TYRANNOSAURS FROM THE LATE CRETACEOUS OF WESTERN CANADA

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RÉSUMÉ

Le nom de famille *Tyrannosauridae* s'applique à un groupe de grands dinosaures théropodes qu'on trouve dans les sédiments du Crétacé supérieur, à l'intérieur de l'Amérique du Nord et en Asie centrale. On reconnaît qu'*Albertosaurus* Osborn est en fait un synonyme plus ancien de *Gorgosaurus* Lambe, et les espèces désignées comme *Gorgosaurus* sont reclassées sous l'ancien genre. *Albertosaurus sternbergi* (Matthew et Brown) et *A. Arctunguis* Parks sont des synonymes plus récents d'*A. libratus* (Lambe) et d'*A. sarcophagus* Osborn respectivement. Un deuxième genre de tyrannosaure, *Daspletosaurus torosus*, qui représente aussi une nouvelle espèce, a été reconnu pour la première fois dans les sédiments des formations Oldman et Edmonton inférieure.

Le crâne du tyrannosaure était essentiellement acinétique, bien qu'il ait pu se produire un certain mouvement médiolatéral dans la région postérieure de chaque moitié du palais. Les éléments médians ventraux de la boîte crânienne et les apophyses paroccipitales contenaient des sinus qui les occupaient presque entièrement. On a comparé plusieurs spécimens d'*Albertosaurus libratus* afin de découvrir dans les proportions des éléments du squelette, les différences qui sont liées à la taille du sujet. On s'est aperçu que les extrémités (main, jambe inférieure, pied et queue) étaient relativement plus grandes chez les individus jeunes, alors que les éléments des régions plus centrales de l'organisme (ceintures de membres, vertèbres présacrées et côtes) étaient relativement plus importants chez les adultes. On attribue la grande fréquence d'humérus malades aux accidents causés par la disproportion entre les bras relativement fragiles et le tronc massif et puissant.

On connaît la présence de tyrannosaures dans plusieurs secteurs du crétacé supérieur de l'Alberta, soient;

Formation Oldman: *Albertosaurus libratus*
Daspletosaurus torosus

Formation Edmonton inférieure: Couche A:
Albertosaurus sarcophagus

Formation Edmonton inférieure: Couche B:
Albertosaurus sarcophagus
Daspletosaurus cf. (*D. torosus*)

Formation Edmonton supérieure (correspond à la formation Lance)
cf. *Tyrannosaurus rex*

SUMMARY

The family group name Tyrannosauridae is applied to a group of large theropodous dinosaurs from late Cretaceous sediments of the interior of North America and central Asia. *Albertosaurus* Osborn is recognized as a senior synonym of *Gorgosaurus* Lambe, and species formerly referred to *Gorgosaurus* are transferred to the former genus. *Albertosaurus sternbergi* (Matthew and Brown) and *A. arctunguis* Parks are junior synonyms of *A. libratus* (Lambe)

and *A. sarcophagus* Osborn, respectively. A second genus of tyrannosaur, *Daspletosaurus torosus* new genus and new species, is recognized in Oldman and lower Edmonton sediments for the first time.

The tyrannosaur skull was essentially akinetic, although some mediolateral movement may have taken place in the posterior region of each half of the palate. The median ventral elements of the braincase and paroccipital processes are filled with sinus cavities. Several specimens of *Albertosaurus libratus* were compared in order to discover differences in the proportions of skeletal elements, which correlate with the size of the individual. It was found that the extremities (manus, lower leg, pes, and tail) are relatively larger in more immature individuals, while elements in more central areas of the body (limb girdles, presacral vertebrae, and ribs) are relatively larger in adults. The high incidence of pathologic humeri is attributed to accidental damage of the relatively fragile forelimb by the massive and powerful body.

Tyrannosaurs are known to occur in several horizons of the late Cretaceous of Alberta as follows:

Oldman Formation:
- *Albertosaurus libratus*
- *Daspletosaurus torosus*

lower Edmonton Formation, Member A:
- *Albertosaurus sarcophagus*

lower Edmonton Formation, Member B:
- *Albertosaurus sarcophagus*
- *Daspletosaurus* cf. *D. torosus*

upper Edmonton Formation (Lance equivalent):
- cf. *Tyrannosaurus rex*

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Introduction

A small number of closely related genera of large theropodous saurischians is known to have existed during late Cretaceous time in North America and Central Asia. These reptiles, which may be termed tyrannosaurs, are noteworthy for their large size (one form attained a length of 47 feet, perhaps weighing over $7\frac{1}{2}$ tons in life; *see* Colbert 1962) and for their extreme adaptation to a carnivorous mode of existence. Their remains indicate that they were completely bipedal, as the lower segments of the hind limbs are proportionally longer than in most other theropods, while the forelimbs are relatively quite small with only two functional digits in the hand. The head is large and is lightly constructed, the neck is short, and the pelvic region is very powerfully developed. The premaxillary teeth are incisiform, as in carnivorous mammals, but the margins of the long, deep muzzle are otherwise armed with sabre-shaped teeth. On this continent the remains of tyrannosaurs have been recovered from sediments deposited on flat deltaic plains bordering the western margin of the old interior sea. They make up only a small percentage of the dinosaur specimens found in these sediments in western Canada (Russell 1967); even so, more tyrannosaur skeletal material has been collected here than in any comparable area of North America.

The type skeleton of *Albertosaurus libratus*, from the Oldman Formation of Alberta, has been thoroughly described and figured by Lambe (1917). Several excellent specimens of this species, collected by the American Museum of Natural History in Alberta, were also briefly described by Matthew and Brown (1923). Lambe (1904) published a study of two incomplete skulls from the Edmonton Formation, which Osborn later made the type and paratype of *Albertosaurus sarcophagus*. A partial skeleton of this species, also from the Edmonton Formation, has been described by Parks (1928). The youngest species of the genus, *A. lancensis*, was established by Gilmore (1946) for a partly crushed skull from the Lance Formation of southeastern Montana. The osteology of *Tyrannosaurus rex*, from the Hell Creek Formation of Montana, but also known from the Lance Formation of Wyoming (Gilmore 1920: 121-2), has been summarily described and well figured by Osborn (1905, 1906, 1912, 1913, 1917). For descriptions and figures of *Tarbosaurus bataar* from the Nemegt beds of Mongolia *see* Maleyev 1955*a*, 1955*b*, 1955*c*, 1964; Rozhdestvensky 1965.

A perusal of the above sources will show that the tyrannosaurs are a small group of highly evolved, but nearly related forms. The author, in collaboration with others, intends to speculate on their systematic position within the Theropoda elsewhere. The object of this paper is to characterize the Canadian forms and to comment briefly on a few of the peculiarities of their morphology. Once again I am very pleased to express my gratitude to Dr. Edwin H. Colbert of the American Museum of Natural History for making tyrannosaur material in the collections of that institution available to me for study. Dr. A. K. Rozhdestvensky has generously forwarded data on *Tarbosaurus* specimens in the collections of the Academy of Sciences of the U.S.S.R. To these gentlemen and to Dr. Wann Langston, Jr., of the Texas Memorial Museum, I am indebted for their courteous counsel on various problems concerning the structure of tyrannosaurs. Special thanks go to Dr. A. G. Edmund of the Royal Ontario Museum, and to Dr. R. C. Fox of the University of Alberta, for allowing me to study tyrannosaur material in the collections under their care. As so often in the past, Dr. C. M. Sternberg, Curator Emeritus of Fossil Vertebrates of the National Museum of Canada, has rendered great assistance through his kindly interest and in making available his great experience in collecting and studying Cretaceous reptiles.

The following abbreviations of institutional names, which precede specimen numbers referred to in the text, identify the place of storage of the specimen:

AMNH—American Museum of Natural History

BMNH—British Museum of Natural History

FMNH—Field Museum of Natural History

NMC —National Museums of Canada, Museum of Natural Sciences

ROM —Royal Ontario Museum

UA —University of Alberta

USNM —United States National Museum

*(Place)—assigned to species, though material insufficient for positive identification.

Family TYRANNOSAURIDAE

Diagnosis

Premaxillary teeth reduced in size relative to those of maxilla, 'U'-shaped in cross-section with carinae bordering opposite edges of flat, posteriorly facing surface. Three antorbital fenestrae within maxilla, anteriormost fenestra small and inconspicuous in lateral aspect. Frontals narrow, parietals represented dorsally as longitudinal crest of bone separating supratemporal fenestrae. Supraoccipital enters dorsal border of foramen magnum, paroccipital processes not depressed laterally. Laterosphenoids meet on midline of skull, separating fenestra for optic nerve from ventroanterior opening of pituitary fossa. Spines of cervical vertebrae most powerfully developed in anterior region of neck, length of cervical centra seldom exceeds 10 per cent of that of femur. Length of dorsal centra less than height of centrum. Length of humerus approximately one-third that of femur, only two functional digits present in manus. The length of the pubic boot in adults greater than half total length of pubis. Shaft of ischium pointed distally, frequently with slight ventral recurvature toward tip. Well-developed alae unite ischial shafts ventromedially. Lateral trochanter of femur large, extends to proximal end of bone. The length of the tibia in adults is about 90 per cent of that of the femur. Shaft of third metatarsal constricted dorsally.

Comments

The family group name 'Tyrannosauridae' was proposed by Osborn (1906: 283) and is based on an unquestionably valid genus of carnivorous dinosaur from the Hell Creek Formation of Montana. The family group name 'Deinodontidae', which has often been used as a synonym of Tyrannosauridae, was proposed by Cope (1866: 279, "Dinodontidae"), with *Deinodon* (Leidy 1857: 72; 1860: 143) as its type genus. The lectotype of *Deinodon horridus* (*see* Cope 1866: 279; Hay 1908: 359) consists of two fragmentary premaxillary teeth of a large theropod from the Judith River Formation of Montana. No topotypic specimens have ever been described from this formation. It has been suggested (Hay 1908: 353; Matthew and Brown 1922: 374, 383) that *Deinodon* is congeneric with *Gorgosaurus* (= *Albertosaurus*) from the Oldman and Edmonton formations of southern Alberta. Gilmore (1946: 17) stressed the point that this identity could not be demonstrated in view of the incompleteness of the type teeth of *Deinodon horridus* and was inclined to doubt that the genus could ever be satisfactorily defined.

Two genera of large carnivorous dinosaurs are now known to be present (*see* below) in the Oldman Formation, a correlative of the Judith River Formation across the International Boundary (L. S. Russell 1964: 13), and it is not possible to distinguish them from each other or from *Deinodon* on the morphology of the premaxillary dentition. *Deinodon horridus* is evidently a *nomen vanum*. Because it is not a useful systematic procedure to perpetuate family group names based on generically unidentifiable material, Deinodontidae is rejected in favour of Tyrannosauridae as an available family group name. The latter name has recently gained widespread acceptance (*see* Colbert 1964; Walker 1964; Charig et al. 1965).

Gilmore (1946: 17) considered *Dryptosaurus aquilunguis* from the late Cretaceous of New Jersey to be closely related to the large theropods of similar age in the interior of North America and suggested that the family group name 'Dryptosauridae' (Marsh 1890: 424) would be available for them should Deinodontidae prove to be based on an indeterminate type genus. In *Dryptosaurus* (for descriptions and measurements *see* Cope 1869–70: 100-08; Huene 1932: 63–4) the manus is larger than in any known tyrannosaur. The ungual phalanx of the first digit is very large, the length of its convex upper surface amounting to 75 per cent of the total length of the humerus. In *Daspletosaurus*, where the manus is relatively large for a tyrannosaur, this length is approximately equal to only 40 per cent of the length of the humerus. The femur in *Dryptosaurus* is very slender, and in contrast to conditions in a half-grown tyrannosaur where the circumference/length ratio of the femur is comparable (AMNH 5423), the tibia is distinctly shorter than the femur. It is unlikely that additional material of *Dryptosaurus* will show that this genus and the western forms should be placed in the same family.

Genus **Albertosaurus** Osborn 1905, p. 265

Gorgosaurus Lambe 1914, p. 13

Type species: *Albertosaurus sarcophagus*

Diagnosis

Premaxilla contacts nasal below external naris. Maxillary teeth relatively smaller than in *Daspletosaurus*, posteriorly become more recurved and smaller still. Anteriormost antorbital fenestra within maxilla visible in lateral aspect, first antorbital fenestra longer than high. Nasals expand between lacrimals, invaded posteromedially on either side by short broad tongue of frontal. Frontal broadly exposed on skull roof, posteriorly recurved vertical cleft in bone above orbit. Prefrontal either unexposed dorsally, or with small process situated between lacrimal and frontal. Lacrimal 'horn' rectangular in lateral aspect, with apex centred well in advance of antorbital ramus of bone; exceeds postorbital 'horn' in development. Anteroexternal edge of antorbital ramus of lacrimal curves anteroventrally across jugal, bounding pocket in jugal laterally. Ventral process of ectopterygoid uninflated, with small ventrally opening sinus; jugular process of bone similarly uninflated. Angular terminates posteriorly behind surangular foramen.

Ventral openings of main basisphenoid sinus situated on either side of midline of skull, dorsomedial to each basipterygoid process. Optic fenestra not bridged medially by presphenoid. Cranial nerves III and IV exit separately on anterior surface of laterosphenoid, although pit for III much larger than that of IV. Exit for cranial nerve V_1 situated close to anterolateral edge of laterosphenoid.

Neural spines of fourth and fifth cervicals subequal, broadly flattened laterally. Spine of sixth cervical narrower, but does not come to point dorsally. Presacral vertebrae tend to be longer and lower than in *Daspletosaurus*; basal caudal vertebrae diminish more rapidly in size posteriorly than in this genus.

The length of the humerus in adults is equal to about 30 per cent of that of femur, forelimb lightly constructed. Anterodistal condyle of metacarpal I large, causing first and second digits to be approximately parallel. First phalanx of digit II slender in adults. Dorsal edge of ungual of digit I passes through arc of about 120 degrees.

Anterior blade of ilium does not cover diapophysis of twelfth thoracic vertebra. The circumference of the femur in adults is equal to 34 to 37 per cent of the femur's length. In comparison with *Daspletosaurus* specimens of similar femur length, the presacral vertebral column is longer, thoracic ribs are slightly shorter, forelimb is shorter, ilium and sacrum are shorter, and metatarsus is slightly longer.

Comments

The generotypic species of *Albertosaurus* is based on two crania found at different stratigraphic levels within the Edmonton Formation. These specimens so closely resemble skulls referable to *Gorgosaurus libratus*, from the Oldman Formation, that there can be little question of their generic identity. *Gorgosaurus* is therefore considered as a junior synonym of *Albertosaurus*, and *A. libratus* is in all probability the immediate ancestor of the Edmonton form. It has been

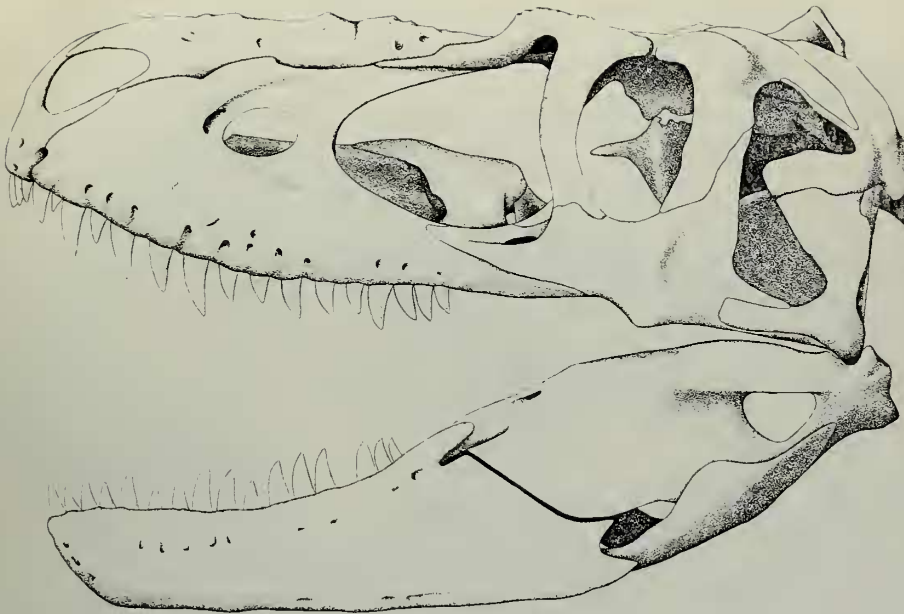

Figure 1—Albertosaurus libratus, reconstruction of the skull in lateral aspect, based primarily on a photograph of FMNH PR308 (negative number 39115, courtesy of the American Museum of Natural History), with the palate restored after AMNH 5336. The skull of FMNH PR308 measures 1050 mm in length (Matthew and Brown 1923: 10).

suggested that interdental plates medial to the marginal dentition (Osborn 1905: 265; Lambe 1914: 14) and an intercoronoid (Lambe 1914: 14) are absent in this genus, although this is not the case. Lambe (1914: 14; 1917: 16) has emphasized the similarity of the first maxillary tooth in the type of *A. libratus* to those in the premaxilla, considering this as characteristic of the genus. The carinae of the anterior maxillary teeth of *A. libratus* (and of *Daspletosaurus* also) are incipiently arranged as in the premaxillary teeth, and the number of small anterior maxillary teeth is variable, ranging from none in FMNH PR 308 to two in AMNH 5664. Although it is partly crushed, the first maxillary tooth of the type of *A. libratus* is probably not so premaxilliform as is indicated in Lambe's figure (1917, fig. 10B).

The dental formula of *Albertosaurus* is as follows: premaxillary teeth 4, maxillary teeth 13–15, dentary teeth 14–16. There are 10–14 (in extreme cases 17) serrations per 5 mm on the carinae of the marginal teeth, the serrations being coarsest near the centre of the jaws and finest near the posterior end of the jaws of immature individuals.

Albertosaurus libratus (Lambe 1914)
Gorgosaurus libratus Lambe 1914, p. 13
Gorgosaurus sternbergi Matthew and Brown 1923, p. 7

Distribution

Oldman Formation, near Steveville, Alberta.

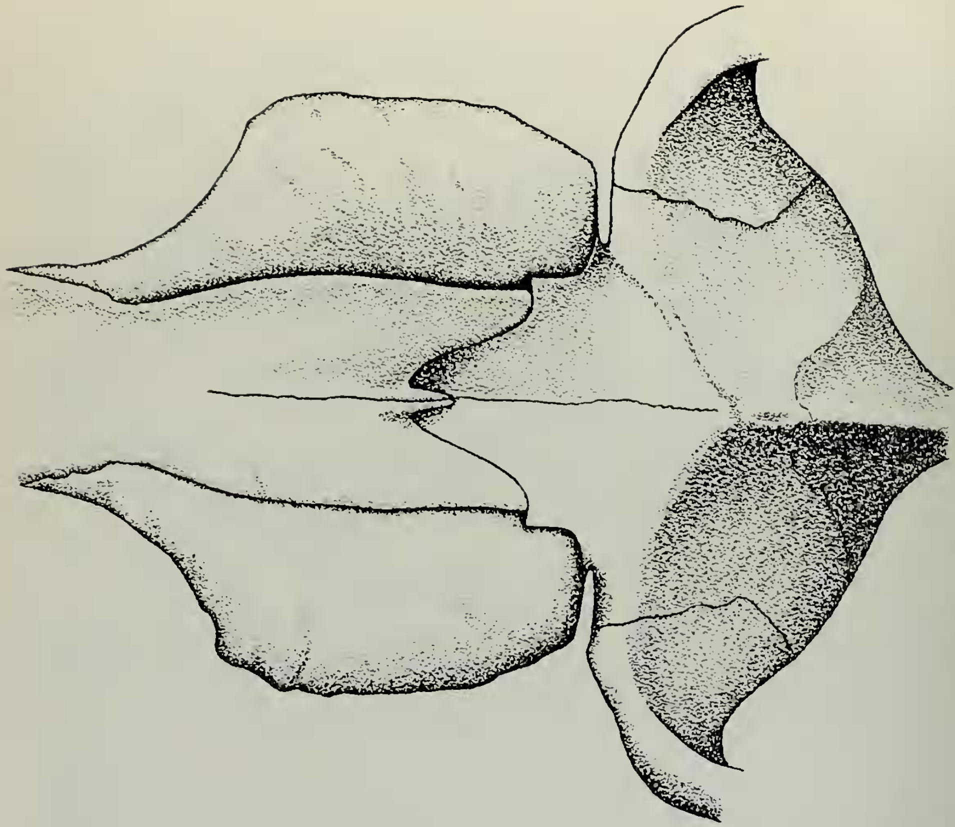

Figure 2—Albertosaurus libratus, median elements of the skull roof restored after USNM 12814. The area shown measures approximately 310 mm in length along the midline of the skull.

Referred specimens

*NMC 8782 incomplete manus and pes, fragments from hind limbs (3 miles south of Steveville, upper half of beds).

*AMNH 5423 jaw fragments, four caudal vertebrae, fragments of pelvis, left hind limb (Little Sandhill Creek basin).

NMC 2270 maxilla.

NMC 12063 maxilla.

ROM 4591 nasals (east side of coulee, at Denhart, Alberta).

AMNH 5664 (type of *G. sternbergi*) nearly complete skeleton (quarry 54 of Sternberg 1950).

USNM 12814 nearly complete skeleton, lacking tail (Little Sandhill Creek basin).

*NMC 2250 ilium.

ROM 1422 fragmentary skull.

ROM 1237 skeleton, lacking presacral vertebrae and right hind limb (quarry 21 of Sternberg 1950).

UA 10 skull, several presacral vertebrae and ribs, right humerus, left metatarsus (quarry 48 of Sternberg 1950).
AMNH 5432 left maxilla, left tibia-metatarsus and some phalanges of pes (quarry 59 of Sternberg 1950).
NMC 11593 pelvis, hind limbs, base of tail (quarry 50 of Sternberg 1950).
ROM 683 maxillae.
ROM 436 left premaxilla and maxilla.
ROM 1247 palatal elements.
AMNH 5336 skull (quarry 57 of Sternberg 1950).
AMNH 5458 skull and nearly complete skeleton (Little Sandhill Creek basin).
NMC 2120 (type of *G. libratus*) nearly complete skeleton (quarry 36 of Sternberg 1950).
NMC 2193 surangular.
FMNH PR308 skull and skeleton, lacking hind limbs and tail (Little Sandhill Creek basin).
NMC 11814 braincase.

Diagnosis

Length of dentary tooth row 71 per cent of length of fourth metatarsal (USNM 12814?, NMC 2120). In adult animals (NMC 2120) combined length of scapula-coracoid greater than that of femur. In adult animals (AMNH 5458, NMC 2120), combined length of tibia and astragalus 95 per cent of that of femur.

Comments

Gorgosaurus sternbergi, with the most complete skeleton known of a North American tyrannosaur as its type, was characterized by Matthew and Brown (1923: 7) as follows: "It is of smaller size and more slender proportions that in *G. libratus*. The jaws are much less massive and the muzzle is more slender, the maxilla more elongate and shallow, the orbital fenestra more circular. The tibia is considerably longer than the femur." Gilmore (1946: 3) suggested that the apparent slenderness of the muzzle in the type was caused by crushing, and Rozhdestvensky (1965) has demonstrated that the tibia/femur ratio decreases during growth in tyrannosaurs (*Tarbosaurus*).

Matthew and Brown (1923: 7) were aware of the possibility that these characters might be due to the juvenility of the type specimen, noting that the pelvic elements were not co-ossified. The sutures between the bones of the skull roof are widely open, and there is nothing in the morphology of the specimen to suggest that it is not an *A. libratus* approximately two-thirds grown. Interestingly, the supraoccipital alae of the parietals are only about one-fourth as large as in adults, indicating that these crests become more powerfully developed with maturity.

Rozhdestvensky's (1965) important studies of growth changes in the limb proportions of *Tarbosaurus* require that North American material be examined for similar growth effects. Although articulated remains of juvenile tyrannosaurs are far from being the commonest of fossils, a barely adequate sample of half-grown to adult specimens of *A. libratus* is available, from which some impression may be gained of allometric growth in the species.

Six specimens of *A. libratus* from the badlands of the Oldman Formation near Steveville, Alberta, have been examined for changes in bodily proportions correlating with the size of the animal. The smallest individual of the series AMNH 5423 was considered as possibly referable to *A. libratus* because the lengths of the tibia and metatarsus continue the same trends seen in larger specimens of the species, because *Albertosaurus* is three times as abundant as *Daspletosaurus* in this area of outcrop of the Oldman Formation, and because only adult specimens of the latter genus have so far been found here. The other five specimens (AMNH 5664, USNM 12814, NMC 11593, AMNH 5458, NMC 2120) have been assigned to *A. libratus* on the basis of their skeletal anatomy (*see* diagnoses). The precise horizon from which each of these specimens was collected is known in only three cases, although dinosaurian fossils are restricted to an approximately 200-foot vertical interval in the area (Sternberg 1950). In view of the great resemblance of *A. sarcophagus* from the younger Edmonton Formation to *A. libratus*, it is improbable that allometric changes would be obscured by evolutionary changes over a stratigraphic interval of this magnitude.

The length of the femur was arbitrarily chosen as a standard to which the lengths of other skeletal structures in a specimen were compared (*see* Table 1). The allometric changes are apparent when the lengths of the skeletal structures

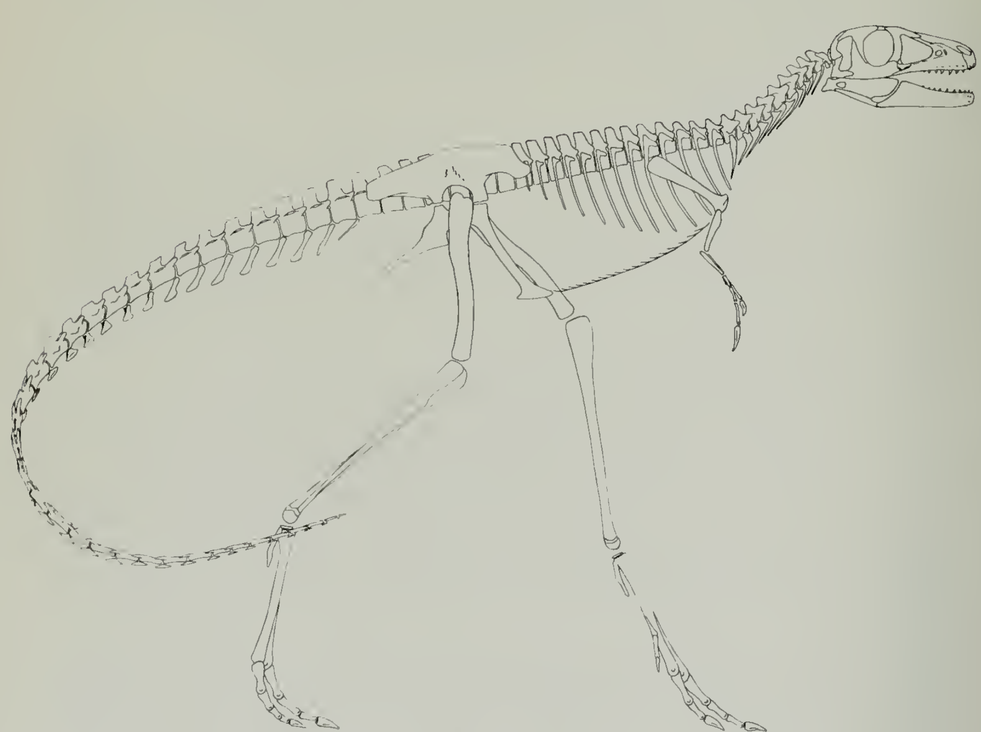

Figure 3—Albertosaurus libratus, restoration of a hypothetical hatchling. The length of the femur is 100 mm.

TABLE 1

	Skull length[1]	Length presacral vertebrae	Length sacrum	Length 24 caudal vertebrae	Length longest rib	Length scapula-coracoid	Length humerus	Length ulna	Length radius
AMNH 5423	–	–	–	–	–	–	–	–	–
AMNH 5664	678(97)	1642(235)	472(68)	2450(350)	800*ca.*(114)	620(89)	205(29)	125(18)	100(14)
USNM 12814	795*ca.*(93)	–	–	–	830(97)	–	254(30)	150(17)	–
NMC 11593	–	–	–	–	–	–	–	–	–
AMNH 5458	990(97)	2550(249)	665(65)	–	–	–	–	–	–
NMC 2120	–		690(66)	3400(327)	1238(119)	1086(104)	324(31)	180(17)	156(15)

	Length manus	Length second mtc	Length ilium	Length pubis[3]	Length ischium[4]	Length femur (=100)	Minimum circ. femur	Length Tib-Ast	Length tibia	Length mtt[3]	Length digit[3]
AMNH 5423	–	–	–	–	–	595	193(32)	–	620(104)	425*ca.*(72)	–
AMNH 5664	245(35)	60(9)	695(99)	610(87)	465(67)	700	–	748(107)	–	480(69)	350(50)
USNM 12814	–	–	–	–	–	860	–	810(94)	780(91)	530(62)	405(47)
NMC 11593	–	–	910(97)	–	–	940*ca*	–	900*ca*(96)	–	580(62)	–
AMNH 5458	–	–	1040(101)	–	–	1025*ca*	357(35)	990(97)	–	625(61)	445(43)
NMC 2120	276*ca.*(27)	98(9)	984(95)	980(94)	762(73)	1040*ca*	378(36)	1000(96)	–	594*ca*(57)	477*ca*(46)

1 Measured from tip of snout to mandibular articulation.
2 Measured along outer curve from tuberculum to end (probably incorrectly estimated in AMNH 5664).
3 Measured from centre of iliac suture to anterior tip of pubic boot.
4 Measured from centre of iliac to distal end of ischium.
Measurements of AMNH 5664 and AMNH 5458 taken from Matthew and Brown (1923); those of NMC 2120 usually from Lambe (1917).

are expressed as a percentage of the femur length and plotted against femur length on a graph. These data, although based on a minimal number of measurements, seem to indicate that as the animal increases in size from half-grown to fully mature, the presacral vertebral column, ribs, scapula-coracoid, pubis, and ischium increase more rapidly in length than does the femur; the skull, sacrum, humerus, and radius-ulna grow at approximately the same rate; and the caudal vertebral column, manus, tibia, metatarsus, and pes grow at a slower rate. These relative rates of growth appear to be rather constant, although in the case of the combined length of the tibia-astragalus the rate of increase is slow, relative to that of the femur, until the animal attains the size of USNM 12814, when the growth rate abruptly changes to equal that of the femur.

The comparative changes in the proportions of skeletal structures may have been of the same general magnitude during the earlier, more rapid stages of growth. Assuming that this was true, it would be possible to estimate the relative bodily proportions of a very young (hatchling) *Albertosaurus libratus*. For a femur length of 100 mm, the lengths of the following structures were estimated graphically as follows: skull 88 mm, presacral vertebral column 210 mm, sacrum 70 mm, anterior twenty-four caudal vertebrae 390 mm, scapula-coracoid 63 mm, humerus 26 mm, ulna 20 mm, manus 48 mm, second metacarpal 7 mm, ilium 100 mm, pubis 68 mm, ischium 54 mm, circumference of femur 28 mm, tibia-astragalus 140 mm, metatarsal three 85 mm, third digit of pes 56 mm.

Using these figures as a guide, an attempt has been made to reconstruct the skeleton of a hatchling tyrannosaur. The adult morphology of *A. libratus* has been modified by reducing the development of muscle scars and tuberosities, and the number of teeth in the jaws and by increasing the size of the orbit. The ungual phalanges of the manus and pes are shown, as in a very immature specimen (NMC 8782), referred to *A. libratus* because the first ungual of the manus, unlike in *Daspletosaurus*, is strongly curved. The lengths of the ribs are entirely conjectural, as the increase in rib length is apparently too rapid in more mature individuals to have been sustained throughout the ontogeny of the animal. It is hoped that this reconstruction (Figure 3) will serve both as an estimation of the actual appearance of a very young specimen of *A. libratus*, and as a means of focusing attention on misinterpretations unknowingly incorporated into it.

Albertosaurus sarcophagus Osborn 1905

Laelaps incrassatus, Cope 1892, p. 240
Dryptosaurus incrassatus, Lambe 1904, p. 6
Albertosaurus sarcophagus Osborn 1905, p. 265
Albertosaurus arctunguis Parks 1928, p. 7

Distribution

Lower Edmonton Formation, Red Deer River, Alberta.

Referred Specimens

NMC 5601 (paratype of *A. sarcophagus*) skull and lower jaws, fragments of sacral vertebrae and ilium, distal end of tibia with astragalus, fourth metatarsal, three ungual phalanges of pes (sec. ?, tp. 33, rge. 22, W. 4th mer., east bank of Red Deer River, Member B of Edmonton Formation).

AMNH 5222 scattered skull (sec. 12 ?, tp. 33, rge. 22, W. 4th mer., 150 feet above east bank of Red Deer River, Member B of Edmonton Formation).

ROM 807 (type of *A. arctunguis*) sacrum and adjacent vertebrae, left scapula-coracoid and forelimb, left half of pelvic girdle and associated hind limb (sec. 27 or 34, tp. 30, rge. 21, W. 4th mer., 100 feet above west bank of Red Deer River, Member A of Edmonton Formation).

NMC 5600 (type of *A. sarcophagus*) palatal region of skull, braincase and lower jaws (sec. 11 ?, tp. 29, rge. 21, W. 4th mer., approximately 100 feet above Red Deer River, along Kneehills Creek, Member A of Edmonton Formation).

?NMC 2196 scapula-coracoid, abdominal ribs (sec. 35 ?, tp. 28, rge. 20, W. 4th mer., west bank of Red Deer River, Member A of Edmonton Formation).

Diagnosis

Length of dentary tooth row 65 per cent of length of fourth metatarsal (NMC 5601). In adult animals (ROM 807, if the distal end of the scapula has not been broken off) combined length of the scapula-coracoid about 80 per cent of that of femur. In adult animals (ROM 807) combined length of tibia and astragalus equal to (or slightly greater than) that of femur.

Comments

In defining *Albertosaurus arctunguis*, Parks (1928: 5–7) stressed the dissimilarities between the distal end of the fourth metatarsal of his specimen (ROM 807) and that of the paratype of *A. sarcophagus* (NMC 5601). The slightly pathologic condition of this portion of the latter element, as Parks himself noted (1928: 7), accounts for some of the differences, while the remainder are due to the fact that the posteroexternal edge of the distal articulating surface has been broken off, which Parks failed to recognize. The ungual phalanges associated with NMC 5601, considered by Parks as belonging to the manus, actually belong to the pes. Altogether, it is not possible to separate the type of *A. arctunguis* from the type and paratype of *A. sarcophagus* on morphological grounds, and the great resemblance of each of these specimens to the corresponding region of the skeleton of *A. libratus* argues convincingly for their inclusion within a single species.

In addition to the characters noted in the diagnosis, the forelimb of ROM 807 seems to be slightly shorter than in *A. libratus* (NMC 2120), and the pubis is slightly larger than in the latter specimen (*see* Parks 1928: 12, 20, 23). *A. sarcophagus* occurs in both member A and B of the lower Edmonton Formation (Russell and Chamney 1967: 10, 12). It is unfortunate that the species is not known from more complete material.

In tyrannosaurs, the bone beneath the brain stem gives the appearance of being solid. However, this region of the skull is almost entirely filled with large sinuses, which are separated from one another only by thin walls. Fenestrae, through which these sinuses communicate with the surface of the bone, have occasionally been confused with openings for nerve or blood vessel conduits (*see* for example Lambe 1904: pl. 7, fig. 15; Gilmore 1946: 10). A reconstruc-

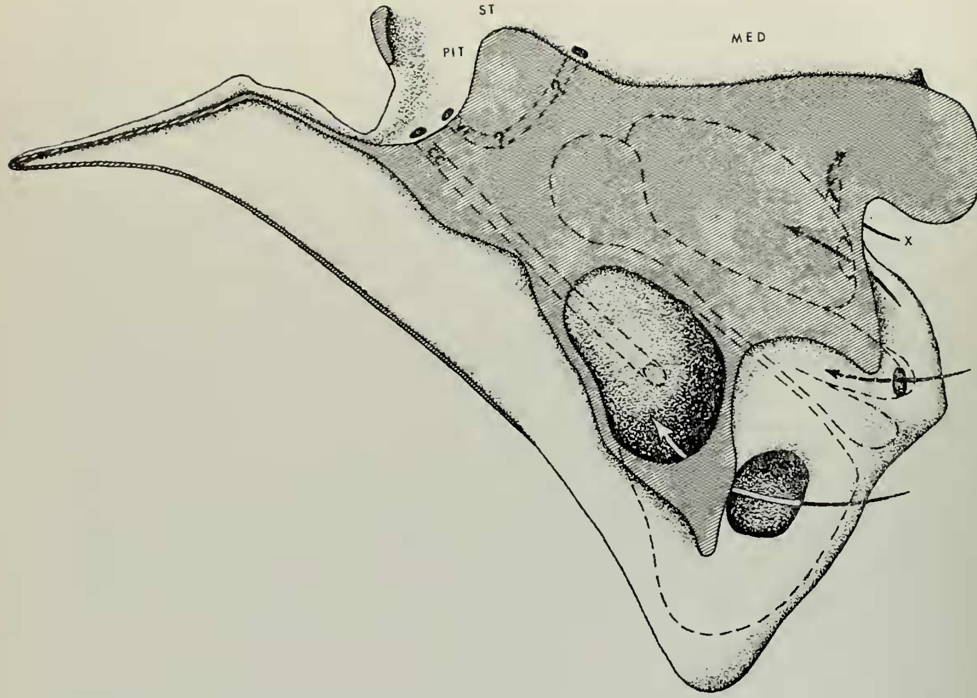

Figure 4—Albertosaurus, reconstruction of the lower half of the braincase seen in sagittal section. Abbreviations: CC carotid canal, MED medullary cavity, PIT pituitary fossa, ST sella turcica, VI hypothetical course of sixth cranial nerve. For further explanation see text.

tion of the ventral part of the braincase in *Albertosaurus* is presented here (Figure 4), based primarily on a partial dissection of the braincase of NMC 5600 (*A. sarcophagus*), with the parasphenoidal area restored from ROM 1237 (*A. libratus*). The large sinuses located in the parasphenoid rostrum and ventral part of the basisphenoid are seen in sagittal section. Dotted lines show the approximate extent of the latter sinus and two other sinus systems on either side of the cranial midline. The fenestrae linking each sinus system with the exterior are indicated by arrows; the arrow labelled "X" passed through the fenestra draining the sinus system in the paroccipital process. The more dorsal sinus systems are partly subdivided by thin webs of bone, which would probably exhibit a high degree of variability in different individuals.

In *Tyrannosaurus* (AMNH 5117), and also in *Allosaurus* (Osborn 1912: figs. 9–10), there is a foramen in the basisphenoid near the anteroventral edge of the laterosphenoid, which Osborn identified as the ventroposterior opening of the carotid canal. Although the distal part of the canal was not observed in NMC 5600, a small foramen in the pituitary fossa may mark its anterior termination. Behind this is another foramen, which may have contained the sixth nerve.

Neither the posterior course of the canal leading to the latter foramen nor the point of penetration of the sixth nerve into the floor of the medullary cavity was identified in this specimen. Not shown in Figure 4 are the conduits for nerves X to XII, which lie in the bone immediately ventrolateral to the medullary cavity and emerge on the occipital face of the skull in three foramina situated beside the neck of the occipital condyle. A small rod of bone, measuring 30 mm between its broken ends and 2.5 mm in diameter, was found in the matrix between the broken right quadrate and paroccipital process in NMC 5600. No doubt it is the stapes.

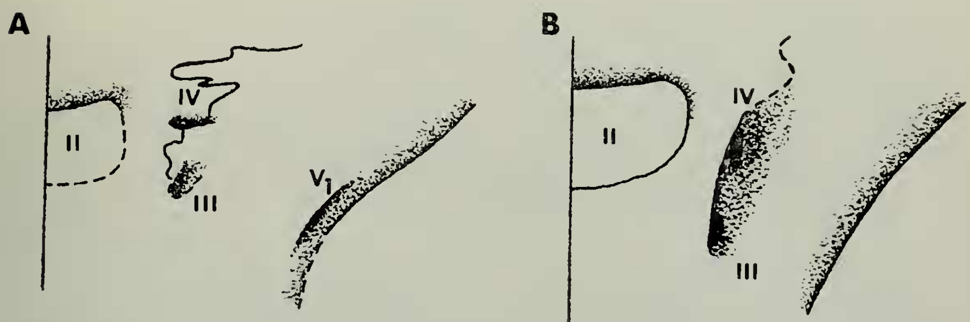

Figure 5—Semidiagrammatic relationships between the exits for cranial nerves II–V_1 on the anterior surfaces of the orbitosphenoid and laterosphenoid. A. *Albertosaurus libratus*, after NMC 11814; B. *Daspletosaurus torosus*, after NMC 8506.

It should be noted that in tyrannosaurs the median elements of the dermal skull roof are solidly sutured to each other and to the braincase below. This rigidity, coupled with the structural weakness of the basipterygoid processes, absolutely precludes any possibility of normal kinetic movement in the skull. Perhaps the diarthroid joint between the quadrate and squamosal, loose overlapping of the basipterygoid processes by the pterygoids, and split nature of the posterior part of the palate would allow some displacement of the temporal muscle mass in a medial direction. In similar fashion, the loose dorsal and posterior contacts of the jugal and quadratojugal, in combination with a vertically flexible antorbital lacrimal bar, may have allowed some displacement of the temporal muscle mass in a lateral direction. It is probable, however, that these suites of structures operated in an entirely passive manner, in response to the struggles of a massive prey held between the jaws. Even movements of the postulated kind must have been very limited, serving only to prevent the breakage of bones within the skull.

Genus **Daspletosaurus** new

Daspletosaurus torosus new species*

Distribution

Oldman Formation, near Steveville, Alberta, except where noted.

*Etymology *Dasplet*, Gr., frightful; *sauros*, Gr., lizard, *torosus*, fleshy, with reference to the large body.

Type

NMC 8506 skull and skeleton, lacking hind limbs (quarry 88 of Sternberg 1905).

Paratype

AMNH 5438 sacrum and adjacent thoracic and caudal vertebrae, pelvis, right femur, left tibia and second metatarsal (Little Sandhill Creek basin).

Referred Specimens

NMC 350 left hind limb (sec. 31, tp. 20, rge. 11, W. 4th mer.).

AMNH 5346 maxilla (Little Sandhill Creek basin).

UA 11 right femur and fourth metatarsal.

NMC 11594 incomplete, weathered skull and lower jaws (Oldman Formation, near Manyberries, Alberta: near centre NW.$\frac{1}{4}$ sec. 36, tp.1, rge. 6, W. 4th mer., about 30 feet below prairie rim or 3,285 feet above sea level).

BMNH R4863 premaxilla, maxilla, dentary.

Diagnosis

Premaxilla does not contact nasal below external naris. Maxillary teeth large, not greatly reduced posteriorly. Anteriormost antorbital fenestra within maxilla minute, hardly visible in lateral aspect, first antorbital fenestra nearly as high as long. Nasals slightly constricted between lacrimals, invaded posteriorly on either side by long slender tongue of frontal. Frontal broadly exposed on skull roof, lacks deep vertical cleft above orbit. Prefrontal broadly exposed dorsally between nasal, lacrimal, and frontal. Lacrimal 'horn' triangular in lateral aspect, with apex centred above antorbital ramus of bone; exceeds postorbital 'horn' in development. Anteroexternal edge of antorbital ramus of lacrimal is not continued across lateral surface of jugal. Ventral process of extopterygoid inflated, with large ventrally opening sinus; jugular process of bone also inflated. Angular terminates posteriorly beneath centre of surangular foramen.

Ventral opening of main basisphenoid sinus situated on midline of skull, behind transverse wall linking basipterygoid processes. Optic fenestra not bridged medially by presphenoid. Exits for cranial nerves III and IV contained in single pit on anterior surface of laterosphenoid. Exit for cranial nerve V_1 situated on lateral surface of laterosphenoid.

Neural spine of fourth cervical vertebra much larger than that of fifth. Neural spine of fifth cervical distally pointed, that of sixth cervical smaller and sharply pointed. Presacral vertebrae tend to be shorter and higher than in *Albertosaurus*; basal caudal vertebrae diminish less rapidly in size posteriorly than in latter species.

In adults length of humerus estimated to equal 38 per cent of that of femur, forelimb powerfully developed relative to that of *Albertosaurus*. Anterodistal condyle of metacarpal I reduced, causing first digit to diverge distally from second. First phalanx of digit II robust in adults. Dorsal edge of ungual of digit I passes through arc of about 90 degrees.

Anterior blade of ilium covers diapophysis of twelfth thoracic vertebra. In adults circumference of femur equal to 38 to 41 per cent of length of femur. In comparison with *Albertosaurus* specimens of similar femur length, presacral vertebral column is much shorter, thoracic ribs are slightly longer, forelimb is longer, ilium and sacrum are longer, and metatarsus is slightly shorter.

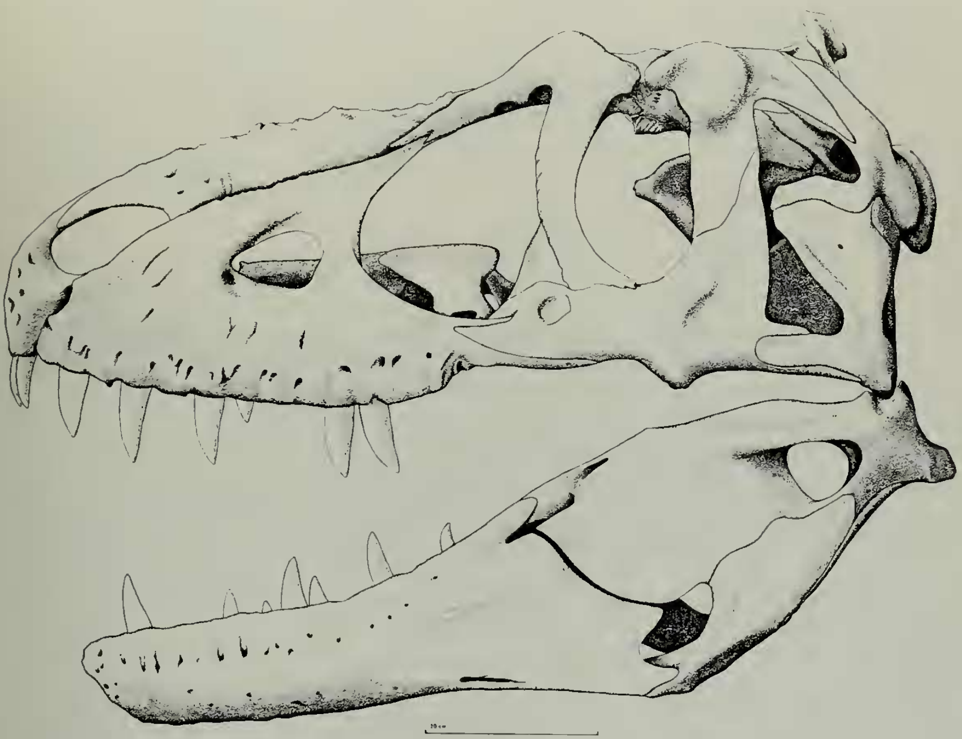

Figure 6—Daspletosaurus torosus, reconstruction of the skull in lateral aspect, based on NMC 8506. The foramen in the quadratojugal is taken from NMC 11315, where the element is better preserved.

Comments

The type specimen of *D. torosus* was collected by C. M. Sternberg late in the 1921 field season. As is usual in large theropod specimens, the head and anterior part of the vertebral column were pulled dorsoposteriorly toward the pelvis before the animal was buried. Although the hind limbs and many of the more distal caudal vertebrae were lost and although the remainder of the skeleton was partly scattered, the specimen is generally very complete and very well preserved. Sternberg's field notes indicate that at the time the specimen was collected he thought it belonged to an undescribed species of *Gorgosaurus* or to a new genus. Photographs of the skeleton in situ have been published by Sternberg (1945: 191; 1946: pl. 15; 1966: fig. 9), and of the skull by Sternberg (1945: 191; 1946: pl. 6; 1966: fig. 17).

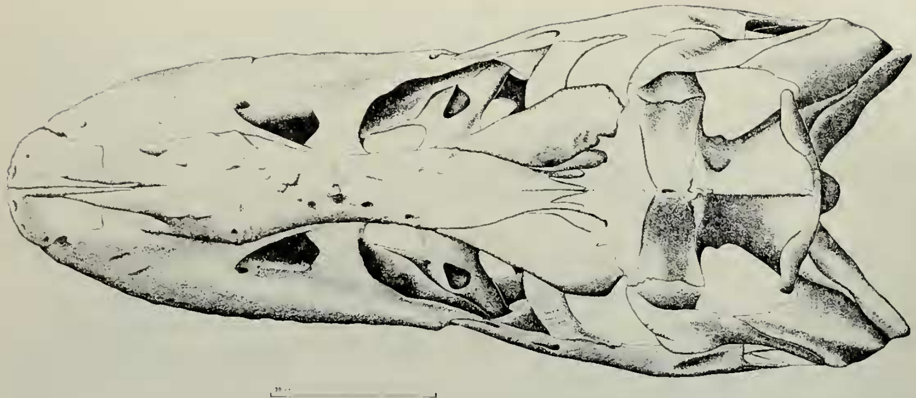

Figure 7—Daspletosaurus torosus, reconstruction of the skull in dorsal aspect, based on NMC 8506.

Daspletosaurus attained approximately the same length (28–30 feet) as its contemporary *Albertosaurus*. However, the body, which measured 1,350 mm (53 inches) through the widest point of the thoracic region in NMC 8506, and the base of the tail are much heavier than in *Albertosaurus*, and the hips and hind limbs are also more powerfully developed. The forelimb, although small, is relatively larger than in any other known tyrannosaur. Interestingly, with the exception of NMC 350, which is subadult, only fully grown specimens of *Daspletosaurus* have so far been collected from the Oldman Formation, while remains of one-half to three-quarters grown albertosaurs are relatively not uncommon in these sediments. The simultaneous existence of these two large carnosaurs indicates the presence in the fauna of two ecologic niches to accommodate them. As the endocranial cavities of both forms are quite small, it might be expected that differences in their gross morphology would rather accurately express their behavioural differences. Perhaps the more powerfully constructed daspletosaurs preyed on ceratopsians, and the more fleet albertosaurs were better suited to subsist on hadrosaurs. Albertosaurs and hadrosaurs are indeed correspondingly more abundant in the Oldman fauna than are daspletosaurs and ceratopsians.

The reconstruction of *Daspletosaurus torosus* (Figure 9) is based principally on the type skeleton (NMC 8506) and the hind limb of the paratype (AMNH 5438). Restored parts include the last two phalanges of the second digit of the manus, acetabular area of the ischium, posterior tip of the pubic boot, all of the metatarsals except the second, the entire pes, and caudal vertebrae 12–14, 18, 19, 21, 22, 26, 28–30, 32, and 36–37. The hind limbs of NMC 350 and NMC 11594 were consulted in drawing elements missing in this region of the type and paratype. Cervical and thoracic ribs are preserved on one side or the other throughout the presacral series of NMC 8506. In the reconstruction they are drawn as seen in lateral aspect, causing the ribs of the posterior thoracic region, which curve away from the vertebrae at a high angle, to appear unusually short. The solid line representing the ventral limit of the body was obtained by projecting the curvature of the anterior thoracic ribs to the midline of the body and by extending this line back to the anteroventral tip of the pubic boot. The abdominal ribs are not shown in the reconstruction.

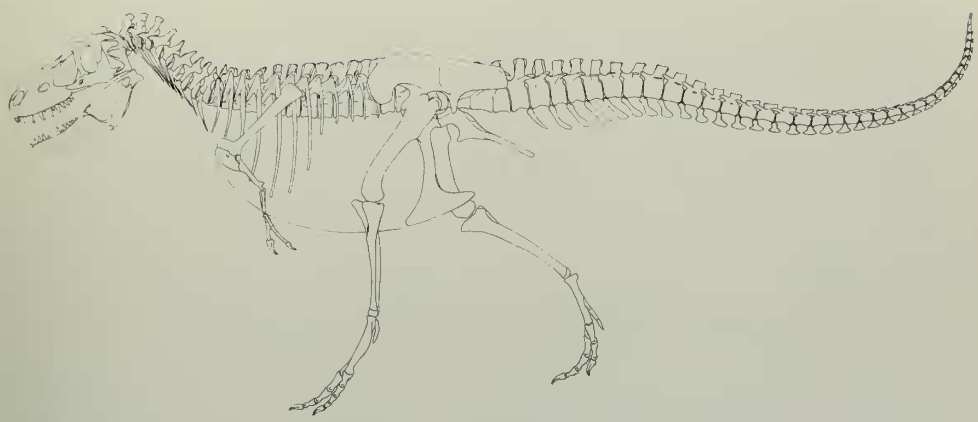

Figure 8—Daspletosaurus torosus, reconstruction of the skeleton. The length of the femur is 1000 mm, for further explanation see text.

The dental formula of *D. torosus*, as indicated by cranial material referred to the species, is: premaxillary teeth 4, maxillary teeth 14 or 15, dentary teeth 15 or 16. There are $11\frac{1}{2}$ to 15 serrations per 5 mm on the carinae of the marginal teeth, the serrations being coarsest near the centre of the jaws.

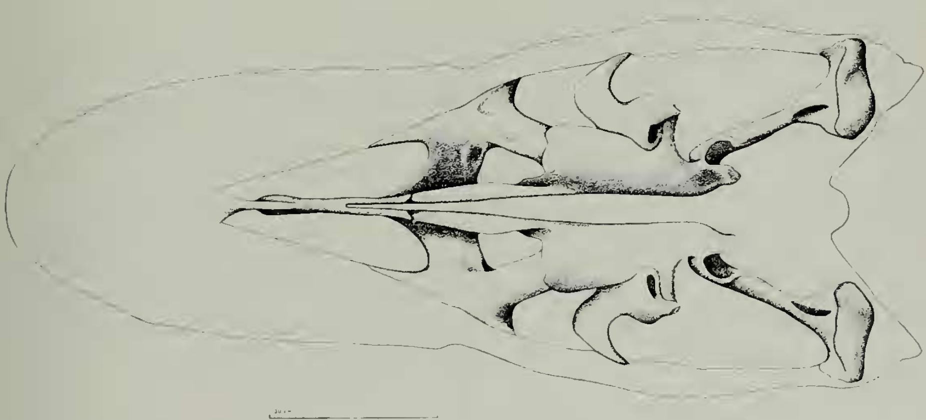

Figure 9—Daspletosaurus torosus, reconstruction of the palate in ventral aspect, based on NMC 8506.

The palate is disarticulated but exceptionally well preserved in NMC 8506 (*see* Figure 8). The vomers are fused together anteriorly dividing posteriorly into two thin vertical sheets of bone. A vertical anterior ala from the pterygoid broadly underlaps each of these vomerine processes. However, the pterygoids do not meet each other on the midline of the skull, nor do they contact the ventral part of the ascending processes of the palatines (the same relations exist in the palate of *A. libratus, see* AMNH negative number 37883, taken of USNM 12814). In *Albertosaurus* (*see* NMC 5600; Gilmore 1946: 11) and probably also in *Daspletosaurus* (NMC 8506) the upper edges of the anterior pterygoid alae loosely but widely contact the upper edge of these palatine processes, with the result that each half of the tyrannosaur palate is separated from the opposite half as far anteriorly as the middle of the vomers. The anterodorsal tip of the ascending process of the palatine is firmly applied to the external dorsoposterior corner of the vomer in *D. torosus* (NMC 8506) and perhaps also in *Albertosaurus* (AMNH 5336?; Gilmore 1946: 11).

Daspletosaurus cf. D. torosus

Distribution

Member B of Edmonton Formation, near Scollard, Alberta.

Referred Specimen

NMC 11315 scattered cranial elements, abdominal ribs, left forelimb, pelvis and hind limbs (SW. $\frac{1}{8}$ sec. 20, tp. 34, rge. 21, W. 4th mer., 150 feet above south bank of Red Deer River).

Comments

NMC 11315 represents the remains of a slightly more than half-grown tyrannosaur. It is referred to *Daspletosaurus* because the humerus, radius-ulna, ilium, and circumference of the femur are longer relative to the length of the femur than would be expected in an *Albertosaurus* of similar femur length. The claw of the first digit of the manus seems less recurved than in the latter genus. The specimen shows that *Daspletosaurus* probably underwent the same ontogenetic changes in limb proportions as did *Albertosaurus*. The foot is very similar to that of *Albertosaurus*, although the metatarsus is slightly shorter than in similarly sized specimens of this genus.

Tyrannosaur humeri are very infrequently found, and of the two *Daspletosaurus* specimens where it is preserved, the distal end of one (NMC 8506) is pathologic. Similarly, of five specimens of *A. libratus* where a humerus is preserved, in two of them (UA 10, FMNH PR308) the bone has also been damaged in life. This is an unusually high incidence of damage and suggests that the small forelimbs were often crushed by the weight of the massive bodies of these reptiles.

Genus **Tyrannosaurus** Osborn 1905, p. 259

Type species: *Tyrannosaurus rex*

Diagnosis (*See* Osborn 1906, 1912, 1917; Matthew and Brown 1923)

Premaxilla contacts nasal below external naris. Maxillary teeth relatively larger than in *Daspletosaurus*. Anteriormost antorbital fenestra within maxilla not visible in lateral aspect, first antorbital fenestra slightly higher than long. Nasals narrowly constricted between lacrimals. Frontal essentially limited to anteromedial wall of supratemporal fenestra, only small rim of bone reaches dorsal surface of skull. Prefrontal exposed dorsally between lacrimal and frontal. Lacrimal 'horn' represented by conical inflation not interrupting dorsal profile of skull. Postorbital 'horn' or rugose area well developed. Antero-external edge of antorbital ramus of lacrimal not continued across lateral surface of jugal. Ventral process of ectopterygoid inflated with very large, ventrally opening sinus. Angular terminates posteriorly behind surangular foramen.

Ventral openings of main basisphenoid sinus situated on either side of midline of skull, dorsomedial to each basipterygoid process. Vertical plate of presphenoid contacts orbitosphenoid and narrow suboptic bridge of laterosphenoid, separating optic fenestra into two openings. Cranial nerves III and IV open into single pit ventrolateral to optic fenestra. Exit for cranial nerve V_1 situated close to anterolateral edge of laterosphenoid, but not so close as in *Albertosaurus*.

Neural spines of fourth and fifth cervical vertebrae subequal, rather narrow in lateral aspect. Neural spine of fifth cervical distally pointed, that of sixth vertebra smaller and sharply pointed. In adults length of humerus equal to about 28 per cent of that of femur. Anterior blade of ilium does not cover diapophysis of twelfth thoracic vertebra. In adults circumference of femur approximately equal to 41 per cent of length of femur. Bodily proportions generally as in *Daspletosaurus*, although adult specimens about 25 per cent larger, humerus more reduced and ilium longer than in this genus.

cf. *Tyrannosaurus rex*

Distribution

Upper Edmonton Formation, Alberta.

Referred Specimens

NMC 9950 phalanx of pes (7 miles east of Huxley, centre sec. 10, tp. 34, rge. 22, W. 4th mer., about 170 feet above Kneehills Tuff).

NMC 9554 fragment of cervical centrum (20 feet below and 200 yards south of locality for NMC 9950).

Comments

The presence of *Tyrannosaurus* in Lance equivalent upper Edmonton strata has been noted several times (*see* Sternberg 1949; L. S. Russell 1964; Langston 1965). This record is based primarily on a badly eroded and shattered skeleton observed by Sternberg in 1946, weathering out of a fractured concretion high on the face of a cliff. Langston revisited the locality in 1960 and collected a phalanx, noting that the skeleton was even more badly damaged than when Sternberg discovered it, and that little of it still remained in situ.

The phalanx (NMC 9950) is the fourth one of the fourth toe and measures 53 mm in length and about 80 mm across its distal articulation. Hence it is larger and broader than the corresponding element in *Albertosaurus* and *Daspletosaurus*. Unfortunately only the first phalanx of the fourth toe is known in *Tyrannosaurus* (Osborn 1906: fig. 11). This bone is relatively broader than in any known Oldman or Edmonton form, and by analogy it seems probable that the above fourth phalanx may indeed belong to *Tyrannosaurus*. The vertebra (NMC 9554) is generically indeterminate.

TYRANNOSAURS NOT KNOWN TO OCCUR IN CANADA

Albertosaurus lancensis (Gilmore)

Gilmore (1946) has described the skull of a small carnivorous dinosaur from the Lance Formation of eastern Montana. The skull is quite different from that of *Tyrannosaurus* and Gilmore founded a new species on it, correctly referring it to *Gorgosaurus* (=*Albertosaurus*). Although the skull is only half as long as that of a fully grown *A. libratus*, the sutures between the bones of the skull roof are tightly interlocking, and some have been obscured through intergrowth; the supraoccipital alae of the parietals are well developed, and a clearly formed tuberosity is present on the ventral border of the jugal (Gilmore 1946). The opposite conditions prevail in the skull of AMNH 5664, a specimen of *A. libratus* of comparable size. The skull of *A. lancensis* is therefore probably from a fully grown individual, and its small size may be characteristic of the species.

Albertosaurus lancensis further differs from *A. libratus* and *A. sarcophagus* (AMNH 5222) in that the frontals meet on the midline throughout their entire length, while in the latter two species these elements are separated anteriorly by a small wedge of bone from the nasals. The frontals are not so deeply cleft above the orbits as is the case in *A. libratus* and *A. sarcophagus*. Gilmore (1946: 6) suggested that the prefrontal may be rather well exposed on the skull roof, unlike in the more ancient species of the genus. Otherwise the skulls of the three forms are quite similar.

Tarbosaurus bataar (Maleyev)

This species is known from the remains of at least seven individuals collected by the Palaeontological Institute of the Academy of Sciences of the U.S.S.R. (Maleyev 1955*b*, 1955*c*) and six more collected by the Polish–Mongolian Palaeontological Expedition (Kielan-Jaworowska 1967), all from the Nemegt basin in strata that may be approximately Edmontonian (*see* L. S. Russell 1963) in age. The form has not yet been thoroughly described, although it has been the subject of several brief reports (*see* Introduction) and a cast of the skull of one specimen (NMC 10422) was available for study through an exchange with the Palaeontological Institute. *Tarbosaurus* seems to be most closely allied to *Tyrannosaurus*. It differs from this genus in that the nasals are not quite so constricted between the lacrimals, the frontals do have some dorsal expression (but not so much as in *Albertosaurus* or *Daspletosaurus*), the surangular foramen is small, and adult animals are smaller than adult specimens of *Tyrannosaurus*. (I am indebted to Dr. A. K. Rozhdestvensky for the above information on the morphology of *Tarbosaurus*.)

TABLES OF MEASUREMENTS

All measurements are expressed in millimetres. The lengths of the phalanges were measured between the lateral edges of the anterior and posterior articular surfaces, along the horizontal midline of the bone.

MEASUREMENTS USNM 12814 *Albertosaurus libratus*
(*see also* Table 1)

SKULL:

Length lower dentition	352

DORSAL RIBS (tuberculum to end):

1	350
2	652
3	793
4	823
5	830

LENGTHS OF PHALANGES OF PES:

Right Pes	*1*	*2*	*3*	*4*	*5*
digit 1	87	–			
digit 2	141	94	131*		
digit 3	157	98	97	115*	
digit 4	103	72	71	–	–
Left Pes					
digit 1	–	–			
digit 2	147	94	ca. 114*		
digit 3	148	–	–	–	
digit 4	ca. 98	–	55	–	ca. 93*

For measurements of the type of *A. libratus*, *see* Lambe (1917). For measurements of specimens of this species in the American Museum of Natural History, *see* Matthew and Brown (1923)

VERTEBRAE

Cervicals	Ant-post width Across Zygopophyses	Height Anterior Face of Vertebra	Length of Centrum
1	–	–	–
2	–	–	65
3	ca. 127	176	ca. 73
4	ca. 145	171	ca. 73
5	ca. 148	161	ca. 70
6	ca. 150	ca. 157	ca. 82
7	ca. 145	175	ca. 87
8	ca. 123	183	–
9	ca. 110	197	–
10	ca. 105	198	–

Dorsals	Length of Centrum	Height of Vertebra
1	ca. 70	–
2	–	–
3	70	243
4	78	271
5	80	269
6	94	277
7	95	297
8	90	291
9	85	303
10	82	293
11	98	308
12	107	310
13	124	330

*Measured along dorsal curve of ungual.

MEASUREMENTS NMC 11593 *Albertosaurus libratus*
(*see* Table 1):

HIND LIMB:

length fibula	795
width astragalus	183
height astragalus	212

LENGTH OF ELEMENTS IN RIGHT PES:

	metatarsal	*1*	*2*	*3*	*4*	*5*
digit 1	–	104	–			
digit 2	520	172	–	–		
digit 3	594	166	–	–	–	
digit 4	–	123	–	–	38	112*
digit 5	–					

LENGTH OF ELEMENTS IN LEFT PES:

	metatarsal	*1*	*2*	*3*	*4*	*5*
digit 1	95	109	–			
digit 2	514	170	105	123*		
digit 3	580	165	110	–	152*	
digit 4	545	124	83	54	–	–
digit 5	223					

CAUDAL VERTEBRAE:

	Height of vertebra	Height of centrum	Length of centrum	Length of transverse process	Length of chevron
1	–	ca. 170	140	–	–
2	348	168	126	125	–
3	ca. 313	155	123	105	–
4	316	150	137	105	–
5	306	140	128	83	–
6	276	130	127	ca. 80	–
7	259	115	132	64	188
8	222	110	138	60	167

*Measured along dorsal curve of ungual.

MEASUREMENTS NMC 8506 *Daspletosaurus torosus*

SKULL:

Premaxilla—mandibular condyle	1040
Premaxilla—occipital condyle	1040
Supraoccipital crest—mandibular condyle	450
Width across quadratojugals	425
Length upper dentition	530
Length lower dentition	420
Length lower jaw	1015/1020
Height muzzle above last maxillary tooth	300
Height of quadrate	248

DORSAL RIBS:

	Length capitulum to tuberculum		Length tuberculum to end	
	left	*right*	*left*	*right*
1	ca. 210	237	–	617
2	243	257	868	–
3	252	265	–	997
4	254	263	1219	1212
5	262	264	1250	–
6	–	273	–	–
7	261	273	933	892
8	233	ca. 248	740	–
9	215	ca. 246	665	–
10	–	236	ca. 540	–
11	202	212	–	455
12	capitulum absent		465	–

FORELIMBS:

length of scapula	772
length of coracoid	170
length of humerus (pathologic)	357
length of ulna	214
length of radius	171

MANUS:

	metacarpal	*1*	*2*	*3*
digit 1	60	133	155*	
digit 2	120	48	–	–
digit 3	71			

PELVIS:

length of ilium	1104
length of pubis	935/902

*Measured along dorsal curve of ungual.

CERVICAL VERTEBRAE:

	Ant-post width across zygopophyses	Height anterior face of vertebra	Height of centrum	Length of centrum	Width of centrum	Width across diapophyses
1	–	–	ca. 60	40	88	–
2	160	300	110	80*	100	ca. 95
3	150	290	ca. 80	74	85	115
4	165	285	88	85	98	132
5	187	280	95	100	90	ca. 175
6	175	260	90	100	85	ca. 190
7	175	273	100	92	105	ca. 255
8	135	305	105	90	110	270
9	135	338	116	90	ca. 120	307
10	118	ca. 345	127	104	124	342

*With axis intercentrum.
Total length of cervical series = 900.

DORSAL VERTEBRAE:

	Length of centrum	Width of centrum	Height of centrum	Height of vertebra	Width across diapophyses
1	96	138	140	356	332
2	91	ca. 138	124	340	290
3	96	126	145	348	282
4	113	127	136	372	276
5	98	125	140	405	293
6	ca. 95	ca. 120	–	415	295
7	ca. 112	ca. 123	ca. 154	430	308
8	104	127	–	440	292
9	ca. 110	ca. 128	ca. 178	458	278
10	ca. 118	ca. 138	–	–	282
11	ca. 108	–	–	–	308
12	ca. 118	–	–	454	313
13	ca. 108	–	–	447	–

Total length of dorsal series = 1470.
Length of sacrum = 752.

CAUDAL VERTEBRAE:

	Height of vertebra	Height of centrum	Length of centrum	Length of transverse process	Length of chevron
1	433	–	ca. 140	ca. 205	–
2	420	195	151	–	–
3	–	–	–	ca. 170	–
4	363	165	134	ca. 165	–
5	359	160	133	ca. 160	252
6	–	145	ca. 134	ca. 130	248
7	297	155	152	ca. 118	242
8	284	150	ca. 146	ca. 115	204
9	274	140	146	ca. 118	188
10	246	130	150	ca. 75	174
11	213	110	162	ca. 88	162

MEASUREMENTS AMNH 5438 *Daspletosaurus torosus*

VERTEBRAE:

Dorsals	Height vertebra	Height centrum	Length centrum
11	434	168	100
12	467	ca. 183	118
13	–	ca. 175	143
Sacrals			
1	–	ca. 173	132
2	–	–	ca. 125
3	–	–	ca. 133
4	–	–	165
5	–	–	173
Caudals			
1	378	174	113
2	ca. 380	ca. 174	–
length of sacrum		712	

PELVIS:

length of ilium	1096

HIND LIMB:

length of femur	1000
circumference of femur	390
length of tibia	870
length of metatarsal II	460

MEASUREMENTS UA 11 *Daspletosaurus torosus*

HIND LIMB:

length of femur	1000
circumference of femur	415
length of metatarsal IV	490

MEASUREMENTS NMC 11315 *Daspletosaurus* cf. *D. torosus*

SKULL:

height of quadrate	164

FORELIMB:

length of scapula	470
length of coracoid	110
length of humerus	225
length of ulna	120
length of radius	96

MANUS:

	metacarpal	*1*	*2*	*3*
digit 1	32	63	57*	
digit 2	58	28	ca. 40	61*
digit 3	38			

PELVIS AND HIND LIMB:

length of ilium	ca. 675
length of pubis	ca. 600
length of pubic boot	365
length of ischium	488
length of femur	655
circumference of femur	226
length of tibia and astrag.	736
height of astragalus	233
width of astragalus	136/118

LENGTH OF ELEMENTS IN RIGHT PES:

	metatarsal	*1*	*2*	*3*	*4*	*5*
digit 1	73	–	–			
digit 2	405	130	ca. 85	90*		
digit 3	448	129	81	60	–	
digit 4	423	87	63	–	28	
digit 5	165					*N*

LENGTH OF ELEMENTS IN LEFT PES:

digit 1	–	74	–			
digit 2	398	127	80	89*		
digit 3	445	130	–	–	110*	
digit 4	420	87	58	40	27	75*
digit 5	165					

*Measured along dorsal curve of ungual.

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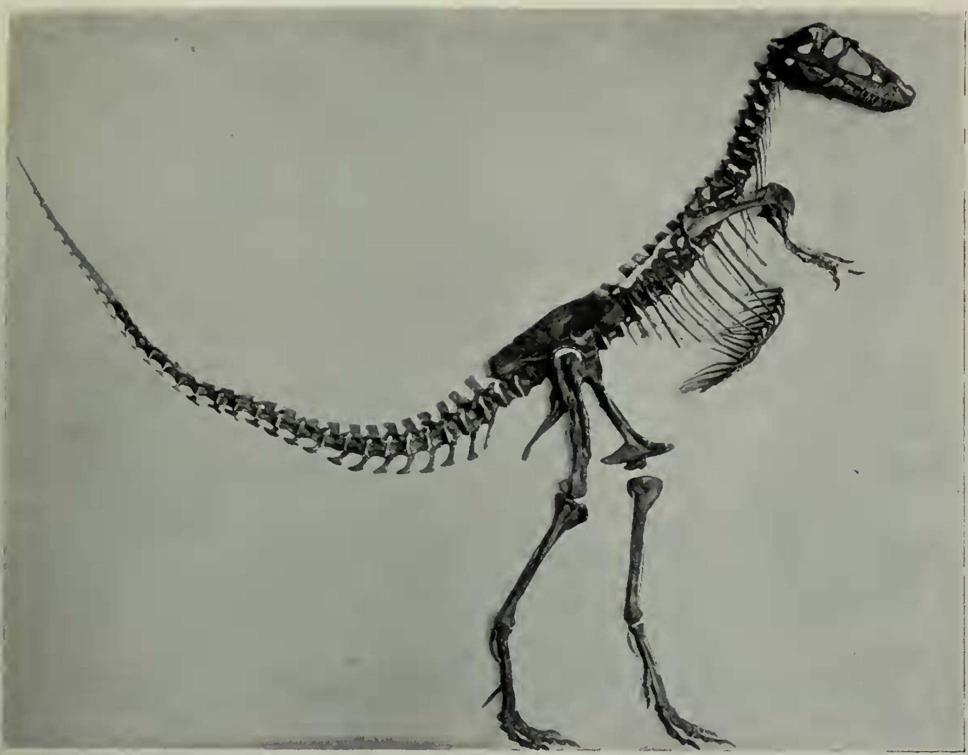

Plate I—Albertosaurus libratus, AMNH 5664. The femur is 700 mm long (Matthew and Brown 1923: 10). Photograph courtesy of the American Museum of Natural History, AMNH negative number 39016.

Plate II—Albertosaurus libratus, AMNH 5458. The femur is approximately 1025 mm long (Matthew and Brown 1923: 10). Photograph courtesy of the American Museum of Natural History, AMNH negative number 39106.

Plate III—Daspletosaurus torosus, NMC 8506. Forelimb seen in dorsal aspect.

Plate IV—Daspletosaurus torosus, NMC 8506. Forelimb seen in ventral aspect.