basisphenoid-basioccipital contact internally, but the suture between the opisthotic and median braincase element continues horizontally back to the center of the anterior edge of a large vertically lunate fissure (vagal foramen), which must have contained the combined roots of cranial nerves 9 through 11.

One of the most striking peculiarities of the endocranial cavity is its great breadth, especially in the anterior medullary region. If the posterior moiety of the brain even approximately filled this space, it must have been very broad indeed. The dorsum sellae is also a very broad structure, with a low, gently rounded, dorso-anterior crest. The area on each side of the midline behind the crest of the sellae may contain the point of entrance of the abducens (sixth) nerve into the basisphenoid, but clearly defined foramina are not preserved. The pituitary fossa is relatively shallow, and terminates below in a shallow, longitudinal sulcus on the dorsal and posterior surface of the parasphenoid rostrum. It is not bounded laterally by flanges from the laterosphenoid, as is the case in the tyrannosaurs. The exits for the internal carotid artery and sixth cranial nerve are not preserved in the posterior wall of the pituitary fossa.

The otosphenoidal crest probably represents the ventralmost development of the laterosphenoid. Within the laterosphenoid, above the otosphenoidal crest and behind the lateral pituitary fenestra, are three prominent foramina representing the external conduits for the three divisions of the fifth nerve, which separate within the braincase wall. The foramen for the profundus branch ( $V_1$ ) lies above the lateral opening of the carotid canal, on approximately the same level as the crest of the dorsum sellae internally. It faces anterolaterally and is bounded posteriorly by a gentle vertical swelling on the external surface of the laterosphenoid. The epipterygoid is reconstructed to have been in contact with the laterosphenoid immediately above this foramen, between it and the posterior rim of the pituitary fenestra. A heavy, overhanging crest extends posteriorly across the face of the laterosphenoid from the epipterygoid contact to fade out in the prootic above the foramen for the seventh nerve. A large, horizontally oval foramen lies beneath this crest about midway between the exits for the profundus branch of the fifth and the seventh nerves. This foramen marks the exit of the mandibular ramus of the fifth nerve ( $V_3$ ), and possibly also the middle cerebral vein. The stapedia branch of the

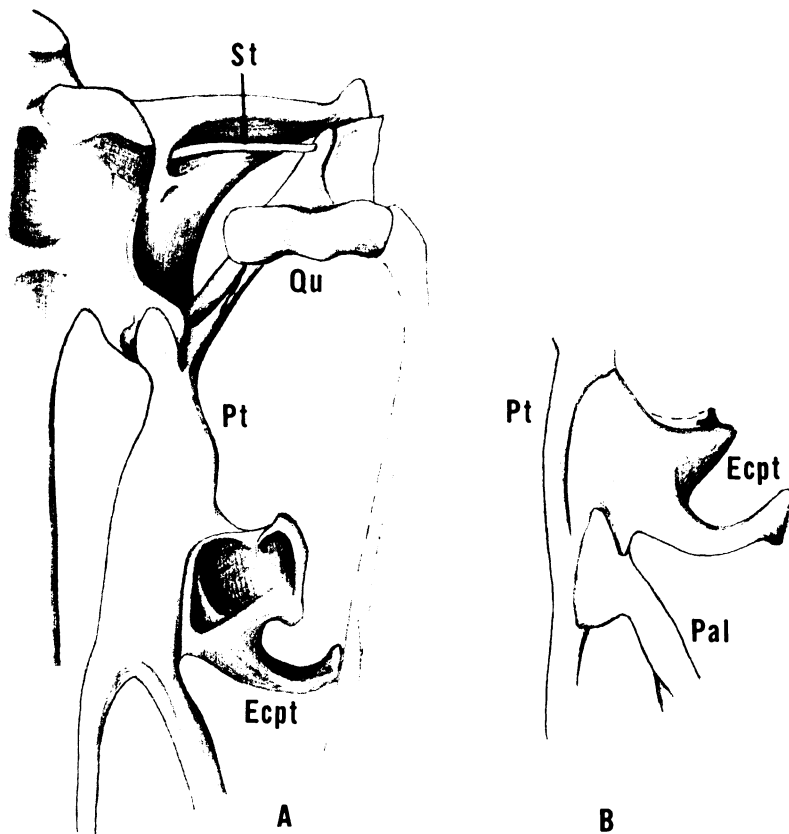


FIG. 10. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type. A. Basicranial and posterior palatal region of the skull, ventral view. Note the deeply "pocketed" ectopterygoid. B. Junction of the pterygoid, ectopterygoid, and palatine bones as seen in dorsal view. Approximately  $\times 1$ .

Abbreviations: Ecpt, ectopterygoid; Pal, palatine; Pt, pterygoid; Qu, quadrate; St, stapes.

internal carotid artery was very likely carried forward from the internal auditory meatus across the laterosphenoid beneath the heavy, gently undulating crest, to pass under the epipterygoid anteriorly. The foramen for the maxillary branch of the fifth nerve ( $V_2$ ) lies directly above the exit for  $V_3$ , near the dorsal border of the heavy longitudinal crest.

The laterosphenoid is not preserved above the exits of the fifth nerve, but if it was in contact with the postorbital behind the orbit in the usual archosaurian fashion, the dorsal portion of the bone must have

risen steeply in front of the pituitary fossa and been unusually elongate. The anterodorsal region of the braincase walls are not well-enough preserved to indicate the presence of orbitosphenoidal elements, although more ventrally there is no evidence of the presphenoids. Altogether the large size of the endocranial cavity in the region of the mesencephalon and the steeply rising laterosphenoid indistinguishably fused to the prootic lend the braincase a superficially lacertilian appearance in lateral view. Evidently the braincase was more broadly open anteroventrally than is normally the case in advanced carnosours and sauropods. In order to meet the olfactory tracts beneath the frontals, the cerebral hemispheres must have lain nearly directly above the pituitary fossa, in a position similar to that reconstructed by Camp (1930, fig. 46) in the phytosaurs.

The prootic is exposed laterally behind the separate exits for the maxillary and mandibular branches of the fifth nerve. No lateral sutural contacts are visible between the prootic and the basisphenoid below, and the opisthotic behind. A tongue of the prootic probably extended over the anterior base of the paroccipital process, above and behind the internal auditory meatus, but no sutures are preserved in this region. A lenticular foramen near the posterior end of the otosphenoidal crest, on a level with the exit for the profundus branch of the fifth nerve anteriorly, marks the lateral exit of both branches of the facial (seventh) nerve.

On the medial surface of the braincase the prootic meets the opisthotic in a vertical suture above a small foramen, which, as noted above, possibly contained the roots of the seventh and eighth nerves. This suture rapidly vanishes dorsally, as the swelling that houses the structures of the internal ear is approached. A rather deep reniform depression (subarcuate fossa) is present on the anteromedial wall of the otic capsule, bounded posteroventrally by a rounded crest of bone which probably contains the anterior vertical semicircular canal. The depression may have contained either the auricular lobe of the cerebellum or the endolymphatic sacculus. Farther anteriorly on the medial braincase wall the prootic-basisphenoid contact descends to the base of a very large foramen for the roots of the fifth nerve. This foramen lies in a shallow concavity, suggesting the presence in life of a well-formed Gasserian ganglion.

The structures of the lateral wall of the inner ear are well preserved on the right side of the braincase. The large channel for the lateral head vein curves dorsoposteriorly beneath the foramen for the seventh nerve and continues laterally across the proximal two-thirds of the

anteroventral region of the paroccipital process. The groove is quite deep in the latter area, where it is approximately parallel to the long axis of the proximal portion of the stapes below. The fenestra ovalis is clearly indicated by the proximal end of the stapes. It is a small foramen situated near the posterior border of the groove for the lateral head vein, on about the same level as that of the foramen for the seventh nerve. The fenestra rotunda, containing the perilymphatic duct and probably also the glossopharyngeal (ninth) nerve, lies on this level as well. It is a very large oval foramen, separated from the fenestra ovalis by a low ridge of bone. The fenestra rotunda communicates internally with the remnant of the metotic fissure (vagal foramen), containing the roots of nerves 9 through 11.

The paroccipital process is a slender structure relative to conditions in the large carnososaurs. It projects laterally, with a posterior inclination of about 70 degrees to the longitudinal axis of the skull, coming to an abrupt termination distally. The distal end is flattened and sharply "twisted," so that a line drawn from the ventrolateral to the dorso-lateral edge would slope upward at an angle of about 50 degrees to the longitudinal cranial axis.

On the occipital face of the skull, the exoccipitals bound a very large foramen magnum, the dorsal border of which is situated about as far above the occipital condyle as the basal tubera of the basioccipital extend below it. There are no indications of a supraoccipital contact dorsally, probably because this region of the skull is not well preserved. The two exoccipitals appear to be widely separated on the upper surface of the occipital condyle, in contrast to the situation in the tyrannosaurids, in which they are nearly in contact. A cluster of three foramina opens directly onto the surface of the exoccipitals on each side of the base of the condylar neck. The most median of these probably contained the hypoglossal (twelfth) nerve, whereas the vagus and accessory (tenth and eleventh) nerves probably passed through the remaining foramina. They are all widely separated from the structures on the lateral surface of the otic capsule by the heavy ventral edge of the paroccipital process.

**STAPES:** Particular mention should be made of the stapes in *Dromaeosaurus*, especially because the stapes, a slender and fragile bone in dinosaurs, is rarely preserved. Fortunately both stapes are present in *Dromaeosaurus* and have been previously studied and described in detail (Colbert and Ostrom, 1958). The description is here paraphrased and summarized.

The stapes in *Dromaeosaurus* is an elongated, slender, rodlike bone,

extending from the fenestra ovalis in the wall of the braincase to a termination near the upper end of the quadrate. Thus it is directed laterally and posteriorly, and such being the case it may be assumed that the tympanum was dorsally situated in *Dromaeosaurus*.

Although the cross section of the stapes is circular throughout most of the length of the bone, it shows some distal flattening, with the long

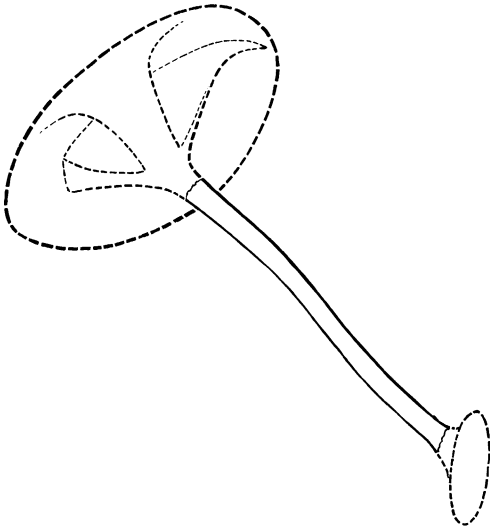


FIG. 11. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, right stapes, with the foot plate, extracolumella, and tympanic membrane restored on the basis of comparisons with crocodylians. From Colbert and Ostrom (1958).  $\times 2$ .

axis of the cross section horizontal in this region. It seems likely that if there was an extracolumella it was cartilaginous and comparatively short, as is the case in the one group of living archosaurians, the crocodylians.

As mentioned above, the stapes lies within a long groove formed mostly by the paroccipital process of the opisthotic but to some extent by the opisthotic as well. It seems probable that in life the elongated cavity that housed the stapes was completed by a cartilaginous ventral floor. A drawing of the stapes, with its footplate as well as the tympanic membrane restored, is shown in figure 11, compared with the stapes and membrane of an alligator.

COMPARISONS: In general appearance the muzzle of *Dromaeosaurus* is similar to that of other small theropod dinosaurs. A wing from the pre-

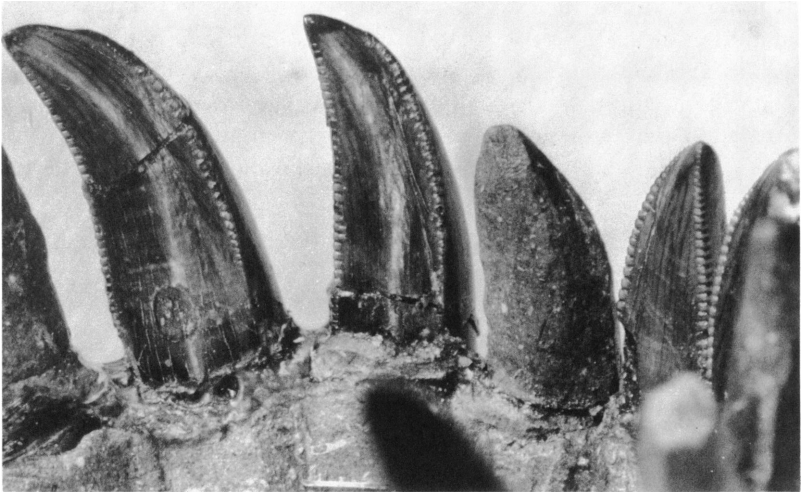


FIG. 12. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, premaxillary teeth, showing the displacement of the serrated ridges to the lingual sides of the teeth.  $\times 4$ .

maxilla bounds the external naris ventroposteriorly as in *Ornitholestes* and *Velociraptor*, whereas in the tyrannosaurids a ventrolateral process of the nasal usually occupies this position. The premaxillary teeth are comparable in size with those of the maxilla, as in these genera and in *Allosaurus*. In *Dromaeosaurus* the anterior serrated edges of the premaxillary teeth are displaced posteromedially, more so in the first two teeth than in the third and fourth teeth. Thus these teeth approach the condition seen in the tyrannosaurids, in which the premaxillary teeth are reduced and bilaterally compressed, with both carinae situated on the posterior surface of the crown. In certain of the more generalized saurischians, such as *Coelophysis* and *Plateosaurus*, the maxillary tooth row extends back to a point beneath the orbits. The alveolar border of the maxilla ends in front of the antorbital ramus of the lacrimal in *Dromaeosaurus*, as in most Jurassic-Cretaceous carnosaur. *Dromaeosaurus* differs sharply from the carnosaur in lacking interdental plates on the medial alveolar surface of the maxilla. The orbits are large, in keeping with the small size of the skull.

In *Dromaeosaurus* the nasals and frontals are broadly exposed on the dorsal surface of the skull, as in most Jurassic-Cretaceous theropods, with the exception of the tyrannosaurids. Apparently the parietals were unusually broad between the supratemporal fenestrae, perhaps as a result



of the small size of the skull and the enlarged endocranial cavity. The paroccipital ala of the parietal is extremely short and perhaps widely separated from the squamosal, whereas in *Ornitholestes*, *Ceratosaurus*, *Allosaurus*, and the tyrannosaurids these elements are in contact above the paroccipital process.

The supratemporal arcade is relatively much longer than in *Ornitholestes* and the large carnosaurs. The supratemporal and lateral temporal fenestrae are correspondingly expanded anteroposteriorly. The elongation of this portion of the skull may be reflected in the great dorso-anterior length postulated for the postorbital ramus of the laterosphenoid, and possibly even in the peculiar slope of the quadrate.

The suspensorium is relatively primitive in *Dromaeosaurus*. The long, straight, quadrate shaft is bounded dorsolaterally by a descending ala of the squamosal, much as in *Plateosaurus* (Huene, 1926a, pl. 1) and *Yaleosaurus* (Lull, 1953, fig. 15). These conditions exist to a lesser degree in *Ceratosaurus*, *Allosaurus*, and *Acrocanthosaurus*, although the head of the quadrate is broadly exposed laterally in these genera. In the tyrannosaurids the ventral border of the infratemporal ala of the squamosal lies on the same level as the squamosal-quadrate articulation. In *Struthiomimus* (Osborn, 1917, fig. 5a) the descending ala of the squamosal is separated from the quadrate dorsally by a slender process from the quadratojugal. The supratemporal ramus of the squamosal does not rise steeply in front of the paroccipital process in *Dromaeosaurus*, as it does in the large carnosaurs. Further, the quadrate and quadratojugal are only tenuously united above the quadrate foramen in *Dromaeosaurus*, if at all. The quadrate shaft has a marked anteroventral inclination, whereas in all other known theropods except the ornithomimids and possibly *Velociraptor*, the quadrate is either vertical or inclined posteroventrally. The quadrate is more extensively exposed laterally than in any other theropod, with the possible exception of *Velociraptor*.

When the braincase of *Dromaeosaurus* is compared with braincases in the tyrannosaurids, the following points of difference may be observed.

The paroccipital processes of *Dromaeosaurus*, although strong, are nevertheless relatively more slender than the same structures in the tyrannosaurids. Moreover, they slope only slightly posteriorly, whereas in the large carnosaurs these processes are directed posteriorly at very strong angles to the transverse face of the occiput. Furthermore, there is no development of sinus cavities within the basioccipital-basisphenoid and paroccipital processes as is the case in the tyrannosaurids. Again the basipterygoid processes are short and the braincase is shallow, whereas in the tyrannosaurids the basipterygoid processes are rather

elongated, and the braincase is deep.

In *Dromaeosaurus* the exits for the trigeminal and facial nerves are widely spaced on the lateral wall of the braincase. The laterosphenoid appears, from present evidence, to have been a slender element in lateral aspect, with its longest dimension in a vertical direction. The prosencephalon must have risen almost vertically above the pituitary fossa, thereby giving the brain stem an even more accentuated L configuration than is the case in the tyrannosaurids. The parasphenoid rostrum is long and slender in *Dromaeosaurus*.

The braincase of *Dromaeosaurus* also differs from that of *Allosaurus* (Osborn, 1912, figs. 9–11) in all the above-listed characters. A fragment of the basioccipital-basisphenoid of the latter genus from the Cleveland Quarry, Utah, now in the collections of the National Museums of Canada, was found to contain large, matrix-filled cavities. In addition, the paroccipital processes of *Allosaurus* are much more sharply inclined ventrodistally than in either *Dromaeosaurus* or the tyrannosaurids. Because the quadrate of *Ceratosaurus* is relatively much longer than that of *Allosaurus* (compare Gilmore, 1920, pls. 4 and 18), the paroccipital processes are directed posteriorly in a horizontal plane in *Ceratosaurus*, as in *Dromaeosaurus*. Huene (1926b, p. 96; see also Gilmore, 1920, pl. 36, figs. 1, 2) noted that the endocranial cavity of *Ceratosaurus* differs from that of *Tyrannosaurus* (Osborn, 1912, pls. 3, 4) in that the cerebral hemispheres are situated almost directly above the pituitary fossa in the former genus, the cerebral hemispheres and diencephalon are much larger relative to the diameter of the foramen magnum, the medullary cavity is shorter, and the vagal foramen is larger and vertically oriented. The endocranial cavity of *Dromaeosaurus* is similar to that of *Ceratosaurus* and differs from that of *Tyrannosaurus* in all these features.

The cranial fragment of *Eustreptospondylus divesensis* figured by Piveteau (1923) and Walker (1964, fig. 17f) resembles the skull of *Allosaurus* and *Ceratosaurus* in the arrangement of the bones of the posterior cranial roof. The braincase itself is more primitive than that of *Allosaurus* and approaches the conditions found in *Dromaeosaurus* in that the broken ends of the basiptyergoid processes and the basal tubera lie on the same level, parallel to the long axis of the parasphenoid rostrum, which is greatly elongated in a horizontal direction. The paroccipital processes slope backward in a horizontal plane as is the case in *Ceratosaurus* and *Dromaeosaurus* and are not depressed distally as in *Allosaurus*. The basiptyergoid processes evidently have not begun their descent, as, accompanying the shortening and deepening of the temporal region, they have in *Allosaurus*, *Acrocanthosaurus*, and the tyrannosaurids. Although

there is no implication of a special relationship between *Eustreptospondylus* and *Ceratosaurus*, it should nevertheless be noted that the two genera resemble each other and differ from *Allosaurus* in that the paroccipital processes are horizontal (*E. divesensis*), the nasal-frontal suture lies in advance of the orbits (*E. oxoniensis*; see Walker, 1964, fig. 17e, and *E. divesensis*), and the prefrontals are broader and do not extend so far posteriorly (compare Walker, 1964, p. 125, fig. 17e, with Gilmore, 1920, p. 81, pl. 18, fig. 1).

#### THE LOWER JAW

**DESCRIPTION:** The lower jaw of *Dromaeosaurus* is comparable with that of *Allosaurus* in proportional depth, being more robust than is normally the case in small carnivorous saurischians, and more slender, especially in its postdentary region, than is the case in the tyrannosaurids. The jaw ends abruptly behind the mandibular cotylus in a broad, shallow, retroarticular process, having the form of a wide shelf. A vertical, columnar-like process rises from the posteromedial corner of the retroarticular region or shelf, to a level above that of the articulation between the quadrate and articular. This vertical process deserves special consideration.

A comparable but not homologous structure is well developed in many modern birds, as, for example, among the North American grackles. In these birds a large process rises obliquely (vertically and medially) from the inner corner of the mandibular cotylus. Proportionally, it is of about the same dimensions as the vertical process in *Dromaeosaurus*. Morphologically it is almost certainly a convergent feature, evolving independently among the birds and in *Dromaeosaurus*. In the dinosaur the process arises from the posteromedial corner of the broad retroarticular shelf; consequently it is behind the quadrate-articular joint. In the birds this process rises from the medial border of the mandibular cotylus; consequently it is medial to the medial condyle of the quadrate. In spite of these differences, pointing to separate and independent origins, the process probably served some similar functions in both the dinosaur and the birds.

Bock (1960) has made a thorough and most illuminating study of this feature in birds. He has shown that this process, which he designates as the "medial process" of the mandible, is variously developed (or even undeveloped) in many families of birds. Moreover, he shows that its functional adaptations are various. In the grackle, for example, the large medial process of the mandible is so situated and shaped that, as the jaw is opened, the process swings forward, its tip moving in a forward arc away from the basitemporal plate of the occiput. The

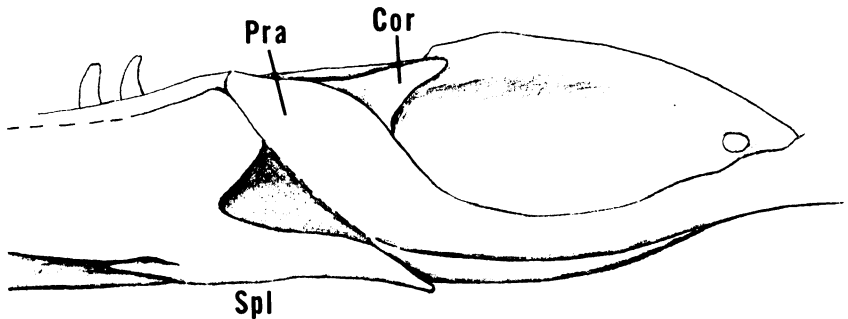


FIG. 13. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, internal view of a portion of the right mandibular ramus, showing the coronoid articulating with the prearticular, and this latter bone, in turn, with the posterior part of the splenial. Note the well-defined surangular foramen on the extreme right. Approximately  $\times 1$ .

Abbreviations: Cor, coronoid; Pra, prearticular; Spl, splenial.

process serves all birds for insertions of the depressor mandibulae muscle and the pterygoid muscle, this being the primary adaptation of the medial process associated with its origin in birds. In certain birds, however, such as, for example, the plovers and skimmers, the medial process of the mandible is so situated and so shaped that its tip abuts against a ventral process, the "lateral basitemporal process," on the basitemporal plate of the skull, forming a secondary articulation between the skull and mandible. Bock has termed this abutment of the medial process against the lateral basitemporal process the "medial brace" of the mandible. He has shown that the medial brace "serves to support the mandible and prevent its disarticulation when the bill is opened" (Bock, 1960, p. 32).

These adaptations in the plovers and skimmers have led us somewhat far afield from *Dromaeosaurus*, but there is good reason to think that the development and function of the medial process of the mandible in birds gives us a significant clue as to the probable function of the comparable process in *Dromaeosaurus*. Perhaps in *Dromaeosaurus*, as in the grackles, the pterygoid and depressor mandibular muscles required this specialized area of insertion which was the original adaptation responsible for the origin of the process. As the process elongated, it curved medially and dorsally until its tip approached or came in contact with the posterior face of the quadrate when the mandible was depressed. Thus this process may have served as a bony "stop," to prevent excessive opening of the mandible and its possible disarticulation when

the jaws were opened widely.

The surangular-articular suture of the *Dromaeosaurus* jaw seems to have crossed the mandibular cotylus anteromedially in the usual manner. The slender prearticular curves forward beneath the Meckelian fossa and rises anteriorly, expanding into a flat, feather-shaped termination.

In front of the mandibular cotylus the angular forms the ventral border of the posterior moiety of the lower jaw. The dorsal edge of the angular is broadly exposed laterally. Anteriorly the bone narrows and curves dorsally over a sulcus in the posterior ramus of the splenial, into the anterior portion of the Meckelian fossa. The upper rim of the surangular is bent dorsomedially to form an area of insertion for the lateral temporal musculature. Anteriorly the rim loses its distinctiveness, and the bone becomes flatter. A small triangular coronoid is present between the anterodorsal end of the prearticular and the dorso-medial edge of the surangular. A portion of the thin, ventral margin of the surangular forms, in the anterior region of the bone, the upper border of a rather small mandibular fenestra, the broadly rounded ventral border of the fenestra being formed by the angular. A small circular foramen is present beneath the inflected dorsal rim of the surangular, well in advance of the mandibular cotylus.

The dentary is rectangularly elongated in lateral aspect, with its posteroventral corner produced backward as a thin flange, so that the splenial is partly exposed laterally. A row of well-marked foramina beneath the alveolar margin, and scattered, more ventrally situated pits mark the exits of terminal branches of the mandibular division of the fifth nerve. There are alveoli for eleven teeth in each dentary. Although the distal end of its broad anterior wing is not preserved, the splenial does cover most of the posteromedial surface of the dentary. The bone is deeply notched posteriorly. It makes a contact with the prearticular posterodorsally and sends a long, slender ramus back to underlap the anterior end of the angular. A slender, horizontal cleft is present on the ventral margin of the splenial, above the posteriormost, medially exposed portion of the ventral edge of the dentary. An intercoronoid strengthened the lingual alveolar margin of the dentary. The mandibular symphysis was obviously ligamentous.

COMPARISONS: The lower jaw of *Dromaeosaurus* exhibits several peculiarities. The large ascending process on the retroarticular process, the possible function of which is discussed above, is similar to, but relatively more powerfully developed than, the same structure in *Allosaurus* (Gilmore, 1920, fig. 15). This process is shortened, deepened, excavated from behind, and closely applied to the posterior rim of the mandibular



FIG. 14. *Dromaeosaurus albertensis* Matthew and Brown, A.M.N.H. No. 5356, type, bones of the left pes in dorsal view, and hyoid bones. The bones of the pes, from left to right, are the distal ends of the first, second, and third metatarsals, with the first and second phalanges of the second digit and the second phalanx of the third digit, and, in the lower right corner, the fourth phalanx of the third digit and the first phalanx of the first digit.  $\times 1$ .

cotylus in tyrannosaurids. In *Dromaeosaurus*, *Velociraptor*, and to some extent in *Ceratosaurus* the splenial is exposed laterally beneath the ventral edge of the dentary, and the angular excludes the prearticular from the ventral margin of the posterior half of the jaw anterior to the mandibular cotylus. In tyrannosaurids a thin tongue from the dentary



FIG. 15. *Dromaeosaurus albertensis* Matthew and Brown. A-C. A.M.N.H. No. 5356, type, metatarsal and phalanges of left second digit. D. N.M.C. No. 12240, ungual. E. N.M.C. No. 12072, right fourth metatarsal. F, G. *Deinonychus antirrhopus* Ostrom, Y.P.M. No. 5205, phalanges of left second digit. Lateral views.  $\times 1$ .

covers the ventroposterior ramus of the splenial, and the prearticular reaches the ventromedial border over all except the most anterior portion of the posterior half of the lower jaw. There is a large circular foramen in the ventral margin of the splenial in tyrannosaurids, in the same position as the horizontal notch in *Dromaeosaurus*, and in *Plateosaurus*, *Velociraptor*, and *Ceratosaurus*. The surangular and angular of *Dromaeosaurus* embraced a mandibular fenestra ventroanteriorly, as in all known theropods except the tyrannosaurids. The foramen in front of the mandibular cotylus in *Dromaeosaurus* probably is homologous with the more posteriorly situated but relatively smaller opening in *Allosaurus* and the comparatively large fenestra in the tyrannosaurids. The opening presumably contained the cutaneous branch of the mandibular nerve.

#### THE PES

DESCRIPTION: A number of scattered foot bones were found in association with the type skull of *Dromaeosaurus albertensis*. These were compared with elements in the manus of *Struthiomimus* and *Gorgosaurus* by Matthew and Brown (1922, pp. 384-385), although it was not specifically stated whether the bones were from the manus or the pes. Gilmore (1924a, p. 2) noted that the distal articulation of one of the metapodials is deeply grooved, unlike conditions in the pes of any of the then-known carnivorous dinosaurs, and that the phalanges of the manus of *Ceratosaurus* relatively were as short as the phalanges in the type of *Dromaeosaurus*. The uncertainty regarding the homologies of these elements is easily resolved when they are compared with the appendicular skeleton of *Deinonychus* (see Ostrom, 1969, and in press). Apparently all of them pertain to the left pes, and the following bones may be identified: distal ends of the first, second, and third metatarsals, first phalanges of the first and second digits, second phalanx of the second digit, and three fragmentary and two complete phalanges from the third and fourth digits, including the proximal corner of one ungual.

The pes of *Dromaeosaurus* resembles that of *Deinonychus* in great detail, and such differences as do appear to exist are minor. An isolated fourth metatarsal (N.M.C. No. 12072), from the Oldman Formation, here referred to *Dromaeosaurus*, seems to demonstrate that the metatarsus in *Dromaeosaurus* was of the same proportional general length and thickness as that in *Deinonychus*. The phalanges of the pes are, however, slightly stubbier than those in the latter genus. An isolated ungual of the second digit (N.M.C. No. 12240), also from the Oldman Formation, greatly resembles the same element in *Deinonychus*, but differs in that it



is less recurved, and the ventral edge is more trenchant.

COMPARISONS: The pes of *Dromaeosaurus* shows some unusual features that are seen in certain other Cretaceous theropods, notably in *Deinonychus*. These characters in particular are the grooved distal articular surfaces of the second and third metatarsals, the large radius of curvature of the distal articulation of the penultimate phalanx of the second digit, and the very large, recurved claw, seen from an isolated ungual (N.M.C. No. 12240), here referred to the second digit of *Dromaeosaurus*, articulating with this specialized articular facet. These same characters are typical of *Velociraptor* as well as of *Deinonychus* and *Dromaeosaurus* and distinguish the pes in the three genera here named from the foot in other theropods. The same three genera further resemble one another in the relative shortness of the metatarsus, in contrast with the metatarsus in *Stenonychosaurus* and many other Cretaceous theropods. In short, it appears that in these three genera the inner toe, with its very large claw, of a functionally three-toed pes was capable of being raised and lowered, and perhaps utilized rather independently of the other toes. This peculiarly specialized toe may have been so adapted for defensive purposes or for digging.

#### FUNCTIONAL MORPHOLOGY

From the foregoing descriptions it is apparent that *Dromaeosaurus* is characterized by certain adaptations which seemingly are shared by some other theropod dinosaurs, notably the genera *Deinonychus* and *Velociraptor*. So far as *Dromaeosaurus* is concerned, these adaptations can be seen only in the skull and jaws, and to some degree in the pes, but, as *Dromaeosaurus* and *Deinonychus* are very close to each other within these limited osteological areas, it may be assumed that resemblances probably were close in other parts of the skeleton as well. Ostrom (1969, and in press) has already described *Deinonychus* from the relatively complete materials available to him, so that a comprehensive view of the many characters distinctive of this group of theropods and their interpretation in terms of functional morphology are obtainable in his work. The skull of *Dromaeosaurus*, however, incomplete though it is, nevertheless offers an opportunity for exploring the problem of its functional morphology in a fairly satisfactory manner.

#### CRANIAL KINESIS IN *Dromaeosaurus*

The skull of *Dromaeosaurus* seemingly was kinetic, as was first recognized by Nopcsa (1928, p. 183) when he placed the genus in his "Megalosaurinae" along with carnosaurian forms he considered to possess kinetic

skulls. A mesokinetic hinge evidently separated the frontal and parietal on the dorsal surface of the skull. The basal articulation between the basisphenoid and pterygoid was movable, and the expanded proximal end of the quadrate was contained in a cotylus on the under surface of the squamosal. Further, the mutual contacts of the jugal, postorbital, and quadratojugal were flexible, and an axis of rotation probably passed transversely through the contact of the latter element with the external condyle of the quadrate.

The small fragment of bone from the right temporal region indicates that the parietal was firmly sutured to the laterosphenoid. A sutural scar on the proximodorsal edge of the paroccipital process also suggests that the parietal was firmly fixed to the braincase posteriorly, so that metakinetic movement was suppressed. A functional mesokinetic axis would require a flexible or movable connection between the frontal and laterosphenoid; the postorbital probably was capable of rotating to some extent on the posterolateral corner of the frontal.

Muscles of the constrictor dorsalis group, a protractor pterygoidei plus the levator pterygoid, linking the pterygoid-quadrate complex with the braincase, were surely present in *Dromaeosaurus*. It is unfortunate that the only surviving archosaurian derivatives are the crocodiles, which are akinetic, and the birds, in which the kinetic system is so different that it cannot be compared in detail with that of *Dromaeosaurus*. The most logical position from which to reconstruct the constrictor dorsalis musculature is in the plane of the epipterygoid, as in *Sphenodon* (Ostrom, 1962) and the lizards (Frazzeta, 1962). The probable origin of the constrictor dorsalis muscles is from the prominent horizontal crest of bone on the laterosphenoid, and their area of insertion can reasonably be interpreted to be along the dorsomedial surface of the quadrate wing of the pterygoid; hence the muscles would run dorsally and somewhat anteromedially from the palate to the braincase.

Kinetic movement in *Dromaeosaurus* is postulated to have operated in the following manner. Activation of the constrictor dorsalis muscles pivoted the pterygoid wing of the quadrate anterodorsally about the quadratosquamosal joint, swinging the base of the quadrate anterodorsally. The flexible connections between bones of the temporal region permitted a slight shift in their relationships, so that the horizontal thrust from the base of the quadrate was transmitted forward, thereby forcing the muzzle to rotate upward about the mesokinetic axis. Vertical force on the palate may have been relieved through a bending of the slender horizontal bar of the pterygoid immediately anterior to the basal articulation. The reverse movement was accomplished by the

horizontal component of the force from the contracting jaw adductor muscles which rotated the quadrate posteriorly and depressed the muzzle about the mesokinetic axis.

This kinetic mechanism resembles that of birds, especially *Archaeopteryx*, as described by Bock (1964), in that the braincase seems to have been fused to the skull roof. In *Dromaeosaurus* and *Archaeopteryx* the horizontal component of force is transmitted between the quadrate and muzzle through the lateral temporal elements and to a lesser extent through the palate. In lepidosaurs, in which the skull roof and braincase remain separate and the infratemporal arcade is absent, the palate carries this thrust. The possible functions of kinetic movements within the reptile skull have been discussed in detail by Frazzetta (1962).

### THE AFFINITIES OF *DROMAEOSAURUS*

Any attempt to estimate the systematic position of *Dromaeosaurus* is much encumbered by our incomplete knowledge of theropod evolution, particularly with regard to the smaller forms. It is doubtful that half of the larger taxonomic groupings of theropods that have been created are known from reasonably complete skeletal material of a single species. The morphologic extremes represented by the crania of *Oviraptor* and *Tyrannosaurus* give some indication of the diversity within the suborder. The sequence of derivation of these two genera from ancestral forms is unknown. These are but two examples of the lack of phylogenetic information so prevalent in this assemblage of dinosaurs.

In the absence of any direct information bearing on the derivation of *Dromaeosaurus*, some attempt must be made to separate those features of its morphology that are specializations peculiar to the animal from those that may be useful in determining its general relationships. Several characters, including the postulated length of the laterosphenoid, the length of the supratemporal arcade and temporal fenestrae, and the slope of the quadrate, seem to be related to a general increase in the length, and to a lesser degree the height, of the upper part of the temporal region. Because this complex of characters has not been modified by subsequent specializations in the temporal region, or accompanied by comparable departures from a generalized morphology elsewhere in the skull, it is assumed that the complex arose only a relatively short time previously in the evolution of *Dromaeosaurus*.

### COMPARISONS WITH OTHER THEROPODS

The skull of *Dromaeosaurus* differs fundamentally from that of the

contemporaneous late Cretaceous tyrannosaurids in the retention of several obviously generalized characteristics. Among these are the primitive construction of the braincase, the breadth of the elements of the dermal skull roof, the relatively large size and only incipiently "incisiform" nature of the premaxillary teeth, and the absence of a significant expansion of the quadratojugal and squamosal into the lateral temporal opening. In these respects the skull of *Dromaeosaurus* resembles the skulls of the late Jurassic to early Cretaceous allosaurids (including *Allosaurus*, *Acrocanthosaurus*, and *Chilantaisaurus maortuensis*). However, it also differs basically from them in that the cranium of the latter group is characterized by distally depressed paroccipital processes, great ventral lengthening of the basiptyergoid process of the basisphenoid, contact or close approximation of the squamosal and parietal behind the supratemporal fenestra, and a shortened quadrate.

A number of imperfectly known forms, principally from the Jurassic of Europe (Huene, 1926b) but with at least one nearly complete skeleton from strata of late Triassic age in North America (Welles, 1954), are usually assigned to the Megalosauridae. As presently constituted the family is surely unnatural, but it does seem to contain carnivorous saurischians of a generally more primitive adaptive level than that of the allosaurids. They can be distinguished from the latter group by the retention of such primitive characters as relatively elongated presacral vertebrae, pubes with a broad, transversely oriented apron and an unexpanded distal end, and large, powerfully developed forelimbs. For comparative purposes *Ceratosaurus* from the late Jurassic of North America is here considered as an aberrant megalosaur.<sup>1</sup> It may be instructive to compare the skull of *Dromaeosaurus* with some cranial remains pertaining to the megalosaurian adaptive grade.

The maxilla of "*Megalosaurus*" sp. (Walker, 1964, p. 126; Owen, 1883, pl. 11, fig. 1) from the early middle Jurassic (lower Bajocian) and that of *Eustreptospondylus oxoniensis* (Walker, 1964, p. 126; Huene, 1926b, p. 54, fig. 12) from the early late Jurassic (upper Callovian) of England both differ from that of *Dromaeosaurus* in their greater size, larger number of dental alveoli (12-14), the presence of interdental plates (Huene, 1932, pl. 43, fig. 6), and the presence of an extensive emargination bordering the external naris posteroventrally. The same characters, except for the absence of a narial emargination, distinguish the maxilla of *Megalosaurus*

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<sup>1</sup> It is not certain that the large pubic foot usually seen in restorations of the pelvis of *Ceratosaurus* was actually present (Gilmore, 1920, p. 108), although field records suggest that such was the case (personal communication, J. S. McIntosh, 1967).

*bucklandi* (Huxley, 1869, pl. 12), of middle Jurassic (upper Bajocian) age, from that of *Dromaeosaurus*. The braincase of *Eustreptospondylus divesensis* (Piveteau, 1923; Walker, 1964), a relatively advanced megalosauroid from the late Jurassic (Oxfordian) of France, is, however, nearly as shallow as that of *Dromaeosaurus*, as pointed out above. Such a similarity suggests that the reduction of the maxillary dentition and the absence of interdental plates and of a narial emargination, may have been subsequent specializations of the *Dromaeosaurus*-lineage, but the braincase remained more primitive than that of this generalized Jurassic carnosauroid.

*Ceratosaurus* (see Gilmore, 1920) from the late Jurassic (Morrison Formation) of Colorado has long been recognized as a morphologically archaic theropod. The similarity of its endocranial cavity to that of *Dromaeosaurus* has already been noted, and the cranium further resembles that of the latter genus in the length of the quadrate, the presumably laterally directed paroccipital process, the absence of a narial emargination from the maxilla, and the exposure of the splenial on the lateral surface of the lower jaw (for the last character, see Gilmore, 1920, p. 90). A large number of maxillary teeth (15), the extension of the maxillary tooth row beneath the orbit, the more anteriorly situated nasal-frontal contact, and the only incipiently developed subnarial process of the premaxilla are all retained within the skull of *Ceratosaurus*—respects in which it is more generalized than that of *Dromaeosaurus*. The skull, however, is deepened as in most carnosauroids, the proximal condyle of the quadrate is exposed laterally, and the squamosal rises steeply in front of the paroccipital process in typical carnosauroid fashion. The genus is slightly aberrant in the possession of only three premaxillary teeth, the exclusion of the jugal from the posteroventral margin of the antorbital fenestra, the absence of any significant expansion of the quadratojugal and squamosal into the lateral temporal fenestra, and the absence of a fenestra within the pterygopalatine contact.

The lower part of the skull and mandible of a small theropod from the middle Jurassic (Bathonian) of England was described as *Megalosaurus bradleyi* by Woodward (1910) and referred to a new genus, *Proceratosaurus*, by Huene (1926b). It is a most unusual carnivore, evidently possessing a large "horn" on the nasals, somewhat in advance of the position of the "horn" in *Ceratosaurus*. It most strikingly resembles *Dromaeosaurus* in its small size, probably low profile of the skull in lateral view, depressed quadratomandibular articulation, wide orbits, wide lateral temporal fenestra, and possibly the lateral exposure of the splenial. Part of the palate is preserved, which indicates that it was not highly vaulted. A

wide fenestra is present between the medial and lateral contacts of the pterygoid and palatine, and the median ramus of the palatine is surprisingly slender. The antorbital fenestra, however, is larger than the orbit, the external naris is extremely large, and the marginal dentition is unreduced (18 maxillary teeth, about 18 dentary teeth), the reverse of conditions in *Dromaeosaurus*. Most significantly, the premaxillary teeth are "incisiform" and distinctly smaller than those of the maxilla. This last progressive character indicates especially that the great similarity of the skull of *Proceratosaurus* to that of *Dromaeosaurus* is probably due to the absence of strong carnosaurian specializations from both genera and a common adaptation to the general ecologic role of a small carnivore.

The skull of "*Megalosaurus*" *wetherilli* from near the Triassic-Jurassic boundary in Arizona is as yet undescribed, although part of it may be seen in a photograph of the type skeleton (Welles, 1954, pl. 1). Additional materials throw new light on this skull, which is now being studied by Welles.

As the group is presently understood, *Dromaeosaurus* should not be included within the Carnosauria. The great deepening of the entire skull in this suborder and the concomitant deepening of the braincase show that these reptiles were undergoing an evolutionary development quite different from that taken by the lineage leading to *Dromaeosaurus*. Both lineages, however, evidently become increasingly alike in successively older horizons. Both probably diverged from common stock during late Triassic time. In the reduction of the marginal dentition and the development of a large excavation within the ventral surface of the ectopterygoid, *Dromaeosaurus* came to parallel the tyrannosaurids. The specializations in the temporal region and the loss of interdental plates are regarded as developments peculiar to the immediate ancestry of *Dromaeosaurus*.

The skull of *Dromaeosaurus* is grossly similar to skulls of the smaller, more primitive theropods, which also lack the cranial peculiarities of carnosaurids. In *Coelophysis*, however, the skull is more delicately constructed than that of *Dromaeosaurus* and possesses a generalized morphology appropriate to the close temporal proximity of the genus to the initial radiation of the saurischians. Conversely, the skull of *Ornitholestes*, from late Jurassic sediments, is too specialized in the relative reduction of the dentigenous portion of the jaws, the ventrolateral inclination of the paroccipital processes, and the broad contact of the parietal and squamosal behind the supratemporal fenestra to have been close to the ancestry of *Dromaeosaurus*. Significantly, the metatarsus and pes of

*Coelophysis*, *Ornitholestes*, *Compsognathus*, and *Coelurus* (*C. agilis*, Y.P.M. No. 2010) are of a normal theropod type and lack any evidence of the specialization seen in the foot of *Dromaeosaurus*.

There is a group of small Cretaceous theropods, typified by *Deinonychus* (Ostrom, 1969, and in press), *Dromaeosaurus*, and *Velociraptor*, in which the skull is relatively unspecialized and the second digit of the pes terminates in a greatly enlarged, sickle-shaped claw. In *Velociraptor* (Djadochta Formation, Mongolia) and *Deinonychus* (Cloverly Formation, Wyoming and Montana), the first and second phalanges of the second digit are short and of subequal length, the radius of curvature of both of the articular surfaces of the second phalanx are subequal, and the distal end of metatarsals II and III are traversed by a deep, medial, vertical sulcus, characters that are also present in the foot of *Dromaeosaurus*. It is obvious that these three genera are closely allied to one another and are somewhat removed from two other generally related genera, *Saurornithoides* from the Djadochta Formation of Mongolia and *Stenonychosaurus* from the Oldman Formation of Alberta. In the latter two genera the first phalanx of the second digit is relatively long. The second phalanx is relatively short, and the radius of curvature of its distal articulation is much shorter than that of the proximal articulation, whereas the distal ends of the second and third metatarsals are smoothly formed as in the ornithomimids.

Tables 1 and 2 show that *Dromaeosaurus* had a fairly wide skull, as did *Deinonychus*. Moreover, in *Dromaeosaurus* the orbit was large in relation to the size of the skull, and also was larger than the large antorbital fenestra, characters seen in *Velociraptor* and *Ornitholestes*. *Dromaeosaurus* apparently had a large, elongated, superior temporal fenestra, as seemingly did *Ornitholestes*. The mandible was moderately deep. In its low dental formula *Dromaeosaurus* approximated *Velociraptor* and *Ornitholestes*. It is interesting to note that the number of tooth serrations per unit length does not appear to be a function of tooth size.

#### DIAGNOSES OF THE THREE ALLIED GENERA

*Deinonychus* (see Ostrom, 1969, and in press): Skull large, and of moderate height. Rugosity present on dorsolateral rim of lacrimal. Orbit deep, smaller than first antorbital fenestra. Supratemporal arcade short. Quadratomandibular articulation depressed relative to alveolar margin of jaws. Pterygoid wing of palatine broad. Dental formula: four premaxillary, 15 maxillary, 16(+?) dentary teeth. Carinae symmetrically placed on anterior and posterior edges of tooth crown. Thirty denticles per 5 mm. on anterior carinae, 17-18 on posterior. Phalanges of pes

relatively more slender than in *Dromaeosaurus*, with unguis of second enlarged and recurved.

*Velociraptor* (A.M.N.H. No. 6516, type of *V. mongoliensis*): Skull small and low. Dorsolateral rim of lacrimal smooth. Orbit circular, larger than first antorbital fenestra. Supratemporal arcade short. Quadratomandibular articulation less depressed below alveolar margin of jaws than in *Dromaeosaurus*. Dental formula: four premaxillary, nine maxillary, 14 dentary teeth. Carinae symmetrically placed on anterior and posterior edges of dorsal part of tooth crown, position of anterior carina uncertain nearer base of crown. Thirty-eight to 40 denticles per 5 mm. on anterior carinae, 25–26 on posterior. Pes similar to that of *Deinonychus*.

*Dromaeosaurus* (A.M.N.H. No. 5356, type of *D. albertensis*): Skull of moderate length and height. Rugosity present on dorsolateral rim of lacrimal. Orbit circular, larger than first antorbital fenestra. Supratemporal arcade long. Quadratomandibular articulation slightly depressed. Pterygoid wing of palatine narrow. Dental formula: four premaxillary, nine maxillary, 11 dentary teeth. Anterior carina of maxillary and dentary teeth displaced medially near base of crown. Sixteen denticles per 5 mm. on anterior and posterior carinae. Pes similar to that of *Deinonychus*, but with relatively shorter phalanges.

Our knowledge of *Dromaeosaurus* is, of course, based on the type specimen of *D. albertensis*, which is composed only of an incomplete skull and scattered elements of a left foot. Several other genera of small theropods have been described from the Oldman Formation, based on similarly incomplete type material. *Stenonychosaurus* (Sternberg, 1932) has already been distinguished from *Dromaeosaurus*. The first metacarpal in the manus of *Chirostenotes* (Gilmore, 1924a) is much too elongated to belong to *Stenonychosaurus*, and in view of the great resemblance of the type material of *Dromaeosaurus* to corresponding elements of *Deinonychus* (see Ostrom, 1969, and in press) it must be too long to belong to *Dromaeosaurus* as well. Perhaps the (?)ornithomimid foot described as *Macrophalangia* by Sternberg (1932) and the manus of *Chirostenotes* belong to the same form. In this connection it may be noted that there is no essential difference between the manus of *Chirostenotes* and that of the Mongolian genus *Oviraptor*. Two additional kinds of small theropod jaws have been described from the Oldman Formation, the mandible Gilmore (1924a) referred to *Chirostenotes* and the dentary of *Troodon* (see Sternberg, 1951). There is no evidence to suggest which, if either, of the jaws should be referred to *Stenonychosaurus* or possibly even *Macrophalangia*. It is unfortunate that the rich fauna of small theropods from the Oldman Formation is known from such incomplete material.



TABLE 1  
MEASUREMENTS (IN MILLIMETERS) OF THEROPODS

	<i>Dromaeosaurus</i> <i>albertensis</i> A.M.N.H. No. 5356	<i>Deinonychus</i> Y.P.M. Various Numbers	<i>Velociraptor</i> <i>mongoliensis</i> A.M.N.H. No. 6515	<i>Gongosaurus</i> <i>libratus</i> A.M.N.H. No. 5336	<i>Ornitholestes</i> <i>hermanni</i> A.M.N.H. No. 619
Skull					
Length, occipital condyle-premaxilla	234.1	310 <sup>a</sup>	168.0	895.0	127.0
Breadth at quadrates	109.0	150 <sup>a</sup>	—	350 <sup>b</sup>	—
Interorbital breadth	41.0	—	32.0	180.0	22 <sup>b</sup>
Height, quadrate-temporal roof	95 <sup>b</sup>	112 <sup>a</sup>	45.0	410.0	50.0
Anterior-posterior diameter of orbit	41.0	45 <sup>a</sup>	37.5	120.0	35.2
Anterior-posterior diameter of anterior fenestra	32 <sup>b</sup>	90 <sup>a</sup>	34.5	212.0	21.0
Length, superior temporal fenestra	43 <sup>b</sup>	40 <sup>a</sup>	16.5	145.0	24 <sup>b</sup>
Length, upper tooth row	106.5	160 <sup>a</sup>	77.5	505.0	51 <sup>b</sup>
Mandible					
Length	202.5 <sup>c</sup>	317 <sup>a</sup>	168.0	965.0	138.0 <sup>d</sup>
	213.0 <sup>d</sup>				
Depth at coronoid	40.5 <sup>c</sup>	58 <sup>a</sup>	21.8	270 <sup>b</sup>	24.0
Length, lower tooth row	88.0 <sup>c</sup>	138 <sup>a</sup>	72.5	425.0	40.0
Number of upper teeth in premaxilla and maxilla	13	18	13	17	14
Number of lower teeth	11	16+	14	16	12
Tooth serrations per 5 mm.	16	17-30	25-40	15	36

<sup>a</sup> Measured from scale drawings.

<sup>b</sup> Approximate measurements.

<sup>c</sup> Right ramus.

<sup>d</sup> Left ramus.

TABLE 2  
INDICES AND RATIOS OF THEROPODS

	<i>Dromaeosaurus</i>	<i>Dimonyichus</i>	<i>Velociraptor</i>	<i>Gorgosaurus</i>	<i>Ornitholestes</i>
Skull, breadth/length	46	48	—	39	—
Skull, interorbital/length	17.5	—	19	20	17
Skull, height/length	41	36	27	46	39
Skull, orbit/length	17.5	14.5	22	13.5	28
Skull, orbit/preorbital fenestra	128	50	108	57	168
Skull, superior temporal fenestra/length	18.5	13	9.8	16	19
Skull, tooth row/length	47	52	46	57	40
Mandible, depth/length	19	18	12.5	28	17.5
Mandible, tooth row/length	42	44	43	44	29

## THE TAXONOMIC POSITION OF *DROMAEOSAURUS* AMONG THE THEROPODS

It seems clear from the foregoing description and discussion that *Dromaeosaurus* represents a distinct and interesting stage of evolutionary development within the saurischian dinosaurs and, more specifically, within those saurischians commonly designated as theropods. Moreover, *Dromaeosaurus* shows close resemblances to certain theropods: to *Velociraptor* from the Cretaceous beds of Mongolia, and particularly to the new genus *Deinonychus* from the Cloverly of North America, recently described by Ostrom (1969, and in press). Indeed, these three genera show so many common characters, to the extent that they are known, and in certain features such unique specializations, that they can be grouped quite justifiably within a family of their own, which is here designated as the Dromaeosauridae.<sup>1</sup> Furthermore, the differences between the genera comprising this family and genera in other families that commonly have been grouped in the two theropod infraorders Coelurosauria and Carnosauria are, we think, sufficiently important to warrant the inclusion of the Dromaeosauridae in an infraorder of its own, which is designated as the Deinonychosauria.<sup>2</sup>

Thus *Dromaeosaurus* and its relatives occupy a position more or less between the Coelurosauria and the Carnosauria as these two taxa are commonly understood. In various characters the deinonychosaurs show close ties to the coelurosaurs, in various other characters to the carnosaurs, and in still other characters this group demonstrates specializations that are not to be seen in either of the two previously named infraordinal groups. To summarize the nature of deinonychosaurian relationships within the theropods, contrasting them with the coelurosaurians and the carnosaurians, certain diagnostic characters are listed and compared in table 3.

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<sup>1</sup> As pointed out above, Matthew and Brown in their original description assigned *Dromaeosaurus* to a new subfamily, Dromaeosaurinae, which they in turn included in the family Deinodontidae. Because we maintain that the genera *Dromaeosaurus*, *Deinonychus*, and *Velociraptor* properly belong within a single family, the name of this family must be Dromaeosauridae (because a subfamily was named on the basis of the type genus, *Dromaeosaurus*, and because "all categories in the family-group are of coordinate status in nomenclature" [International Code, Article 36]).

<sup>2</sup> The Code specifies that names within the family group must be based on a type genus, but there is no specification for the derivation of names in categories higher than the family. It seems advisable to use a name for this infraorder based on the genus from the Cloverly Formation of North America, because *Deinonychus* is known from materials far more complete than those that represent the genera *Dromaeosaurus* and *Velociraptor*.

TABLE 3

## COMPARISON OF DIAGNOSTIC CHARACTERS IN THE THEROPODS

Coelurosauria	Deinonychosauria	Carnosauria
Small	Small	Large
Bones with thin walls	Walls thicker than in Coelurosauria	Thick walls
Skull small, equal to or shorter than femur	Skull large, equal to or longer than femur	Skull large, equal to femur
Orbit rounded, larger than antorbital opening	Orbit rounded, subequal to antorbital opening	Orbit deep, smaller than antorbital opening
Skull relatively low	Skull moderately high	Skull very high
Quadrate vertical or slanted anteriorly	Quadrate vertical or slanted anteriorly	Quadrate slanted posteriorly
Parietal broad and flat	Parietal broad and flat	Parietal broad, or narrow and crested
No supraorbital rugosities	Rugosities on lacrimal	Heavy rugosities on lacrimal and postorbital
Elongated braincase	Broad braincase	Short, deep braincase
Ectopterygoid simple	Ectopterygoid expanded, with ventral pocket	Ectopterygoid expanded, with ventral pocket
No interdental plates	No interdental plates	Interdental plates
Premaxillary teeth with anterior and posterior serrations	Premaxillary teeth trending to "incisiform"	Premaxillary teeth variously "incisiform," with serrations posteriorly placed
Mandible shallow	Mandible moderately deep	Mandible posteriorly very deep
No mandibular interdental plates	No mandibular interdental plates	Mandibular interdental plates
No surangular foramen	Surangular foramen	Surangular foramen
Neck long	Neck moderately short	Neck short
Pubes not distally expanded	Pubes expanded into plate	Pubes often with distally expanded "foot"
Forelimb about equal to 1/2 of hind limb	Forelimb exceeds 1/2 of hind limb	Forelimb less than 1/2 of hind limb
Tibia longer than femur	Tibia longer than femur	Tibia shorter than femur
Pes birdlike, slender	Pes specialized, with second digit, especially claw, greatly enlarged; perhaps didactyl during locomotion	Pes birdlike but broad
Tail normal	Tail, posterior to tenth caudal, stiffened by long, overlapping, ossified tendons	Tail normal

**REDIAGNOSIS OF THE THEROPODA:** Saurischian carnivorous dinosaurs with strongly bipedal adaptations, forelimbs not adapted for locomotion. Pelvis of dolichoiliac type (see Colbert, 1964), with four to six sacral vertebrae. Manus showing progressive reduction of digits from lateral to medial side of hand. Pes generally birdlike, with pollex reduced and fifth digit reduced. Skull small to extremely large. Teeth, when present, sharp.

To indicate in a little more detail the position of *Dromaeosaurus* and its close relatives among the theropods, a listing of the infraorders and families of this saurischian suborder is here presented. A more detailed consideration of theropod classification will be published by the present authors in collaboration with John H. Ostrom.

#### Theropoda

##### Coelurosauria

Podokesauridae; Triassic

Segisauridae; Jurassic

Coeluridae; Jurassic, Cretaceous

Ornithomimidae; Cretaceous

##### Deinonychosauria

Dromaeosauridae; Cretaceous

##### Carnosauria

Megalosauridae; Triassic, Jurassic, Cretaceous

Allosauridae; Jurassic, Cretaceous

Spinosauridae; Cretaceous

Tyrannosauridae; Cretaceous

### CONCLUSIONS

In this new study and re-evaluation of the genus *Dromaeosaurus*, as based on the monotypic species, *Dromaeosaurus albertensis* Matthew and Brown, an attempt is made to present in some detail the nature of a dinosaur well established in the literature, but concerning which little has been known. As a result of the study and the several comparisons, some interesting and unexpected results have been forthcoming.

Thus it is evident that *Dromaeosaurus* is neither coelurosaur nor carnosaur, but rather that it belongs to a new group of theropod dinosaurs, of which we have recently been made aware by the studies of Ostrom on the Cloverly fauna. This group of dinosaurs, here accorded the rank of an infraorder, and designated by us as the deinonychoosaurs, is specialized along lines that are in part intermediate between and in part quite distinct from the other two theropod infraorders. The deinonychoosaurs are characterized by numerous specializations in the skull for strong predaceous habits, and by remarkable specializations in the forelimbs and hind limbs, also for predation. The specialization of the pes is par-

ticularly noteworthy, for it shows an enlargement of the inner digit as a powerful digging or tearing weapon, with a probable concomitant stress on the middle and outer digits for locomotion. Possibly these dinosaurs were in effect didactyl.

Moreover, as a result of the study of *Dromaeosaurus* in comparison with *Deinonychus*, it is becoming apparent that theropods of this type were rather abundant and widespread during Cretaceous times; thus the study of *Dromaeosaurus* and its relatives has opened new vistas of theropod relationships. There is much still to be learned about the relationships and adaptations of the theropod dinosaurs.

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