

Article **XLIII**.—SKELETAL ADAPTATIONS OF *ORNITHOLESTES*, *STRUTHIOMIMUS*, *TYRANNOSAURUS*.

By HENRY FAIRFIELD OSBORN.

PLATES XXIV–XXVII, AND TWENTY-THREE TEXT-FIGURES.

INTRODUCTION.

A revision of the previous description by the author (1903) of *Ornitholestes* and a preliminary study of the skeletons of *Struthiomimus* (*Ornithomimus*) and of *Tyrannosaurus* forms the subject of this article.

The new subgeneric or generic name **Struthiomimus** is proposed for the Belly River (Fort Pierre) stage of the Ornithomimidæ.

The discovery of the skull of the Belly River "*Ornithomimus*" occasioned one of the greatest surprises in the whole history of vertebrate palæontology because it proved that both in head and limb structure this animal was non-raptorial. *Struthiomimus* (*Ornithomimus*) has no adaptations in its limbs nor in its jaws for seizing an active prey; on the contrary, the extremely small head and slender jaws entirely without teeth most nearly resemble those of the ostrich (*Struthio*). Nor is the recently discovered fore limb analogous to that of any of the carnivorous dinosaurs; it is in some characters like that of the peaceful herbivorous tree sloths *Bradypus* and *Cholæpus*; in other characters it is unique. The pes has long been known as of the purely cursorial type, the phalanges closely resembling those of certain of the struthious birds.

These surprising discoveries necessitate a reconsideration of the structure and habits of *Ornitholestes*, which at the time of its first description by Osborn derived its name from its supposed bird catching propensities (*Ornithos*, ὄρνις, bird, *lestes*, ληστής, robber). *Ornitholestes*, an Upper Jurassic animal, is doubtless related as a family to *Struthiomimus* (*Ornithomimus*) of the Upper Cretaceous, there being a striking general resemblance, as shown in the comparative restorations of Plate XXV. *Ornitholestes* connects *Struthiomimus* (*Ornithomimus*) with the true carnivorous dinosaurs since it is more of the raptorial type. In the light of our fuller knowledge of the *Struthiomimus* (*Ornithomimus*) skeleton a restudy of *Ornitholestes* indicates that it also has partially lost its raptorial characters; the teeth are small and feeble, in the manus the two central digits, D II–III, are closely appressed and not adapted to seizing or holding a struggling live prey, as Osborn

imagined in restoring this animal<sup>1</sup> as seizing *Archæopteryx*; the manus is relatively feeble, and the phalanges while not fully known appear to be elongating in the direction of the *Struthiomimus* (*Ornithomimus*) type. In brief, *Ornitholestes* is a small, subcarnivorous dinosaur of the cursorial, bipedal type, the body balanced by a very elongate tail which shows the beginnings of characters evolving for a new mode of life, in adaptation to which there appears to be a secondary elongation of the fore limb, which is carried to a further extreme in *Struthiomimus* (*Ornithomimus*).

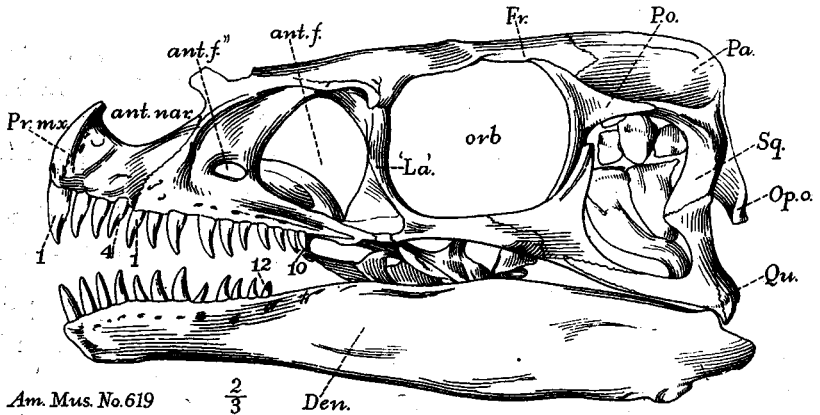


Fig. 1. Reconstructed skull of type of *Ornitholestes hermanni*, Amer. Mus. No. 619, replacing the original figure (1903). Two-thirds natural size.

*Ornitholestes* does not point directly toward the *Struthiomimus* type for it displays a somewhat different adaptive evolution of the manus. Yet *Ornitholestes* appears to agree with *Struthiomimus* in the separation or divergence of the phalanges of the pollex (Digit I) from those of Digits II, III, which are closely appressed (see Figs. 2, 3) to each other.

The illustrations for this bulletin have been made with great accuracy by Mr. Erwin S. Christman, Mrs. Lindsey Morris Sterling, and Mr. A. E. Anderson. The orthogonal scale projection of the vertebral column of *Tyrannosaurus* by Mr. Christman and the photographs by Mr. Anderson are especially accurate and remarkable.

<sup>1</sup> Osborn, H. F. "Fossil Wonders of the West, the Dinosaurs of the Bone-Cabin Quarry, being the First Description of the Greatest "Find" of Extinct Animals Ever Made." *Century Mag.*, Vol. LXVIII, No. 5, Sept., 1904, pp. 680-694.

RESTUDY OF *ORNITHOLESTES HERMANNI* OSBORN.

Text-figs. 1-3, Plate XXVI.

The original reconstruction of the skeleton (Osborn, 1903, fig. 1, p. 460)<sup>1</sup> is very inaccurate. It was based partly upon Marsh's restoration of the skeleton of *Anchisaurus*. The cervical ribs are incorrectly restored; the presacral vertebræ, restored as twenty-eight, are certainly too numerous; the digits of the manus (Osborn, 1903, figs. 1, 2, 3) are restored as spreading instead of closely appressed; the skull is incorrectly drawn.

The following characters may be pointed out in the new reconstruction shown in Plate XXVI, which is based upon a restudy of the type specimen (Amer. Mus. No. 619) supplemented by the manus of the second specimen (Amer. Mus. No. 587).

*Vertebral formula.* The vertebral formula is uncertain; it is estimated in comparison with that of other Theropoda as follows:

	<i>Ornitholestes</i>	<i>Struthiomimus</i>	<i>Allosaurus</i>	<i>Tyrannosaurus</i>
Cervicals	? 9	10	9e	10-9
Thoracic dorsals	?13	13	14	13-14
Cervico-thoracics, presacrals	23e	23	23	23
Sacrals	4	?5	5	5
Caudals	?39-44	?40		?53

It will be observed that there is a constant number of twenty-three pre-sacrals in *Struthiomimus*, *Allosaurus*,<sup>2</sup> and *Tyrannosaurus*, which renders it probable that *Ornitholestes* also had not more than twenty-three pre-sacrals.

The boundary line between the cervical and thoracic vertebræ in the American Museum skeleton of *Ornitholestes* is uncertain because the two vertebræ C9 and C10 are missing, but in *Struthiomimus*, in which the cervical series is complete, the boundary line is clearly indicated by the change in the character of the ribs from the fixed, coalesced condition (C10) to the movable bicipital condition (Th. 1).

*Skull.* (1) Teeth: premaxillary 4, maxillary 10; crowns not so serrate or prehensile as in typical carnivorous dinosaurs. (2) Cranium with two antorbital openings, prominent premaxillaries, typical theropod arrangement

<sup>1</sup> Osborn, H. F. "Ornitholestes hermanni, a New Compsognathoid Dinosaur from the Upper Jurassic." Bull. Amer. Mus. Nat. Hist., Vol. XIX, Art. xii, July 23, 1903, pp. 459-464.

<sup>2</sup> In the National Museum series of *Allosaurus* there were found nine cervicals, fourteen dorsals, and five sacrals; there were two breaks in the series, but evidently the whole number was present. Letter of C. W. Gilmore, January 8, 1916.

of lacrymals, frontals, postorbitals, parietals, squamosals, quadratojuggals, opisthotics. (3) Dentary with twelve small upright or slightly recurved teeth. (4) Jaw with sessile coronoid process.

*Vertebrae.* Cervicals nine or ten in number, gently opisthocœlous; dorsals amphicœlous; caudals amphicœlous. The supposed 7th and 8th cervicals are moderately elongate, slightly opisthocœlous, with separate attachments for the capitulum of a freely articulated rib on the anterior portion of the centrum and for the tuberculum on the broad diapophysial extension of the neural arch. The neuro-central suture is faintly indicated. It appears that the cervical ribs were slender, free, and two-headed in *Ornitholestes* while in *Struthiomimus* they are firmly coalesced with the sides of the cervical centra and arches, a progressive character. For other details of the vertebrae see original description (Osborn, 1903, p. 460). Four

firmly coalesced sacral ribs are suturally distinct. Caudals 39-44e, anterior caudal ribs coalesced. The very characteristic rod-like elongation of the zygapophyses of the caudal vertebrae begins with the vertebra supposed to be C13; it reaches its maximum between C16 and C24. In these vertebrae the chevrons are depressed, elongate, bifurcated in front, with a posterior keel. In *Struthiomimus* the rod-like elongation of the prezygapophyses begins with C12 and reaches the maximum in C26-C30, which are so rigidly articulated by the elongate zygapophyses and chevrons as to admit of little or no movement.

*Pelvic girdle.* The pelvic girdle is broadly similar in contour to that of *Struthiomimus*, but ilium, pubes, and ischia are suturally separate, while in *Struthiomimus* they are firmly coalesced; pubes with deep sym-

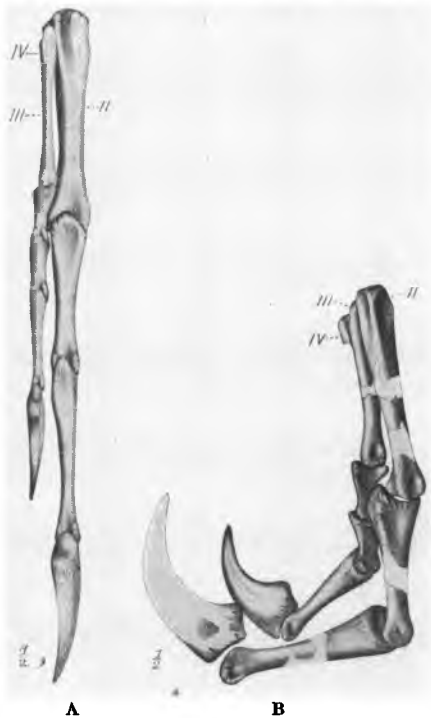


FIG. 2. Incomplete manus of *Ornitholestes hermanni*; Digit I is missing in this specimen. Amer. Mus. No. 587. Palmar (A) and internal (B) views, one-half natural size. After Osborn, 1903.

physial union; ischia more slender, with proximal anterior processes united distally; peduncle of pubes missing in the type.

*Hind limb.* Femur (.207m.) and tibia (.159m.) estimated to be of unequal length, the femur being the longest bone. In *Struthiomimus* the tibia is more elongate, a cursorial adaptation. The pes tridactyl; median metatarsal, Mts. III (.117 m.), relatively less elongate than in *Struthiomimus*: condition of Mts. V unknown. The total length of the hind limb is

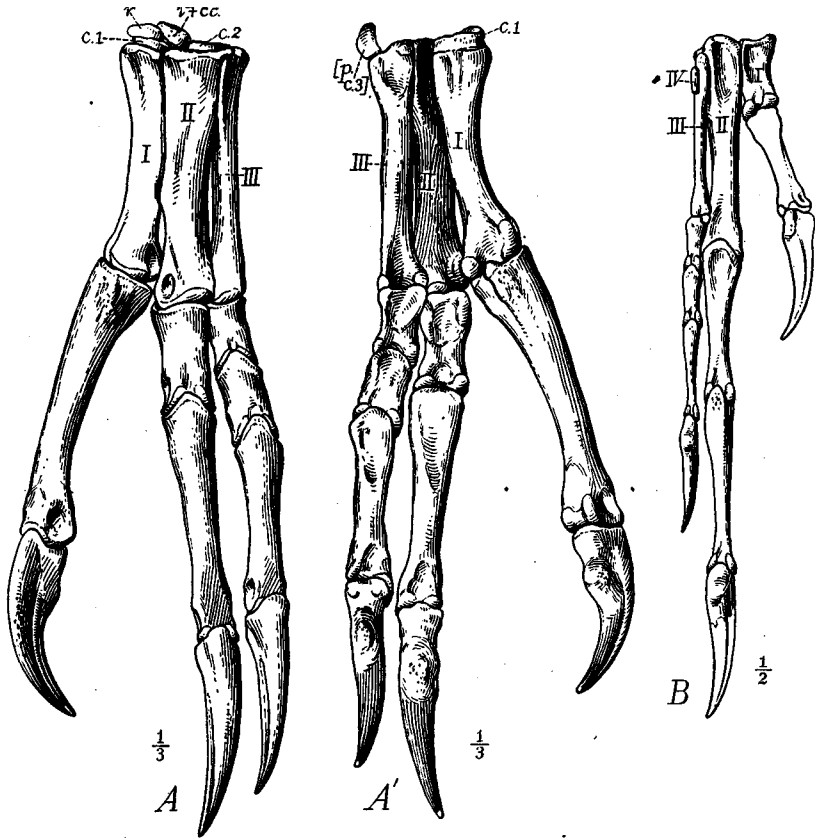


Fig. 3. Composition of complete manus (B) palmar view of *Ornitholestes hermanni*. Amer. Mus. 587, partly restored (Digit I) from Amer. Mus. 619, type. One half natural size.

Manus of *Struthiomimus altus*, Amer. Mus. 5339. (A), dorsal aspect; A', palmar aspect. *r.*, radiale, *i.*, intermedium (?) coalesced with *cc.*, centrale. C1, C2, p. C3 carpalia and (?) p. tendinosa ossicle. One third natural size.

.483 m., the tibio-femoral ratio is .706, which indicates that the movement of this animal was not so swift as that of *Struthiomimus* (*Ornithomimus*), in which the tibio-femoral ratio is: 1.11 (T. 540-F. 480). It appears from the preserved terminal phalanges that they were more recurved and claw-like than in *Struthiomimus* (*Ornithomimus*).

*Fore limb.* In the fore limb of *Ornitholestes* the humerus is somewhat longer (.127 in.) than the ulno-radius, which is also the proportion observed in *Struthiomimus*. In the figures accompanying the original description of *O. hermanni* (Amer. Mus. 587, see Figs. 7A, 7B, p. 748) the proportions are correctly represented.

We observe a marked anisodactyly and lateral compression of the manus (Figs. 2, 3 B). Mtc. II is enlarged and greatly elongate while Mtc. III is reduced and abbreviated, and Mtc. IV is vestigial; Digit I is partly known in the type as being short and somewhat divergent (Plate XXVI); Mtc. I and Ph. I. 2 only are preserved. This manus may, therefore, be described as functionally *anisotetradactyl* whereas that of *Struthiomimus* is comparatively *isotridactyl*, indicating a very marked difference in habit. In other words, the manus of *Ornitholestes* while subraptorial is more highly reduced than that of *Struthiomimus*. The central digits are closely appressed to each other (as in *Struthiomimus*) while the claws are relatively more powerful and recurved (Fig. 7B) than in *Struthiomimus*. The *Ornitholestes* manus is losing its fitness as a raptorial grasping type, it is too feeble and too much reduced; it represents a species adaptation to another purpose, recalling in some features the slender and greatly elongated digits of the Aye-Aye (*Cheiromys*). In (Fig. 3) *Ornitholestes*, *Struthiomimus*, and the manus associated with *Ornithomimus* (Fig. 3a) metatarsal I is closely appressed to metatarsal II. The phalanges of the pollex are divergent and rotated inwards in the two genera first named, *Ornitholestes* and *Struthiomimus*.

The fact that the central digits of *Ornitholestes* are closely appressed and incapable of spreading laterally harmonizes with the incipient coalescence of Mtc. I and Mtc. II in *Struthiomimus*. Another harmony is the divergence of the phalanges of Digit I.

## STUDY OF STRUTHIOMIMUS AND ORNITHOMIMUS.

### TYPE LOCALITIES OF STRUTHIOMIMUS, ORNITHOMIMUS, AND TRICERATOPS.

The known *Ornithomimidae* belong to two phases of Upper Cretaceous age which are widely separated in geologic time, as follows:

1. *Ornithomimus velox*. The genotype specimen of *Ornithomimus velox* Marsh is probably of *Triceratops* zone age. It consists of leg bones found in 1892 by G. L. Cannon about twelve miles from Denver, Colorado, near where the old Morrison should have left the mesa going down into Beaver Creek Valley at the head of a small arroyo east of road and near a small

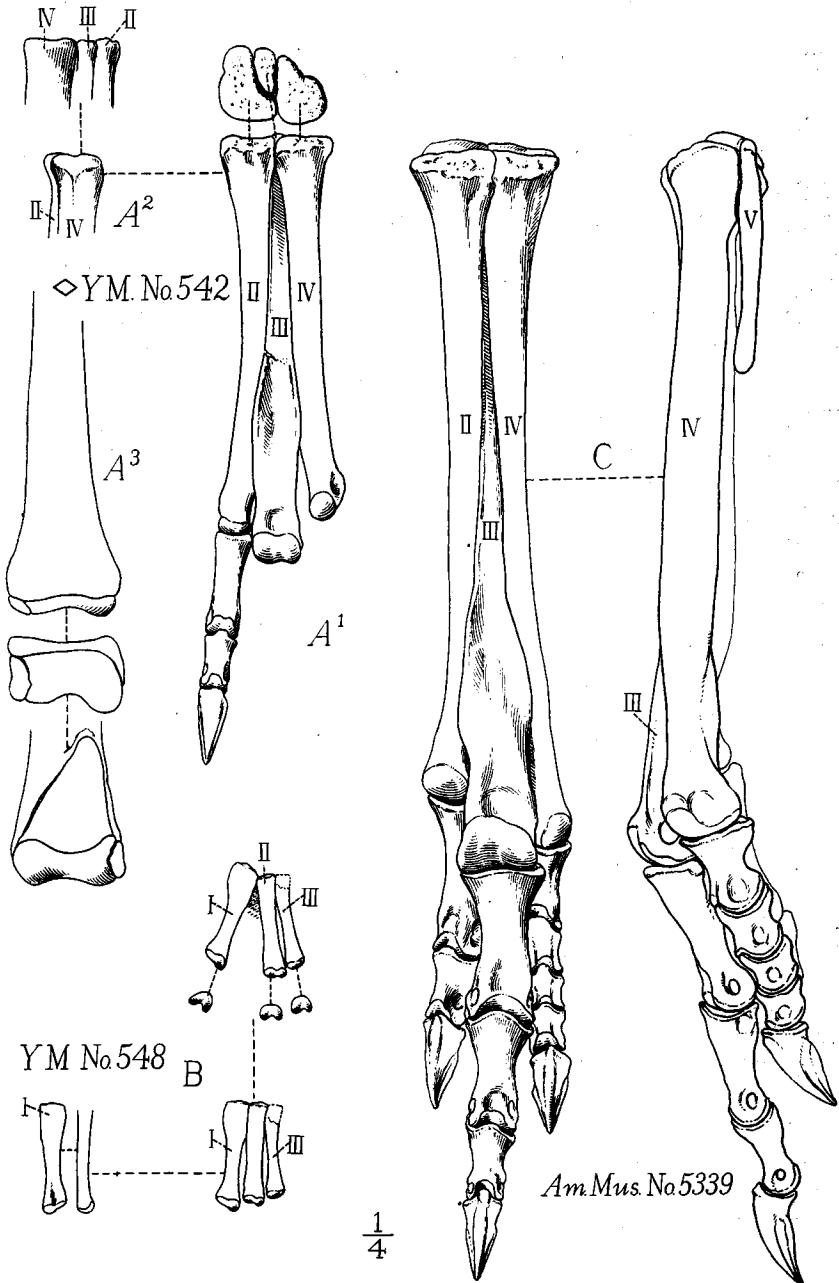


Fig. 3a. (A<sup>1</sup>-A<sup>3</sup>). Genotype specimen of *Ornithomimus velox* Marsh. Yale Mus. 542. (A<sup>1</sup>), dorsal aspect of the type left pes, superior aspect of Metatarsals II-IV. (A<sup>2</sup>) posterior aspect (upper) and exterior aspect (lower) of metatarsals II-IV. (A<sup>3</sup>) Type tibio-tarsus, anterior, inferior, posterior aspects. (B) Portion of right manus of another individual (Yale. Mus. 548) associated by Marsh with *Ornithomimus velox*; (upper) metacarpals I-III as they appear in the matrix, (lower) as placed in natural position. (C) Left pes of *Struthiomimus allus*, genotype specimen, Amer. Mus. 5339. Anterior and exterior aspects of digits II-V. One fourth natural size. After original drawings by the present author. One-fourth natural size.

white school house.<sup>1</sup> The geologic age of this genotype still remains to be determined precisely; it is probably the *Triceratops* zone. The records of the Peabody Museum, Yale University, are as follows: The genotype of *Ornithomimus velox* bears the catalogue number Yale Museum 542, collected by George L. Cannon June 30, 1889, in the Denver sandstone, in the southwest quarter of section 27, tier 4 S., range 69 W. The locality note in Professor Marsh's handwriting is as follows: "Foot of *Ornithomimus* ? found on Bear Creek road from Morrison to Denver, where it leaves the creek and goes on hills, 6 m. from Morrison. (Right hand side road). 20 ft. from road bed, near end of gully within 100 yards of house of left of road (white house with chicken coops and the only house on slope of hill near top.) 6 ft. below road bed and near end of gully." The presumption is that this is the same horizon as that of *Triceratops (Bison) alticornis*, but that specimen is now in the United States National Museum, Washington.<sup>2</sup> The locality of the type of *Triceratops (Bison) alticornis* is in the suburbs of the city of Denver. The records of the United States National Museum give the locality of the type of *Triceratops alticornis* as Green Mountain Creek, near Denver, Colorado.<sup>3</sup> Marsh in his description says: "Portions of the same specimen were subsequently secured by Whitman Cross of the U. S. Geological Survey."

2. *Struthiomimus tenuis*. The type of the geologically more ancient "*Ornithomimus*" *tenuis*<sup>4</sup> Marsh bears the catalogue number U. S. Nat. Mus. 5814. It is of Monoclonius-Ceratops zone age, from the Judith River formation as exposed on Birch Creek, Montana, and was collected by J. B. Hatcher in 1888. Hatcher states<sup>5</sup> that he found Marsh's type of this species, consisting of a foot and a portion of a limb, on Cow Island, Missouri River, at a level which he estimates from 1,500 to 1,600 feet below the summit of the Judith River beds and 500 to 600 feet below the level of Marsh's type of *Ceratops montanus*.

3. "*Ornithomimus*" *grandis*. The type of "*Ornithomimus*" *grandis* Marsh has not been located in the United States National Museum; its generic and family reference is therefore doubtful at present. It may belong to the genus *Deinodon* Leidy. Hatcher's record regarding its geological position (Bull. U. S. Geol. Surv. 257, pp. 12-41-87) is that it was found in the Eagle Sandstones.<sup>6</sup>

<sup>1</sup> Notes given for the writer by G. L. Cannon to Mr. Barnum Brown orally on June 29, 1916.

<sup>2</sup> Letter of R. S. Lull to the writer, January 12, 1916.

<sup>3</sup> Gilmore, Charles W. Letter to the author, January 15, 1916.

<sup>4</sup> If the genus *Struthiomimus* is established this species should be transferred to it.

<sup>5</sup> Hatcher, J. B. *Science*, N. S., Vol. XVI., no. 412, November 21, 1902, pp. 831-832.

<sup>6</sup> Gilmore, Charles W. Letter to the writer, Jan. 15, 1916.



	Ceratops-Monoclonius Zone		Anchiceratops-Leptoceratops Zone	Typical Triceratops alticornis zone	Triceratops-Torosaurus zone
	Judith River Formation Montana	Belly River Formation Alberta	Edmonton Formation Alberta	Denver Basin Colo.	Hell Creek Montana
1. <i>Ornithomimus velox</i> Marsh, genotype				×	
? <i>Ornithomimus velox</i> ?sp., Amer. Mus. Nos. 5016, 974, 975, 1006, 5003, 5014, 5015, 5018, 5019, 5051, 5884, 5891, ?5017, ?5050					XXXXXXXXXX XXXXXXXXXX
? <i>Ornithomimus velox</i> ?sp., Amer. Mus. Nos. 5201, 5255, 5257, 5262, 5264			XXXXXX		
2. " <i>Ornithomimus</i> " (= <i>Struthiomimus</i> ) <i>tenuis</i> Marsh, type.	×				
3. " <i>Ornithomimus</i> " (= ? <i>Deinodon</i> ) <i>grandis</i> Marsh, type	×				
" <i>Ornithomimus</i> " (= <i>Struthiomimus</i> ) <i>altus</i> Lambe, type		×			
4. <i>Struthiomimus altus</i> , genotype, Amer. Mus. Nos. 5339, 5355		XX			

The American Museum expeditions have secured abundant remains of the *Ornithomimidæ* in three zones, viz.: Belly River (= Fort Pierre), Edmonton (= intermediate), Hell Creek (= Lance).

4. *Struthiomimus altus*. The type of *Struthiomimus* (*Ornithomimus*) *altus* Lambe is from the Belly River series, Red Deer River, Alberta, Canada, now regarded as of approximately the same age as the Judith River. It consists of a "complete right hind limb (including the foot), the phalanges

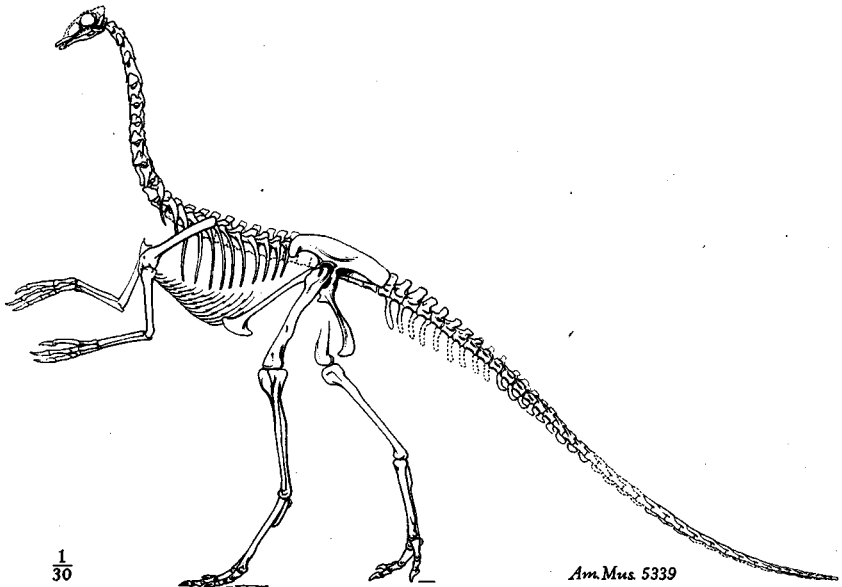


Fig. 4. First restoration of the skeleton of *Struthiomimus altus*, Amer. Mus. 5339. Digit I is set too close to digits II, III. One-thirtieth natural size.

of the left foot in place, a pubic bone, and an ischium, of one individual" (p. 50).<sup>1</sup> Catalogue number 930f Ottawa Museum. "The right hind limb with the phalanges of the left foot, were found in 1901, below Berry Creek." (p. 53).

#### MATERIALS IN THE AMERICAN MUSEUM.

Year after year the trying search for *Ornithomimidæ* remains has been encouraged by the author.

The American Museum expeditions under the leadership of Barnum Brown, aided by Peter Kaisen, have resulted in securing fourteen specimens of *Ornithomimidæ* from the *Triceratops* zone of Hell Creek, Mon-

<sup>1</sup> Osborn, H. F., and Lambe, Lawrence M. "On Vertebrata of the Mid-Cretaceous of the North West Territory." Geol. Surv. of Canada, Contributions to Canadian Palæontology, Vol. III, Pt. II, pp. 7-81, 24 text figs., 21 pls.

tana, the very close of the Cretaceous, five specimens from the intermediate Edmonton formation of Alberta, also a number of specimens from the ancient Belly River formation of Alberta, including especially the nearly complete skeleton, American Museum No. 5339, which forms the basis of the present description and affords the first complete knowledge and restoration of the animal. As bearing on the habits of these animals it is noteworthy that the geologic occurrence is invariably in shore deposits, with remains of molluscs, ripple marks, and plant life, indicating littoral conditions and affording ground for the association of these animals with shore feeding habits.

The specific reference of this skeleton of the Belly River series is probably to the species *Struthiomimus* (*Ornithomimus*) *altus* Lambe, the comparative measurements being as follows:

	Type of <i>Struthiomimus</i> ( <i>Ornithomimus</i> ) <i>altus</i> Lambe 930f Ottawa Museum	<i>Struthiomimus altus</i> . Complete skeleton Amer. Mus. 5339
Length of femur . . . . .	.430	.480
“ “ tibia (from 2 specimens) . . . . .	.560e	.540
Antero-posterior diameter of shaft of femur at mid-length . . . . .	.045	.044e
Transverse diameter of same tibia above distal end . . . . .	.041	.041
Length of Mts. IV . . . . .	.335	.370
“ “ “ V (non-functional) . . . . .	.100	.119
“ “ Digit II . . . . .	.164	.150
“ “ “ III . . . . .	.213	.210
“ “ “ IV . . . . .	.143	.150

It is noteworthy that only a single genus or species of dinosaur is known to pass from the Monoclonius-Ceratops zone into the Triceratops-Torosaurus zone; this is the genus *Trachodon*. The known carnivorous and herbivorous dinosaurs underwent profound modifications, and it is not probable, therefore, that the Ornithomimidæ remained generically unchanged. This specimen of the Ornithomimidæ comes from a much older geologic horizon than that of the genotype of *Ornithomimus*, which is from the Triceratops zone; it belongs to a distinct genus, or subgenus for which the name *Struthiomimus*, 'Ostrich mimic,' is proposed in reference to its mimicry of the ostrich (*Struthio*) in the skull, neck, and foot structure.

*Ornithomimus*, as a geologically more recent stage, is distinguished by the loss of Metatarsal V in the pes (Fig. 3a) for which no facet remains (Fig. 3a A<sup>2</sup>), and other characters. It was rightly defined by Marsh as possessing only three metatarsals. The geologically more ancient *Struthiomimus* retains a splint of metatarsal V.

**Struthiomimus** gen. nov.

*Generic characters of Struthiomimus.* Stage of evolution of the Ornithomimidæ, corresponding with the Judith River or Belly River formation, Monoclonius-Ceratops zone. Skull relatively small, edentulous; manus isotridactyl, with elongate and slightly recurved terminal phalanges, metacarpals I-II incipiently coalescent; pollex phalanges separate, divergent; pes anisotetradactyl, Mts. II, III, IV incipiently coalescent, Mts. V present, reduced; Digit III relatively elongated.

The generic characters are based upon the complete skeleton of *Struthiomimus altus*, Amer. Mus. 5339.

## DESCRIPTION OF SKELETON OF STRUTHIOMIMUS ALTUS.

Text-figs. 2, 3, 4, 5, 6, 7, 8, 9, Plates XXIV, XXVI.

*Proportions.* In comparing this skeleton with that of *Ornitholestes* (Plate XXVI) we are immediately impressed with the extremely small size of the skull, elongation of the neck, abbreviation of the back, relative elongation of the tibia and of the tarso-metatarsus. These are the struthious analogies.

	mm.
Vertebral column, total length of . . . . .	4.085
Pre-acetabular vertebræ, total length of . . . . .	1.56
Post-acetabular vertebræ, " " " . . . . .	2.525
Caudals, total length of . . . . .	2.31

Non-struthious is the balancing power of the tail. The vertebræ behind the acetabulum exceed those in front of it by nearly a meter, and the posterior half of the tail is very stiff and rod-like and was thus doubtless used as a balancing organ in rapid cursorial motion.

As compared with *Ornitholestes* the fore limb is of the same relative length, but the manus is a very strong and fully functional organ.

*Table of Measurements of Struthiomimus altus*, Amer. Mus. 5339.

	mm.
Skull, length of, tip of premaxillary to back of quadrate . . . . .	.240
" lower length, tip of dentary to back of articular . . . . .	.215e
Cervical vertebræ, series of 10 inclusive . . . . .	.770
Thoracic " " " 13 " . . . . .	.760e
Sacral " " " 5e " . . . . .	.230e
Caudal " " " 39 " . . . . .	2.31e

	mm.
Fore limb, total length.....	.850
Scapulo-coracoid, total length.....	.445
Scapula " ".....	.335
Humerus " ".....	.310
Ulna-radius " ".....	.230
Manus, including phalanges, approximate length.....	.315e
Digit I: Mtc. I ".....	.085
Pollex I.1 ".....	.110
Pollex I.2 ".....	.065
Digit II: Mtc. II ".....	.100
Phalanx II.1 ".....	.040
" II.2 ".....	.090
" II.3 ".....	.085
Digit III: Mtc. III ".....	.095
Phalanx III.1 ".....	.025
" III.2 ".....	.035
" III.3 ".....	.075
" III.4 ".....	.080
Pelvic girdle: ilium, length of.....	.450
pubis " ".....	.475
ischium " ".....	.335
Hind limb, total length including femur to tips of phalanges.....	1.530
femur, length of, extreme measurement.....	.480
tibia, " ".....	.540
Mts. III, " ".....	.370

*Proportional Measurements, Indices, and Ratios.*

Fore limb, brachium, total length humerus to tip of phalanges.....	.850
Hind limb, crus; " " " " " " " ".....	1.530
Brachio-crural ratio (proportion of fore to hind limb).....	55%
Femoro-tibial ratio (proportion of femur to tibia).....	88%

*Skull.* The unique feature of the skull is the total absence of teeth and indications that the premaxillaries and dentaries were sheathed in narrow horny beaks somewhat similar to those of *Struthio*. The skull as a whole (Fig. 5A, B) is only one-third longer than that of *Struthio* although it is attached to a vertebral column over thirteen feet in length. The dentary is relatively deeper and more powerful than that of *Struthio* and apparently closes on the inner side of the premaxillaries. All the areas of muscular attachment are very slight as compared with those of the carnivorous dinosaurs. The muscles of the jaws are relatively feeble as compared with those of the carnivorous dinosaurs but more powerful than in *Struthio*.

The relations of the dentary, surangular, angular, articular, lachrymal,

jugal, quadrate are totally different from those of *Struthio* and indicate direct derivation from the theropod dinosaur type. The chief distinctions from the cranium of *Allosaurus* and *Tyrannosaurus* (Osborn, 1912, p. 28, figs. 25, 26<sup>1</sup>) are: (1) the great size of the orbit, which is relatively as large as in *Struthio*; (2) the constriction of the post-temporal fossa; (3) the vertical elongation of the quadrate-quadrate-jugal; and (4) the anterior inclina-

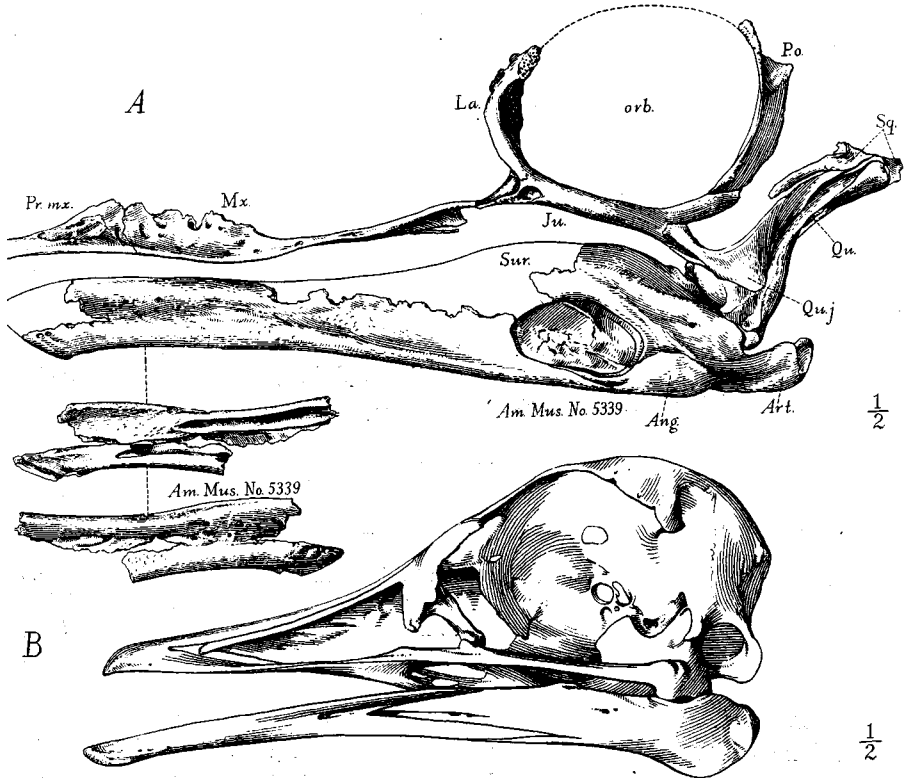


Fig. 5. Skulls of *Struthiomimus* and *Struthio* compared. A Portions of the skull and jaws of *Struthiomimus allus*, Amer. Mus. 5339, showing the left dentary, also the outer and inner aspect of the right dentary. B Skull of *Struthio*. Both figures one-half natural size.

tion of the lower end of the quadrate as distinguished from the backward inclination of the same element in *Allosaurus*. The cranium thus presents a very wide contrast to that of *Allosaurus* and the widest possible contrast to that of *Tyrannosaurus*, indicating a profound change of function.

<sup>1</sup> "Crania of *Tyrannosaurus* and *Allosaurus*." Mem. Amer. Mus. Nat. Hist., N. S., Vol. I, Pt. i, June, 1912, pp. 1-30, pls. i-iv, figs. 1-27.

*Cervicals.* The cervical centra are uniformly elongate and the cervical ribs, instead of being loosely attached as in *Ornitholestes* and in the typical Theropoda, are abbreviated and closely coalesced to the sides of the centrum and neural arch in C3-10. Cervicals 6-11 are amphicoelous. C12 is procoelous. C4 is slightly procoelous. C3 is opisthocelous. This is an indication of a long, flexible, and powerful neck, as in *Struthio*.

*Thoracics.* The thoracic or dorsal vertebræ, T1-13, are distinguished by elongate bicipital ribs, the anterior pair of which (T1-T2) are freely movable, while in T3-T10 the thoracic ribs are connected below with the sternal rib elements. In T12 and T13 the ribs are not observable in this specimen, but were probably attached to the inner side of the anterior crest of the ilium. The centra of T1-3 are preserved and seem to be gently

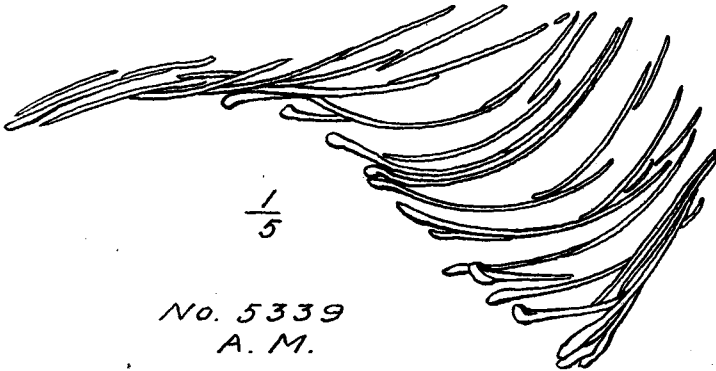


Fig. 6. Detail of the actual arrangement of the abdominal ribs in *Struthiomimus altus*, Amer. Mus. 5339, as preserved on the left side of the thorax. One-fifth natural size.

opisthocelous; from T4-13 the centra are not observable; the neural spines indicate progressive increase in size and abbreviation in length.

*Sacrals.* The sacral centra cannot be clearly distinguished; the indications are that there were five sacrals closely coalesced. S3-?5 are visible behind the acetabulum (compare *Tyrannosaurus*, Plate XXVII). The supposed S5 is coalesced laterally with the postero-internal plate of the ilium. Superiorly the sacral spines unite in a continuous single, closely compressed plate, wedged in between the iliac borders (compare *Tyrannosaurus*, Fig. 17).

*Caudals.* Seventeen caudals are preserved in continuous series in this specimen, Amer. Mus. 5339, the typical theropod characters of which are clearly shown in Plate XXVI. Then follows an unknown interval in which five vertebræ have been inserted, behind which fifteen vertebræ are added from the specimens American Mus. Nos. 5355, 5262. These vertebræ,

C 12-C 26, C 30, exhibit the remarkable rod-like elongation of the prezygapophyses, so that the apex overlaps the base of the prezygapophysis in front. The postzygapophyses are greatly reduced. The chevrons are elongate and rod-like also.

*Sternal ribs.* These elements consist of at least thirteen rows (corresponding with the thirteen thoracic ribs) each including a triple series on each side as represented in Fig. 6 and Plate XXVI, namely: (1) a short, very slender *proximal* series; (2) a slender *median* series about twice the length of the proximal; (3) a stouter *ventral* series, of about three times the length of the proximal, which terminate in club-shaped expansions in the median

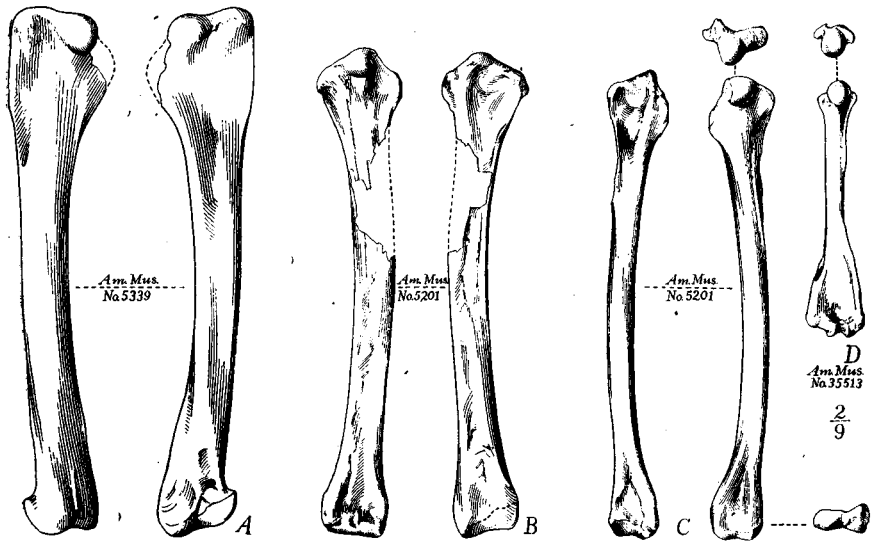


Fig. 7. Humerus of *Struthiomimus altus* and of *Cholepus didactylus* compared.

A Crushed left humerus of *S. altus*, Amer. Mus. 5339. B Normal left humerus of *S. altus*, Amer. Mus. 5201. C Right humerus, anterior and posterior views of *S. altus*, Amer. Mus. 5201. D Right humerus of two-toed sloth, *Cholepus didactylus*, Amer. Mus. 35513, posterior view. All figures two-ninths natural size.

line. The sternal rib apparatus as a whole is exceedingly delicate and indicates a feeble development of the pectoral muscles.

*Fore limb.* Figs. 3 A, 8. The scapula is slender and firmly coalesced with the coracoid. The humerus (Fig. 7) is relatively slender as observed in two specimens (Amer. Mus. Nos. 5339, 5201). The small, backwardly directed head (Fig. 7 C) is supported by the lesser and greater tuberosities, which are somewhat more strongly developed than in the arboreal two-toed sloth, *Cholepus didactylus* (Fig. 7 D). The shaft is relatively longer and



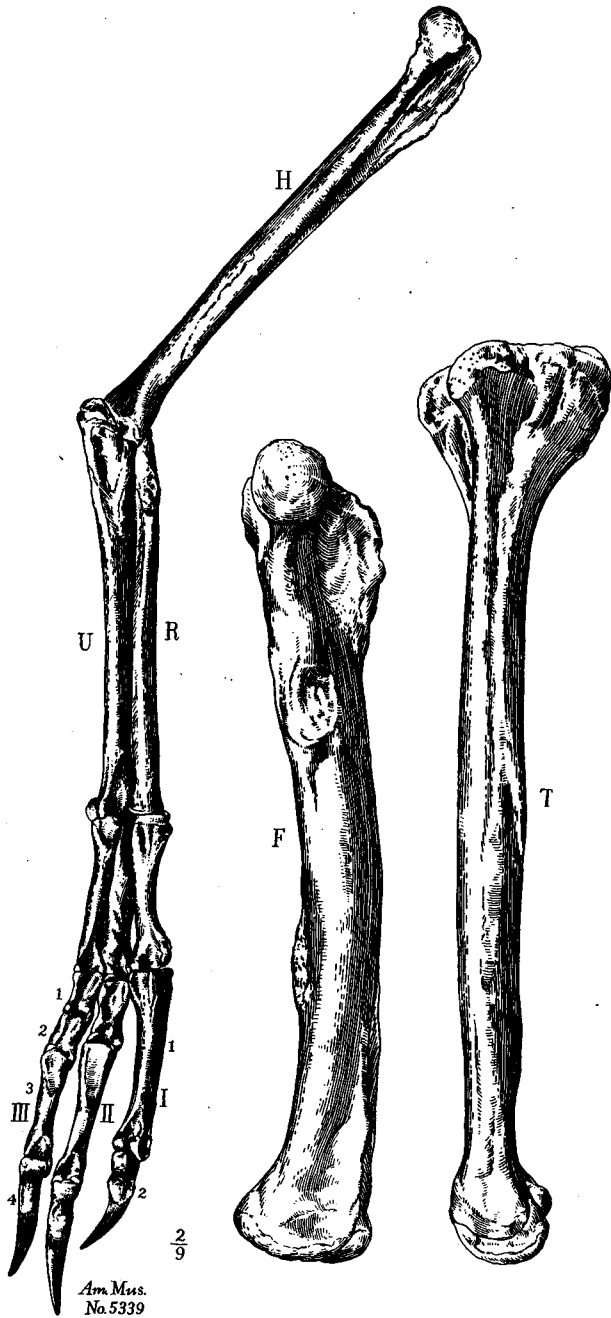


Fig. 8. Fore and Hind limb bones, H, U, R, of *Struthiomimus altus*, Amer. Mus. 5339, to same scale. Palmar aspect of left fore limb. F Left femur, internal aspect. T Left tibio-tarsus, internal aspect. All figures two-ninths natural size. Manus more correctly drawn in Fig. 3.

more slender than in *Cholæpus* and the distal extremity is relatively narrower and has less provision for muscular attachment than in *Cholæpus*. The absence of muscular attachments on the pronator and supinator condyles of the humerus as well as the generally slender structure of this bone forbid the assumption of fossorial function for this peculiar limb. The ulna and radius are attached somewhat obliquely to the perpendicular axis of the shaft. A small sesamoid or vestigial Mtc. IV appears at the junction of the ulna and Mtc. III. The carpal series is represented by five separate elements, Fig. 3 A; it includes the radiale, intermedium, ulnare, carpale 1 and carpale 2, much flattened. Mtc. I-III are short and equal in length, and Mtc. II-III are firmly fitted to each other; Mtc.

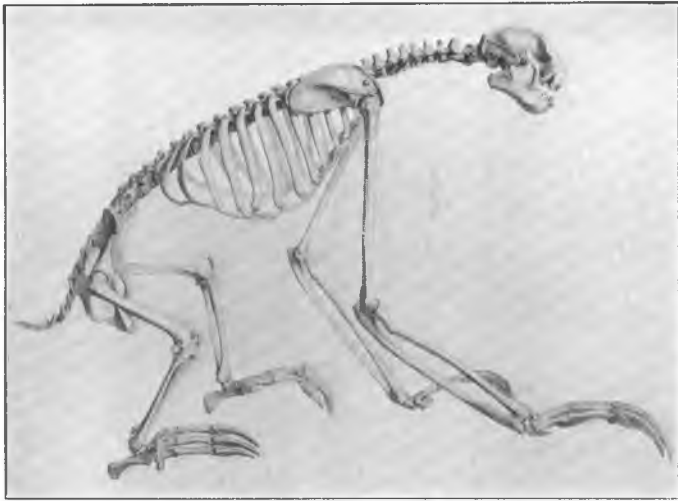


Fig. 9. Skeleton of the three-toed Sloth, *Bradypus tridactylus*. After De Blainville.

I and Mtc. II exhibit an incipient coalescence; they are synmetacarpal but not syndactyl.

The phalanges of Digit I, the pollex, are separate and divergent from those of Digits II, III which tend to be appressed and syndactylous; there are indications of more or less rotation and opposition or grasping power in the pollex.

*Manus*. The very unequal elongation of the *phalanges* is a peculiar feature of the manus; especially the first phalanges of Mtc. I, II, III are of totally different lengths. This is compensated for by the elongation of phalanx D II.2 which is unusually long. These three digits, therefore,

through the abbreviation of D III and the elongation of D I are approximately isotridactyl as in *Bradypus tridactylus* (Fig. 9). This arrangement is quite different from that of *Ornitholestes hermanni* (Fig. 3) in which D I is reduced but D II is very much more elongate than D III. The lateral motion of these phalanges is partly provided for in the joints between the metacarpals and the proximal phalanges. The remaining interphalangeal joints tend to confine the digits exclusively to an opening and closing movement as in many edentates or strict flexion and extension such as is also observed in *Ornitholestes* and in *Bradypus*. The distal phalanges are extremely long, slender, and slightly recurved, with strong attachments for the flexor perforans, less recurved, claw-like, or raptorial than those of *Ornitholestes* (Fig. 2). They are relatively longer and more slender than those of the greater or lesser anteaters and entirely lack the fossorial powers of the manus of these Myrmecophagidæ.

*Hind limb.* The hind limb (Fig. 8) is relatively robust, the femur (Fig. 8 F) having on a small scale the general form and areas of muscular attachment characteristic of the larger theropoda such as *Tyrannosaurus* (Fig. 18A<sup>1</sup>), with greater relative elongation. The tibio-tarsus (Fig. 10 T) is also a powerful bone, relatively more elongate than the femur. The fibula (Plate XXIV) is relatively slender.

The tarso-metatarsus, as previously described in *Ornithomimus* (Figs. 10, 11), consists of three closely coalesced median digits, D II-IV, in which Mts. III is thrust backward at the proximal end so that it only appears on the posterior face, while it is thrust forward at the distal end so that it makes up the greater part of the anterior face of the pes, in which D III is much the longest digit. Metatarsal V is greatly reduced, extending one-third down the shaft of Mts. IV.

The terminal phalanges are very slightly recurved, less elongate and pointed than in *Dinornis* among the struthious birds and slightly more pointed than in *Struthio*. This structure points to strictly cursorial rather than to raptorial function in the pes.

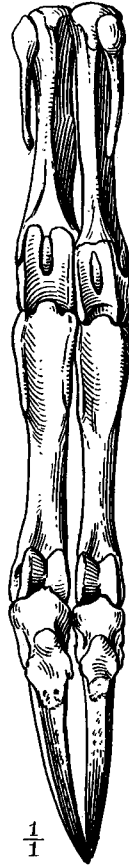


Fig. 10. Manus of two-toed Sloth, *Choloepus didactylus*. Palmar aspect. Natural size.

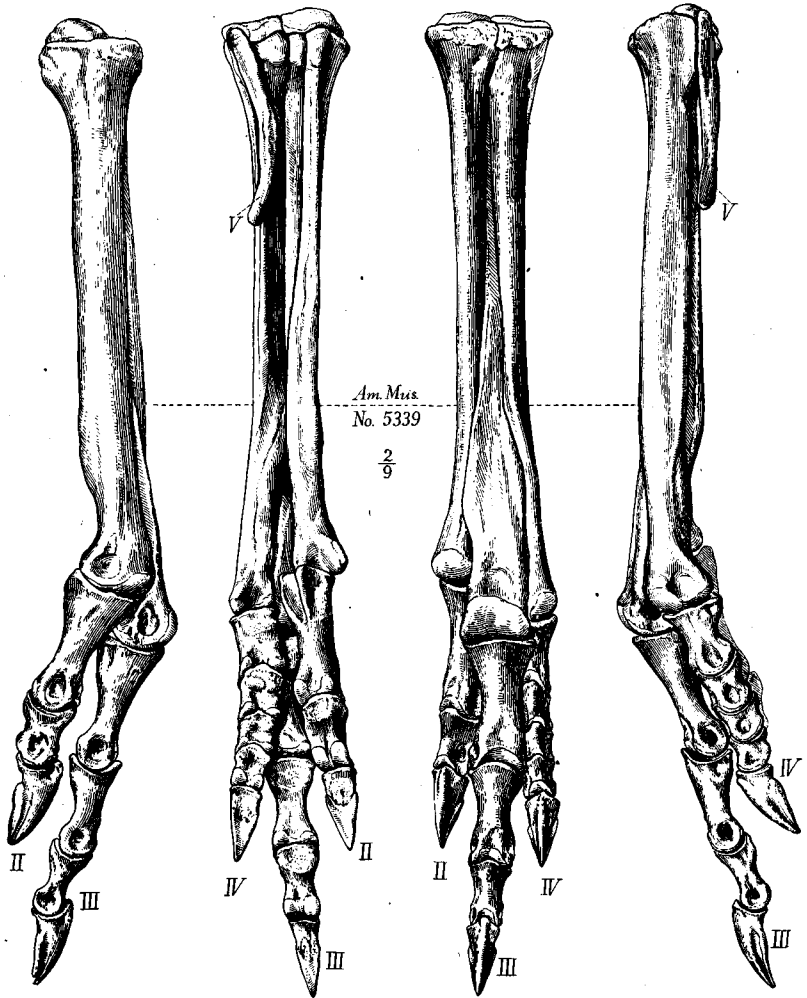


Fig. 11. Left pes of *Struthiomimus altus*, Amer. Mus. 5339. Internal, posterior, anterior, external aspects. Mts. II, III, IV, with three functional digits, Mts. V reduced. Two-ninths natural size. Compare Fig. 3a.

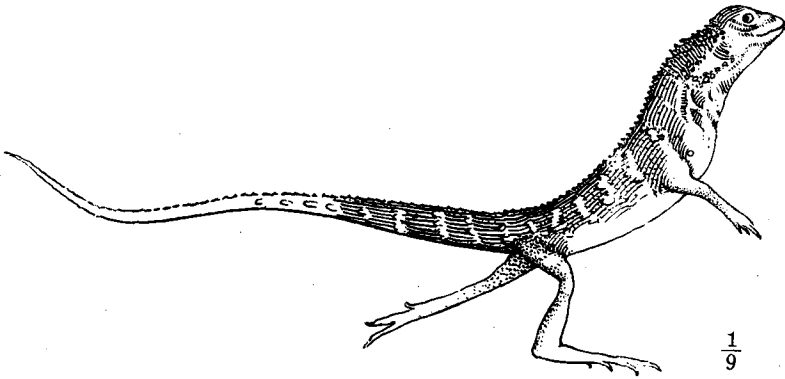


Fig. 12. Australian water lizard, "Lesueur's lizard" (*Physignathus lesueurii* Gray), Queensland variety, family Agamidæ, from instantaneous photograph of running pose.

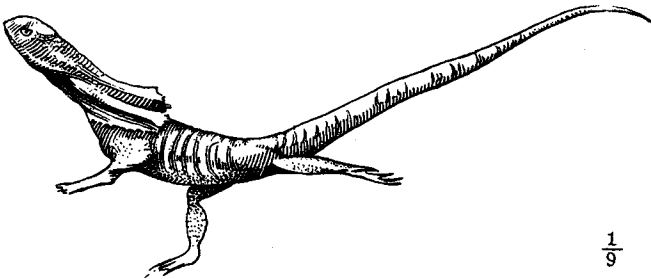


Fig. 13. Frilled lizard *Chlamydosaurus*, family Agamidæ. Instantaneous photograph of swift running pose. After Saville Kent.

### *Habits of Struthiomimus.*

In view of the ostrich-like structure of the skull and of the pes, and the partly suspensory, partly grasping structure of the fore limb and manus of *Struthiomimus*, it is very difficult to form a consistent hypothesis of the habits of this remarkable animal. It may be compared with certain of the lizards, the struthious birds, the tree sloths (*Bradypus*, *Choloepus*), and the Aye-Aye (*Cheiromys*).

*Comparison with lizards.*<sup>1</sup> The habit of lizards of running upon the hind

<sup>1</sup> Notes given to the author by Mr. Raymond L. Ditmars, Curator of Reptiles, N. Y. Zoölogical Park.

legs (Figs. 10, 11) with the body reared upward has been observed among representatives of three families, namely, the Old World Agamidæ (Agamas), the New World Iguanidæ (Iguanas) and Teiidæ (Tegus, Race Runners). (1) The two first named families have a distinct affinity, arising either from parallelism of development among varied genera or from actual relationship as alleged by some writers. The systematic separation of the Agamidæ and the Iguanidæ is mainly by the dentition, which is acrodont in the former and pleurodont in the latter. The family Teiidæ is of remote relationship to both of the first named families. (2) Among the species of lizards observed at times to rear and use the hind legs only for locomotion are highly active types, large and small, that live under various conditions. The habit has been observed among large arboreal species as well as among lizards of diminutive size, several of the latter frequenting the deserts. (3) The lizard never rears, in fact, appears unable to do so, unless moving at a high rate of speed. The bipedal trait may be indicated immediately after the beginning of a dash over the ground, or the lizard may rear upward after it has run a considerable distance. In all cases the animal drops to all fours as its speed materially decreases. During the reared running pose the front legs appear to involuntarily droop forward and not to be used as balancers, but the position of the tail indicates the marked importance of this organ in balancing and a voluntary rearing or curving upward of the tail in order to keep the body upright. Mr. Ditmars has not observed the habit except in long-tailed species. (4) Lizards resorting to anthills are mostly burrowing and more or less limbless forms which present no analogy with *Struthiomimus*. (5) The grasping powers of the manus are developed in the tree-living chameleon, the fingers terminating in strong claws, two on each grasping knob, which should be compared with those of *Struthiomimus*.

*Running gait of Struthiomimus and Ornithomimus.* From these studies of the lizards the running gait of *Struthiomimus* is suggested in the pose represented in Fig. 14A in which the rod-like tail balances the anterior half of the body. The estimated total length of the vertebral column being M 4.085, the length of the tail is estimated at M 2.525; thus the post-acetabular vertebræ are slightly longer than the pre-acetabular. The hind limbs are relatively longer than in any of the running lizards but relatively shorter than in the ostriches. It is noteworthy as compared with the running lizards that the ratio between the length of the fore and hind limbs is less in *Struthiomimus*. Its very awkward position in the supposed quadrupedal gait is shown in Fig. 14B.

*Insectivorous theory of C. William Beebe.* The ornithologist, C. William Beebe, has suggested that the feeble fore limbs of *Struthiomimus* may have

been adequate for attacking sandy and gravelly anthills, as represented in Fig. 14B. There are three objections to this theory: first, the fore limb gives no evidence of any fossorial musculature; second, the beak affords no evidence of a protrusible tongue analogous to that of the Myrmecophagidæ; third, the terminal phalanges of the hind limb afford little evidence of power to scratch or dig but are rather of the cursorial type.

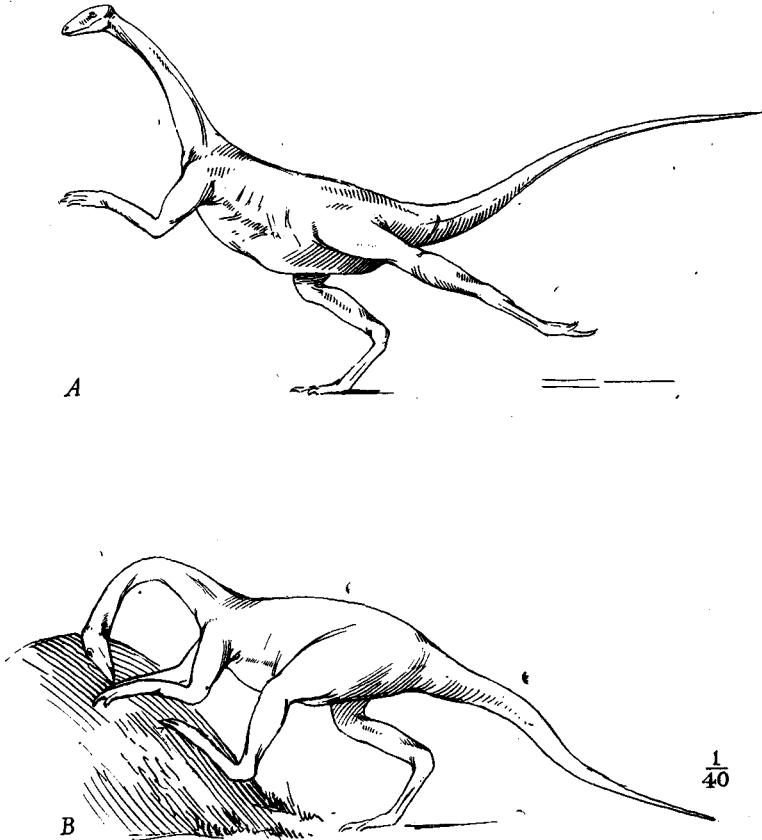


Fig. 14. Restorations of *Struthiomimus altus*, Amer. Mus. 5339. A Running pose suggested by Osborn. B Insectivorous theory, anthill-attacking pose suggested by C. William Beebe. One-fortieth natural size.

*Sea-shore theory of Barnum Brown.* Influenced by the fact noted above that the remains of *Struthiomimus* and *Ornithomimus* are invariably found in littoral deposits, Barnum Brown has suggested the theory that this animal waded along the shores, feeding upon small crustaceans and

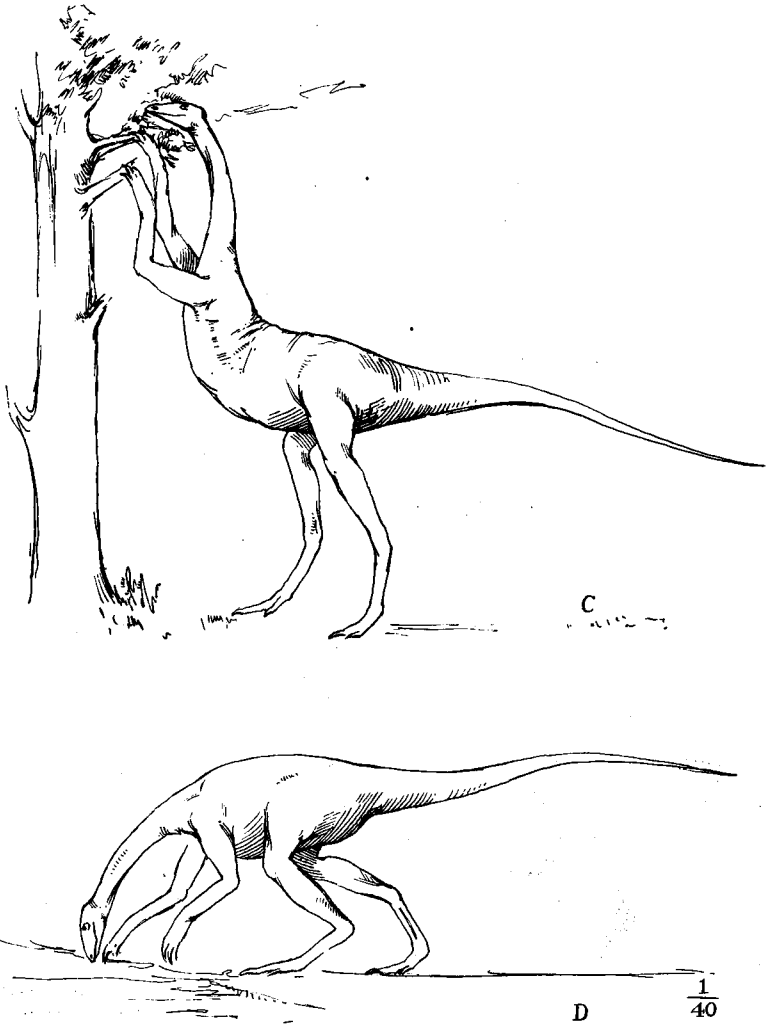


Fig. 15. Restorations of *Struthiomimus altus*. C Herbivorous, tree-browsing pose, suggested by Osborn. D Carnivorous, shore-living pose, hunting for Crustacea and small Mollusca, suggested by Barnum Brown. One-fortieth natural size.



molluscs, using its long anterior claws partly to scrape the sand and partly to seize these shore-living animals. The objections to this theory are three. First, neither the beak nor the terminal phalanges are adapted to seizing an actively moving crustacean prey of any kind although they may have been adapted to securing sessile Mollusca. Second, the feeble musculature of the forearm is non-fossorial, and non-raptorial; that is, it does not indicate powers of pronation and supination of the manus. Third, as pointed out by Beebe, neither the structure of the beak nor of the phalanges of the pes is analogous to that of the shore-living birds (grallatores) which partly live upon small invertebrates. Brown points out that while the attachments of the muscles are but slightly developed and the arm is of feeble power as a whole, the manus shows wonderful adaptability of finger movement, since while Mtc. II and Mtc. III are coalesced D I has an articulating face with Mtc. I which allows of a rotating movement and the opposition of D I to D II, III. The points noted are to Brown conclusive proof that this dinosaur in securing food depended chiefly on the movements of its neck and the prehensile power of the digits of the manus and that crustaceans were the favorite article of food, which the construction of the neck and manus were well adapted to capture.

*Ostrich-like theory of Struthiomimus, Osborn.* This theory, which seems the most probable one to the author, is depicted in Fig. 15C, namely, an herbivorous browsing pose in which the ostrich-like beak, sheathed in horn, is represented as securing leaves and buds while the fore limbs, two digits of which are analogous to those of *Bradypus tridactylus*, are used in supporting the fore part of the body and drawing down the smaller branches; the grasping power of the thumb, D I, may have facilitated this action.

First, in defence of this theory, a chiefly suspensory and limb-grasping function of the fore limb is indicated by its analogy to that of the tree sloth, *Bradypus tridactylus* (Fig. 9), the analogy consisting in the slenderness of the humerus and of the ulno-radius, the apparent slenderness and suspensory character of the muscles and especially the *isodactyly* of the manus, a highly distinctive feature of the tree sloths. Second, the bird-like and especially ostrich-like structure of the neck, which is totally unlike that of the carnivorous dinosaurs and very similar to that of the struthious birds especially, in which very rapid fore-and-aft motions of the head are observed during the act of browsing. Third, the bony structure of the upper and lower jaws indicates the possession of a horny beak similar in shape to that of the browsing birds especially of the struthious type. There is no curvature of the beak suggesting analogy to the carnivorous birds, nor broadening of the beak suggestive of that of the wading birds (grallatores). Fourth, it appears probable that the pes was purely curso-

rial, adapted to dry or hard earth, since its analogy to that of the various members of the ratite order, such as *Struthio*, *Rhea*, *Casuaricus*, *Dinornis*, is very close. Such feet are used primarily in locomotion, secondarily for the scratching of sand for the burying of eggs, and thirdly as weapons of defense; they are not adapted for assisting the fore limb and the beak in the prehension of food.

*Notes on the Habits of Struthiomimus by Dr. William K. Gregory.* (1) "Were the forearms used in pulling food toward the mouth, either up from the ground or down from the trees? Probably yes. (2) Were the forearms used in climbing up low trees? Probably no. (3) Were the forearms provided with a small patagium, which could be used in swift flight on the ground? [Hypothetical.]"

"The long slender forearm of *Struthiomimus* had a long reach and great freedom of motion at the shoulder, as shown by the form of the head of the humerus. The elbows were undoubtedly everted, in reptilian fashion. While the radius could not be twisted around the ulna so that true supination was very limited, yet merely by moving the elbow in toward the body the palms of the opposite manus were turned toward each other (partly supinated), while by moving the elbows outward from the body the manus was brought into the position of pronation and the opposite manus brought together. The wrist joint was very stiff, capable of very little extension; the three metacarpals were closely appressed; there was considerable motion between the metacarpus and the proximal phalanges. In the third digit the second and third metacarpals were closely appressed and in the way of coalescence, but the distal phalanges of the second and third digits could be sharply flexed. By virtue of the twisting of the first metacarpal the phalanges of the first digit could be turned partly toward the other digits so that the manus was to a certain extent prehensile. The ungual phalanges were large and falcate, deeply grooved at the sides and evidently bore stout and sharp claws, larger than those of a grizzly bear. The deep pits at the sides of the distal ends of the penultimate phalanges testify to the great strength of the ligaments connecting the distal and penultimate phalanges, while the large size of the claw phalanges and their swollen proximo-inferior bases indicate a powerful development of the flexor profundus (perforans). The manus as a whole, as observed by Professor Osborn, partly suggests that of the tree sloths, not only in its general form, but in the tendency toward coalescence of two of the successive phalanges, and in the large size of the claws. It differs from the sloth type, however, in the lateral mobility of the first digit and of the proximal phalanges of all the digits."

"The reconstruction of *Struthiomimus* errs in representing the forearm

in the position in which it is mounted, namely with the elbow drawn well in toward the body and with the dorsum of the manus turned fully outward. That this position is erroneous is apparent from the fact that the head of the humerus is thereby wrenched out of the glenoid and appears exposed in the lateral view. By placing the head of the humerus fully within the glenoid, everting the elbows and opening the radio-humeral angle, the manus will be partly pronated."

"We speak of the fore limb of *Struthiomimus* as 'slender', but it is so only because the longitudinal dimensions of the principal elements greatly exceed their transverse dimensions. The fore limb is, however, by no means weak. It is at least as strong as the fore limb of a man and was armed with very large sharp claws."

"With the elbows everted in reptilian fashion and the body swung downward from the acetabulum, the powerful manus could be brought near to the ground, although I think there was not sufficient mobility for the fingers to be extended so that the palm could rest upon the ground. But I believe that the animal could stoop down and with its powerful claws tear up shrubs from the ground and perhaps scrape away the surrounding earth by the sweeping movements of the whole forearm after the fashion of a kangaroo. These heavy claws might also have been useful in tearing off the husks of fruits or for tearing and pulling down the branches and fruits of palms, cycads, figs, bananas, etc. Perhaps the claws served also as weapons of defense, if they were swiftly drawn across the flanks of an opponent. The pulling up of vegetation from the ground and the tearing of husks would be assisted by the broad, ostrich-like beak and the powerful neck, which was capable of strong vertical movements."

"Some features of the fore-limbs might indicate that *Struthiomimus* was a climbing animal, but the large size of the body and the nonprehensile character of the pes are against this view."

"The jaws of *Struthiomimus* unquestionably suggest those of an ostrich, and the animal seems too large to thrive exclusively upon an insectivorous diet. *Struthiomimus* was not necessarily exclusively a vegetarian. The ostrich itself is said to be omnivorous in the wild state, feeding on lizards, small mammals, fruits, berries, seed grass, etc., and the slightly more powerful beak of *Struthiomimus* might have been equally adapted for a varied diet, including some animal food."

"The fact that the remains of *Struthiomimus* were found in littoral deposits does not in my judgment indicate that the animal lived after the fashion of wading and shore-living birds."

"In conclusion we can be sure only that *Struthiomimus* was a swift running biped; that in seeking its food it made well-coördinated use of its

ostrich-like bill, powerful neck, and strong, heavily clawed manus; that a good deal of pulling and clawing was accomplished by these wide-reaching fore limbs."

"The animal seems to be too big for arboreal life, and its hind limbs were built rather for great speed on the ground, purely as a protective function. It seems possible that the fore limbs bore a narrow patagium, which might be of use in rapid flight along the ground as indicated in the accompanying restoration (Fig. 16). By throwing the head and forearms well forward the thrust of the femora would be turned more forward than upward, while at the same time the forearms if provided with patagia would serve to keep the fore part of the body from pitching downward."<sup>1</sup>

*Author's conclusion.* The above observations by the several expert anatomists who have coöperated with the author in attempting to solve

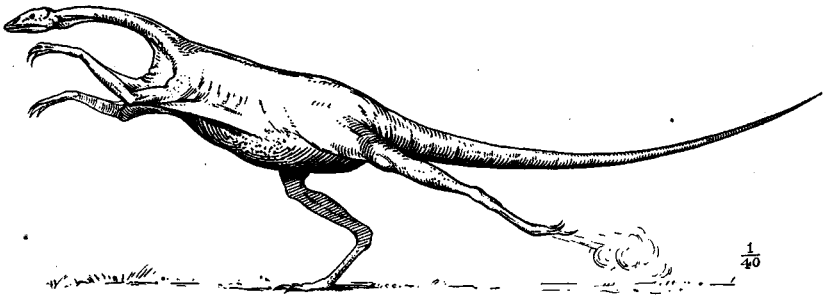


Fig. 16. Running pose of *Struthiomimus*, with a rudimentary patagium as suggested by W. K. Gregory. One-fortieth natural size.

the very difficult problem of the habits of *Struthiomimus* indicate a very great diversity of opinion and interpretation. The author adheres to the opinion, very gradually formed, that *Struthiomimus* presents prevailing analogies of structure in the head, neck, and feet, and consequently of habit, to the ostriches. Its fore limb structure, entirely unique among reptiles, is analogous partly to the suspensory type of fore limb such as we observe in the tree sloths, with the exception of the phalanges of the pollex, Digit I, which are set apart from the other digits and exhibit a grasping or opposable function.

Comparison of the *Struthiomimus* manus with that of the fossorial anteaters (*Myrmecophagidæ*) shows that the structure is totally different, for anteaters and, in fact, many other fossorial animals are *anisodactylous*, that is, the different digits vary greatly in length, in size, and in the develop-

<sup>1</sup> Notes by Wm. K. Gregory, 1916.

ment of the claws, whereas in *Struthiomimus* we have the *isodactyly* peculiarly suited to the suspensory, limb-grasping power of arboreal types. This does not preclude fruit- and shrub-grasping powers, but appears to exclude the grasping of living or actively moving prey.

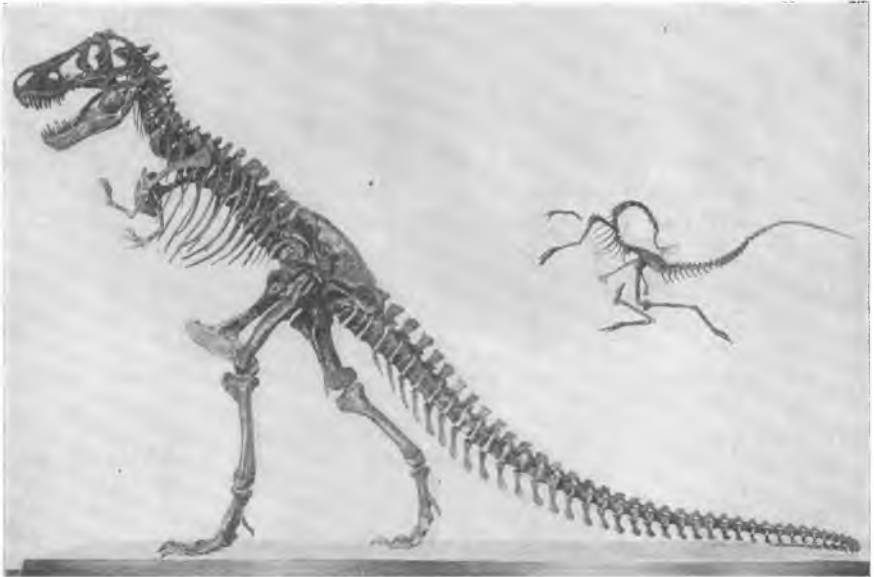


Fig. 17. *Tyrannosaurus* and *Struthiomimus* mounted skeletons, reproduced to same scale, about one-seventy-fifth natural size, and showing relative size and proportions of the fore and hind limbs.

### THIRD STUDY OF TYRANNOSAURUS.

#### INDETERMINATE TYPE OF *Manospondylus gigas* COPE 1892.<sup>1</sup>

The genotype (Amer. Mus. Cope Coll. 3982) of *Manospondylus* originally consisted of two dorsal vertebræ, which Cope recorded verbally to Hatcher<sup>2</sup> as from South Dakota. Of these original two dorsal vertebræ one was figured by Hatcher (*op. cit.* p. 114, fig. 105) and correctly referred to the Theropoda. Unfortunately the remaining vertebra has been misplaced

<sup>1</sup> Cope, E. D. "Fourth Note on the Dinosauria of the Laramie." *Amer. Naturalist*, Vol. XXVI, Sept. 1892, pp. 756-758 (p. 757).

<sup>2</sup> Hatcher, John B. (with O. C. Marsh and R. S. Lull) "The Ceratopsia." *Monogr. U. S. Geol. Surv.*, Vol. XLIX, 1907.

in or lost from the American Museum collections. It most nearly resembles in size and other characters the posterior cervical or first dorsal of *Tyranno-*

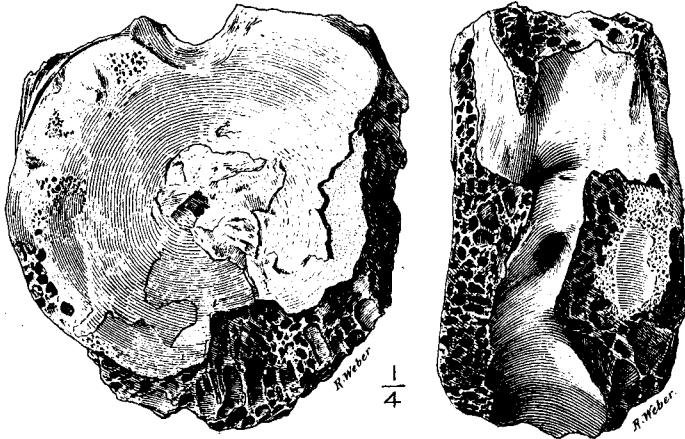


Fig. 17a. Vertebral centrum of *Manospondylus gigas* Cope, type, Amer. Mus. Cope Coll. 3982. One-fourth natural size. After Hatcher, 1907.

*saurus rex* (Amer. Mus. 5866). The comparison with the measurements given by Cope is as follows:

	DIAMETERS OF CENTRUM	
	Type 3982 <i>Manospondylus gigas</i> Cope ? Cervical	Amer. Mus. 5866. <i>Tyrannosaurus rex</i> 10th Cervical
Articular face, vertical.....	205.....	175
Articular face, transverse.....	200.....	167
Antero posterior.....	.090.....	110

This type is so incomplete and so imperfectly preserved that the genus and species which were founded upon it are regarded as indeterminate.

#### SKELETON OF TYRANNOSAURUS REX OSBORN.

Text-figs. 17-21, Plates XXV, XXVII.

*Tyrannosaurus* is the most superb carnivorous mechanism among the terrestrial Vertebrata, in which raptorial destructive power and speed are combined; it represents the climax in the evolution of a series which began with the relatively small and slender Triassic carnivore *Anchisaurus*.

*Materials.* The fortunate discovery of two skeletons of exactly the same size (Amer. Mus. Nos. 973, 5027), secured by the American Museum of Natural History expeditions to Hell Creek, Montana, in the years 1902

and 1908 respectively, affords complete knowledge of all parts of the skeleton except the sternal ribs, the fore arm, and the manus. The mounted animal here represented (Fig. 15, Plate XXV) is chiefly composed of the specimen found in 1908, Amer. Mus. 5027, with the missing complementary parts, especially the humerus and the femur, cast from the genotype specimen Amer. Mus. 973, discovered in 1902.

*Mounting.*<sup>1</sup> The anterior, lateral, and posterior aspects of this remarkable mount are shown in Plate XXV, reproduced from the superb photographs taken by Mr. A. E. Anderson in 1915 which were subsequently perfected by his skilful retouching of the negatives whereby all trace of the powerful steel frame work which supports the mounted skeleton has been removed. The absolutely perfect skull of this specimen (Amer. Mus. 5027), which has been described in great detail by Osborn (1912),<sup>2</sup> is not mounted with this specimen because of its great weight but is replaced by a *fac simile* cast. The pose of this animal has been the subject of prolonged study by the author<sup>3</sup> with the coöperation especially of Mr. Barnum Brown and Mr. Erwin Christman. It is proposed ultimately to mount the pair of skeletons in the offensive and defensive attitudes respectively.

*Resemblances to the Ornithomimida.* The resemblances which the skeleton of *Tyrannosaurus* presents to that of *Struthiomimus* and *Ornithomimus* are due to inheritance from a remote common ancestor of Lower Jurassic or even Triassic age. The many striking differences are due to the extremely wide divergence in the habits and adaptations of these animals, and are here represented in a form preliminary to more complete description in a memoir. The chief resemblances are the following:

1. A similar vertebral formula, namely: C 9-10, T 14-13, S 5.
2. Ornithic adaptation of the pelvic arch and sacrum, and a close analogy in adaptation to bipedal locomotion, cursorial and saltatory.
3. Functional tridactylism of the pes with strong reduction of DI, and lateral compression of Mts. III between Mts. II, IV.
4. Relatively feeble development of the fore limb.
5. Retention of a complete series of sternal ribs.

The obvious ancestral resemblances cease or are masked by the widely divergent adaptations of *Tyrannosaurus* to exclusive carnivorous habits and aggression, and of *Struthiomimus* and *Ornithomimus* probably to herbivorous habits and defencelessness, compensated for, doubtless, by alert powers of vision and rapid locomotion. The relative scale of development

<sup>1</sup> The work of mounting was performed, under the direction of the author and of Mr. Barnum Brown, by Mr. Charles Lang.

<sup>2</sup> Osborn, H. F. "Crania of *Tyrannosaurus* and *Allosaurus*." Mem. Amer. Mus. of Nat. Hist., N. S., Vol. I, Pt. i, June, 1912, pp. 1-30, pls. i-iv, figs. 1-27.

<sup>3</sup> "*Tyrannosaurus*, Restoration and Model of the Skeleton." Bull. Amer. Mus. of Nat. Hist., Vol. XXXII, Art. iv., Apr. 11, 1913, pp. 91-92, pls. iv-vi.

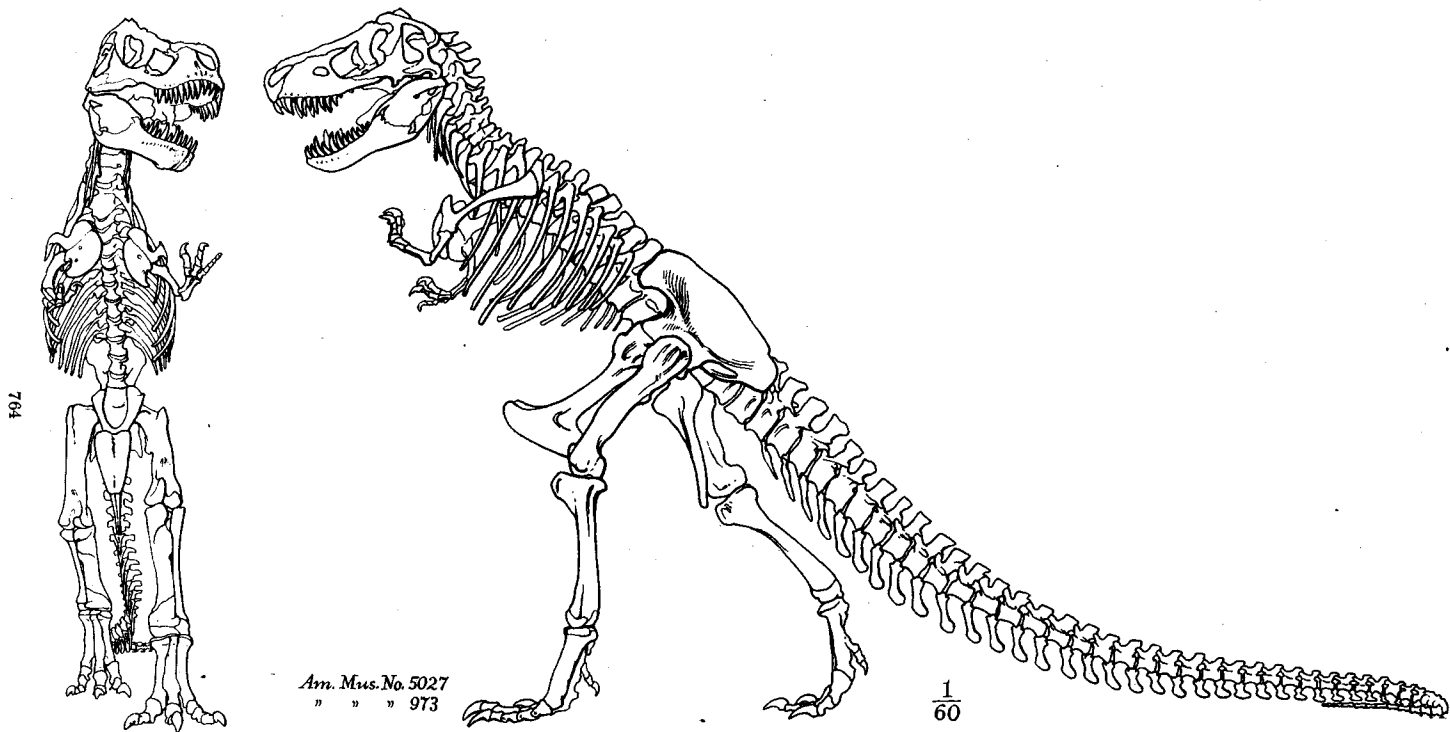


Fig. 18. Mounted skeleton of *Tyrannosaurus rex* Osborn, anterior and lateral views. One-sixtieth natural size. The structure of the manus is conjectural. The other parts are mounted by combination of the skeletons Amer. Mus. Nos. 5027, 973. The sternal ribs are omitted. The manus is represented as tridactyl, but it may be didactyl.



of the skull and the various parts of the skeleton in these two types of animals is well shown in the accompanying figures (Fig. 17), both one-seventieth natural size.

#### ADAPTIVE DIVERGENCES AND CONTRASTS.

##### *Tyrannosaurus.*

Extremely large-headed, megaloccephalic  
Dentition powerful, of extreme raptorial, carnivorous type  
Neck extremely abbreviated, cervical ribs elongated, loosely articulated  
Fore limb greatly abbreviated, small, prehensile manus with powerful recurved phalanges  
Hind limb very powerful with subprehensile phalanges, recurved claws

##### *Struthiomimus.*

Extremely small-headed, microcephalic  
Dentition atrophied, jaw sheathed in horn, probably of herbivorous type  
Neck extremely elongated, cervical ribs coalescent, with narrow centra, flexible.  
Fore limb moderately elongate, extremely slender, isotridactyl, phalanges greatly elongated, straightened, non-prehensile of living prey  
Distal segments and metatarsals greatly elongated. Non-prehensile.

#### CHIEF CHARACTERS OF THE TYRANNOSAURUS SKELETON.

In a previous description of the *Tyrannosaurus* skeleton (1906)<sup>1</sup> a preliminary description was given of the parts preserved in the genotype (Amer. Mus. 973). The present description is based upon the parts preserved in both the specimens (Amer. Mus. Nos. 973, 5027):

*Pre-sacral vertebræ* (Plate XXVII). There is little doubt that the total number of pre-sacral vertebræ is twenty-three, but the line of division between the cervicals and the thoracics is not positively demarkated. The formula is either:

Cervicals 9, Thoracics 14 = 23, or Cervicals 10, Thoracics 13 = 23. On the whole, close examination of C 10 appears to indicate that this should be regarded as the posterior cervical, since the capitulum of the rib is depressed as in C 9-5, whereas in the first thoracic, D 1, the capitular and tubercular articulations of the rib are widely separated as in the thoracics D 2-D 9.

*Cervicals.* The cervical series, C 1-10, is extremely abbreviated by the fore-and-aft compression of the vertebræ. C 1 (atlas) is extremely short, C 2 (axis) has a somewhat more elongate centrum, with a bifid spine,

<sup>1</sup> Osborn, H. F. "Tyrannosaurus, Upper Cretaceous Dinosaur." Bull. Amer. Mus. of Nat. Hist., Vol. XXII, Art. xvi, July 30, 1906, pp. 281-296.

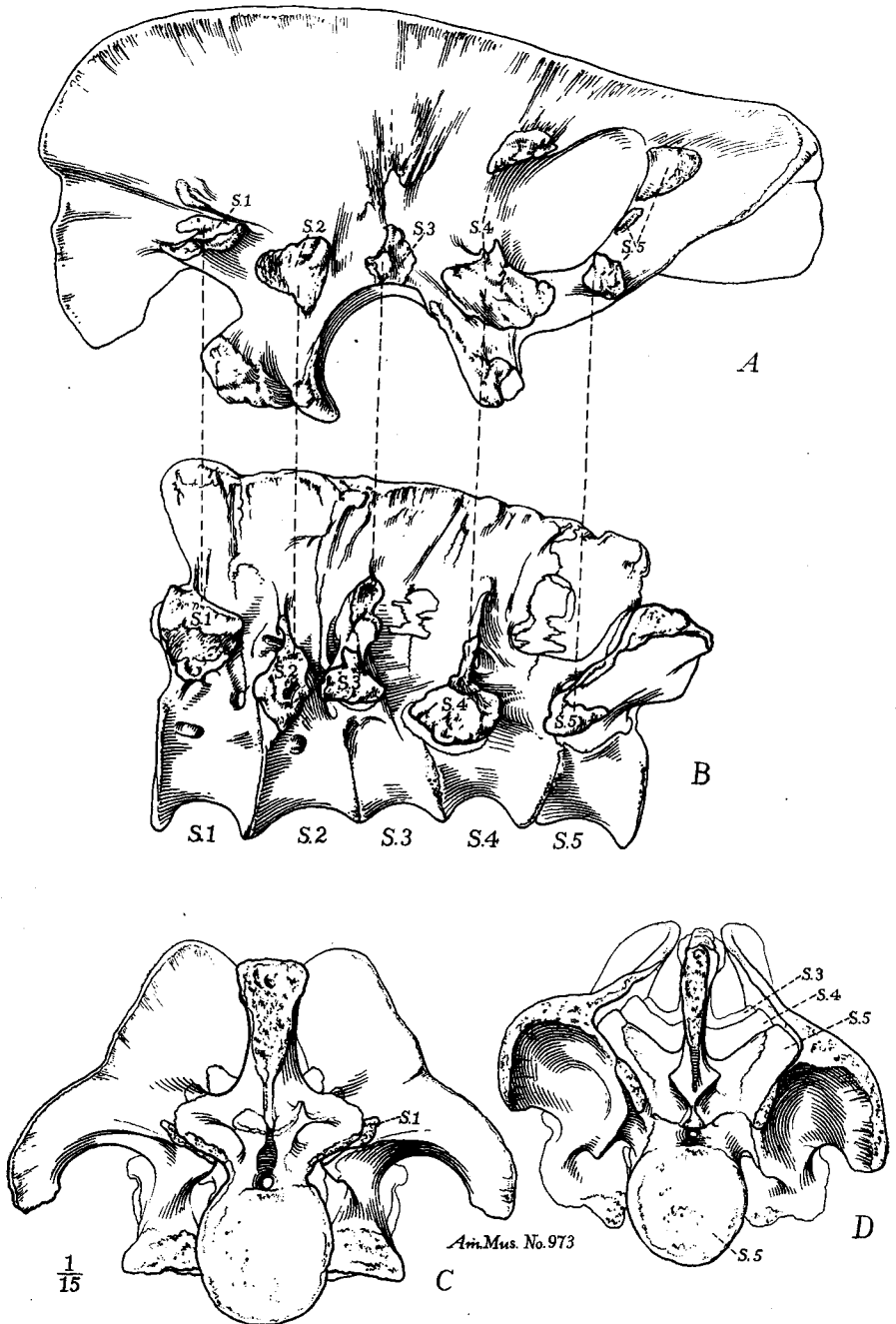


Fig. 19. Sacro-pelvic arcade of *Tyrannosaurus rex* of the genotype specimen Amer. Mus. 973, discovered in Hell Creek, Montana, in 1904. A, Sacral aspect of the right ilium showing the respective attachments of the five sacra S 1-5. B, Left lateral aspect of the sacrum, exhibiting centra of S 1-5, also the sacral rib attachments S 1-5 to the inner aspect of the left ilium. C, Anterior aspect of the sacro-iliac arcade, S1, the first sacral vertebra. D, Posterior aspect of the sacro-iliac arcade showing S5, the fifth sacral. All figures one fifteenth natural size.

coalesced intercentrum, and a monocipital rib, C 3 exhibits a powerful spine and a bicipetal rib (as partly restored). In C 5-C 10 the neural spines gradually diminish in height; lateral cavities (pleurocœlia) appear at the sides of the centra; the tubercular processes of the ribs expand into a broad tuberculo-capitular head, in which the capitulum is abbreviated and no longer articulates with the posterior face of the centrum in front. The centra of the last cervical and the first dorsal, D1, are more or less coalescent.

*Thoracics or dorsals.* The ten successive vertebræ exhibit the following characters: (1) the centra progressively elongate; (2) the faces are amphiplatyan or slightly opisthocœlous; (3) lateral cavities (pleurocœlia) are present in D 2, are faint in D 3, D 5, present in D 6, D 13, rising gradually from the middle of the centrum in D 4 to the top of the centrum in D 13; (4) the capitular articulations of the ribs rise from near the base of the centrum in D 1 to the middle of the neural arch in D13; (5) the articulations for the tubercles of the ribs are elevated on the metapophyses (transverse processes) throughout, diminishing in size from D 1-D 12, in which the capitular and tubercular processes are brought nearer together. The under surfaces of the metapophyses are sculptured and pitted with two facets or cœlia; (6) the neural spines increase steadily in size from D 1-D 13; (7) between D 7 and D 13 there is a tendency of the adjacent neural spines to coalesce at the summits; (8) in D 9-D 12 there are traces of a neurocentral suture; (9) the metapophyses of D 12-D 13 tend to unite with the antero-internal face of the iliac crest (Fig. 17); (10) the centrum of D 13 tends to unite with that of the first sacral (Fig. 17).

As a whole the pre-sacral series, the cervico-thoracic, is greatly abbreviated so that the extremely heavy and powerful skull is brought very near the powerful sacral arcade.

*Sacral vertebræ* (Figs. 19, 20, Plate XXVII). Of the two superbly preserved sacral arcades that of the first specimen (Amer. Mus. 973) shows best the normal condition of the five sacral vertebræ since the second specimen (Amer. Mus. 5027) is unnaturally compressed and deformed. It is noteworthy that the five vertebræ composing the sacrum coalesce by their centra, also that S 2, S 3 are laterally compressed, as shown normally in Amer. Mus. 973. S 1 is directly opposite the anterior (pubic) peduncle of the ilium, while S 3 is opposite the posterior (ischiac) peduncle of the ilium. These are probably the primary sacrals, while S 4, S 5 are probably caudo-sacrals. The sutures between the sacral centra and sacral ribs are still apparent in the ventral view of Amer. Mus. 973. An instructive view of the sacro-iliac arcade is shown in Plate D, in which it is observed also that the anterior (pubic) and posterior (ischiac) peduncles of the ilium coincide with S 1 and S 3 respectively.

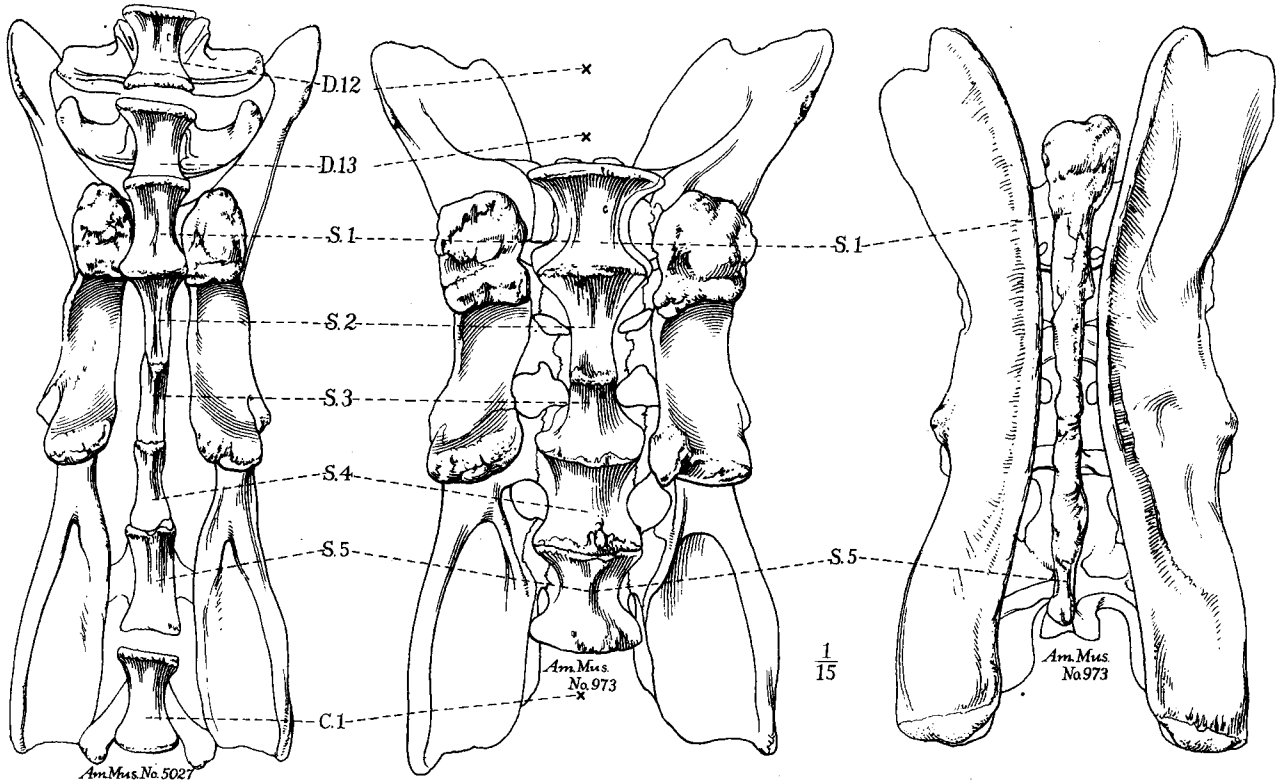


Fig. 20. Comparative views of the sacro-iliac arcade in *Tyrannosaurus rex*. To the right, superior and inferior views of the type specimen Amer. Mus. 973. To the left, inferior view of the second specimen, Amer. Mus. 5027, including dorsals, D.12, 13, also the first caudal, C.1. S.2, S.2-5 are strongly crushed laterally, deforming their proportions.

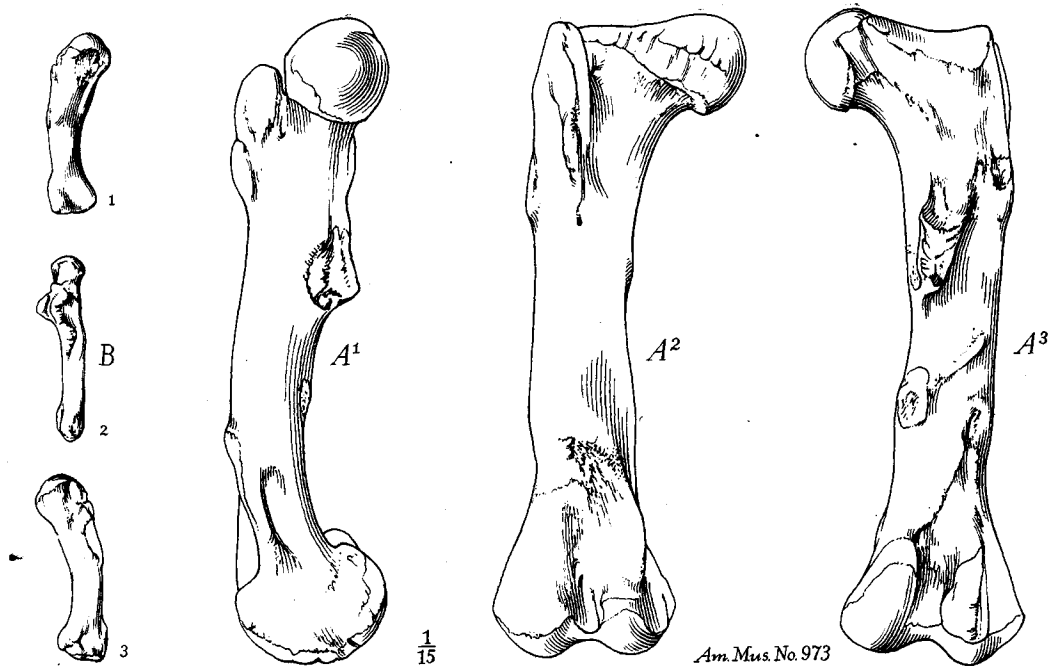


Fig. 21. Humerus and femur of *Tyrannosaurus rex*, type specimen Amer. Mus. 973. One-fifteenth natural size. B Humerus in three aspects, (1) posterior, (2) exterior, (3) anterior. A<sup>1</sup> right femur, internal aspect, A<sup>2</sup> the same, anterior aspect, A<sup>3</sup> the same, posterior aspect. One-fifteenth natural size.

*Caudal vertebræ* (Fig. 17, Plate D). The anterior caudal, C 1 (Fig. 17), partly unites by its caudal rib with the horizontally expanded internal plates of the ilium (Fig. 17, Amer. Mus. 5027). The caudal series so far as preserved in the specimen (Amer. Mus. 5027) is represented in the shaded vertebræ figured in Plate D, namely C 1-C 15, C 17, ?C 21-22. The intermediate vertebræ as well as the terminal vertebræ, C 23-53, are conjecturally restored. As in other carnivorous dinosaurs the caudals gradually diminish in size and increase in relative length. The centra are amphiplatyan or slightly procœlous. Neuro-central sutures are observed in Cd 2, Cd 11. The tail is an elongate balancing organ for the anterior part of the body, having considerable flexibility and exhibiting no indications of the extreme rigidity observed in the inflexible tail of the Ornithomimidæ.

*Sternal ribs.* Remnants of the doubly paired, or more probably triply paired series of abdominal ribs are preserved with specimen Amer. Mus. 973 and have already been described (Osborn, 1906). Brown observes:<sup>1</sup> "As yet we cannot definitely say as to the triply paired disposition of the abdominal ribs in *Tyrannosaurus* although I doubt not that this was the placement. It is true in all other forms in which the abdominal plates are found in position, and when the median series of abdominal ribs of *Tyrannosaurus* are placed in position the ends do not reach the costal ribs, so that it appears that there were two additional abdominal rib segments on each side."

*Problematic Dermal plates.* The dermal plates previously described by Osborn (1906) are still unique in the American Museum collections; they are totally unlike those of the armored herbivorous dinosaurs or the armored Ceratopsia. In a type specimen of *Ceratosaurus* recently mounted in the U. S. National Museum there is part of a row of dermal plates present above the tips of the neural spines. It is, therefore, quite possible that plates of the character attributed by Osborn to *Dynamosaurus* (= *Tyrannosaurus*) extended down over the sides of the body.

*Pelvic arcade* (Fig. 17, Plate XXVII). The pelvic arcade is distinguished by the following characters: (1) the antero-posterior extension of the ilium; (2) the firm articulation of the ilium with the sacral ribs (Fig. 16, S 1-S 5); (3) the articulation of the ilium with the metapophyses of the three posterior sacrals (Fig. 16, S 3-S 5); (4) the anterior expansion of the iliac plates (Fig. 16 C); (5) the postero-internal iliac horizontal plates (Fig. 16 D).

The pubis, firmly coalesced with the ilium and ischium, terminates in an enormously expanded peduncle. The ischium is comparatively slender with contracted rod-like extremity.

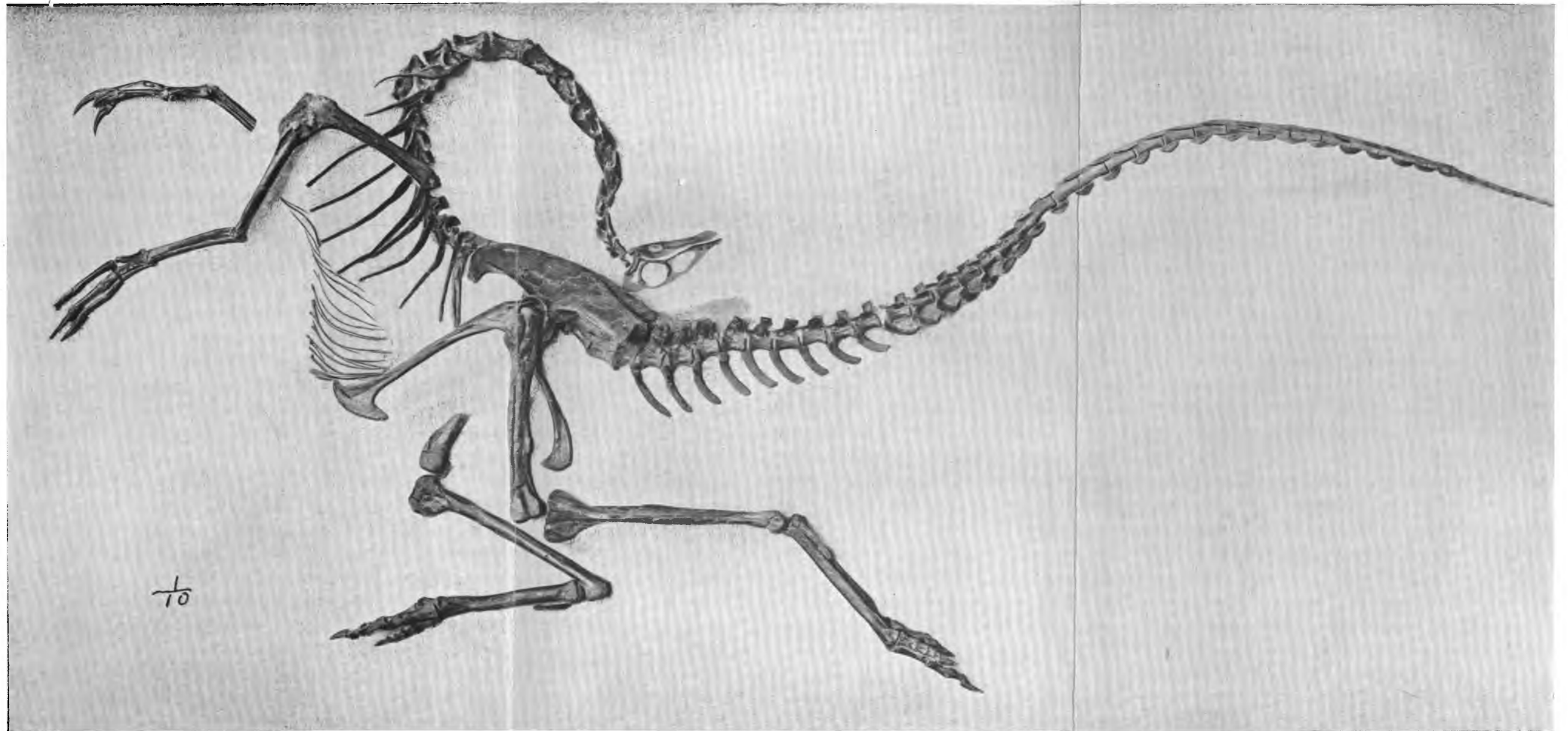
<sup>1</sup> Brown, Barnum. Letter to the author Jan. 7, 1916.

*Fore limb.* The great disparity between the fore limb and hind limb is illustrated in the contrast (Fig. 18) between the humerus (B) and the femur (A<sup>1</sup>, A<sup>2</sup>, A<sup>3</sup>) of the genotype specimen (Amer. Mus. 973).

As to the number of digits in the still unknown manus of *Tyrannosaurus* Gilmore regards it as probable that *Tyrannosaurus* will prove to be functionally didactyl with a vestigial D III as in the genus *Gorgosaurus*, in which D III is reduced to a vestige being represented only by Mtc. III without phalanges. It has recently been shown by Gilmore and Lambe that the manus of the Theropoda is greatly reduced not only in size but in the number of its parts.

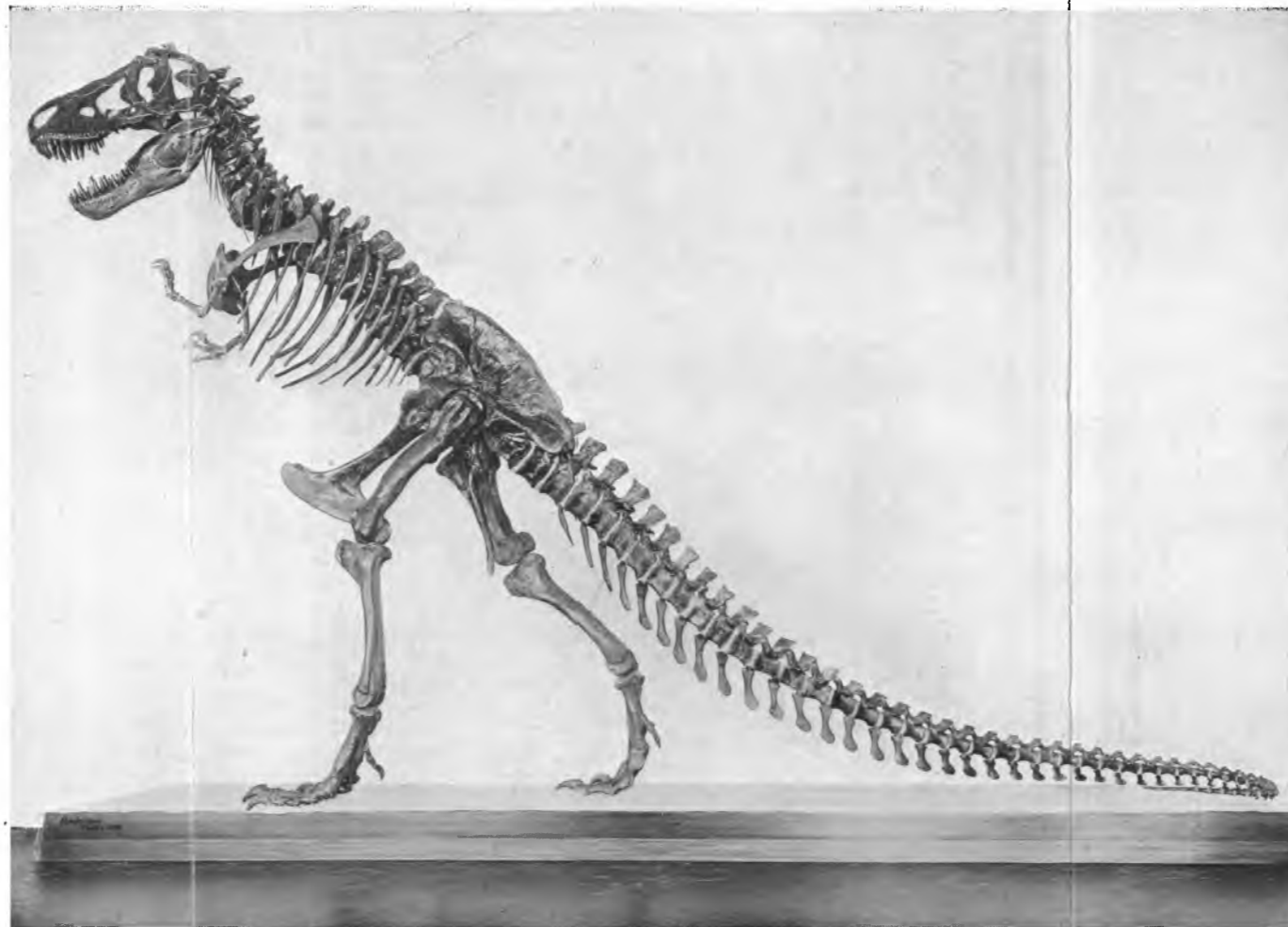
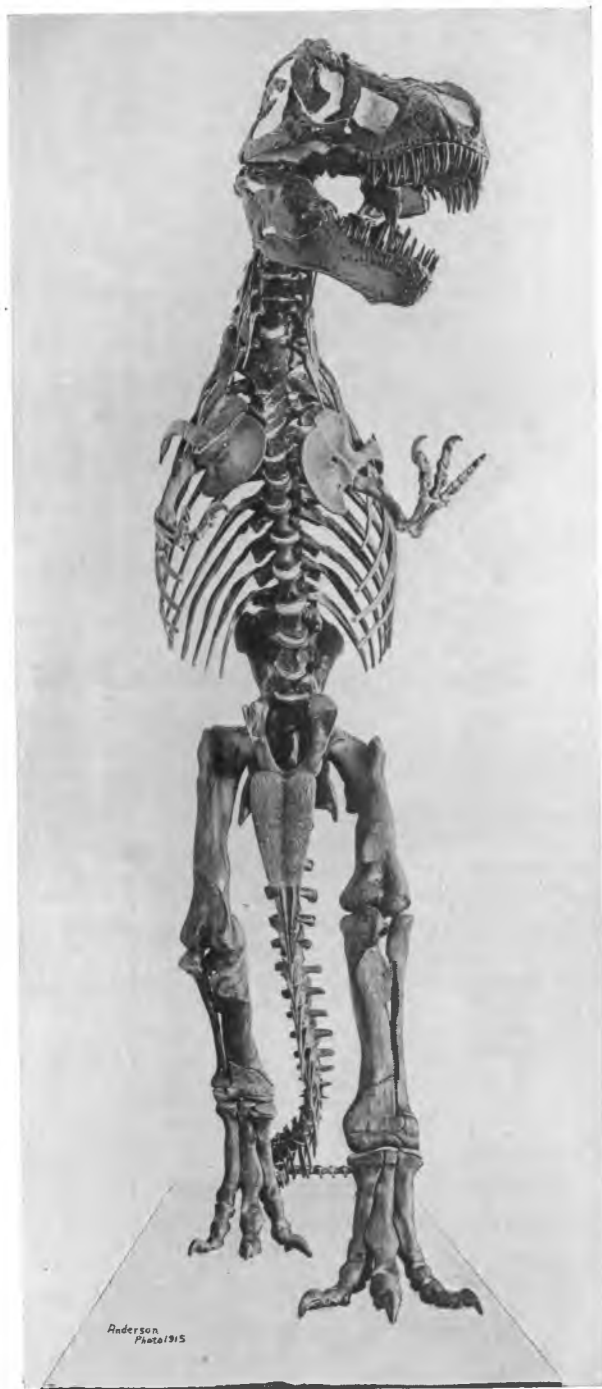
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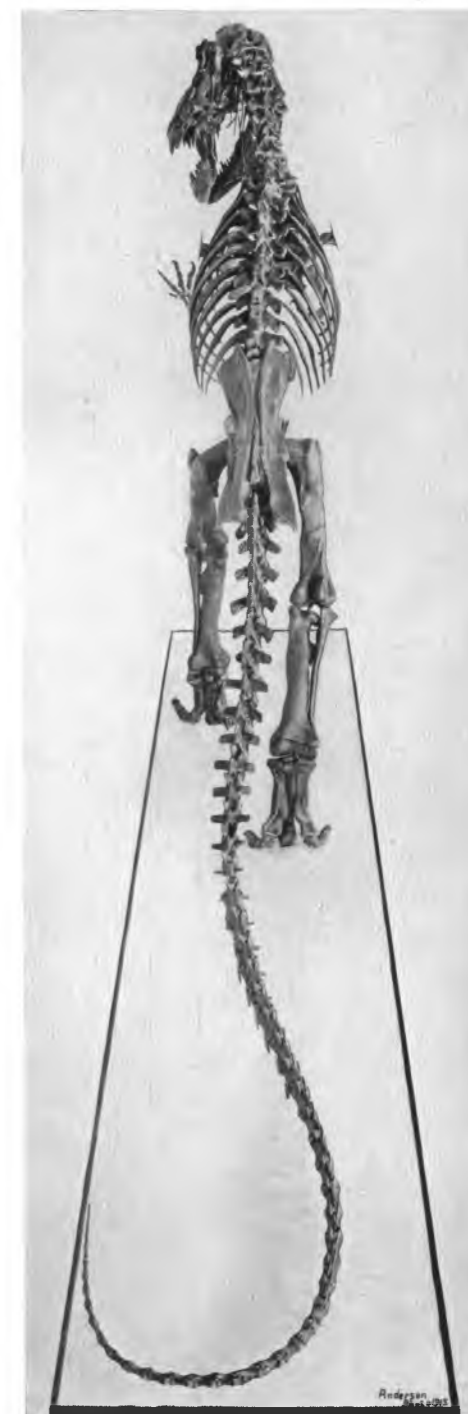


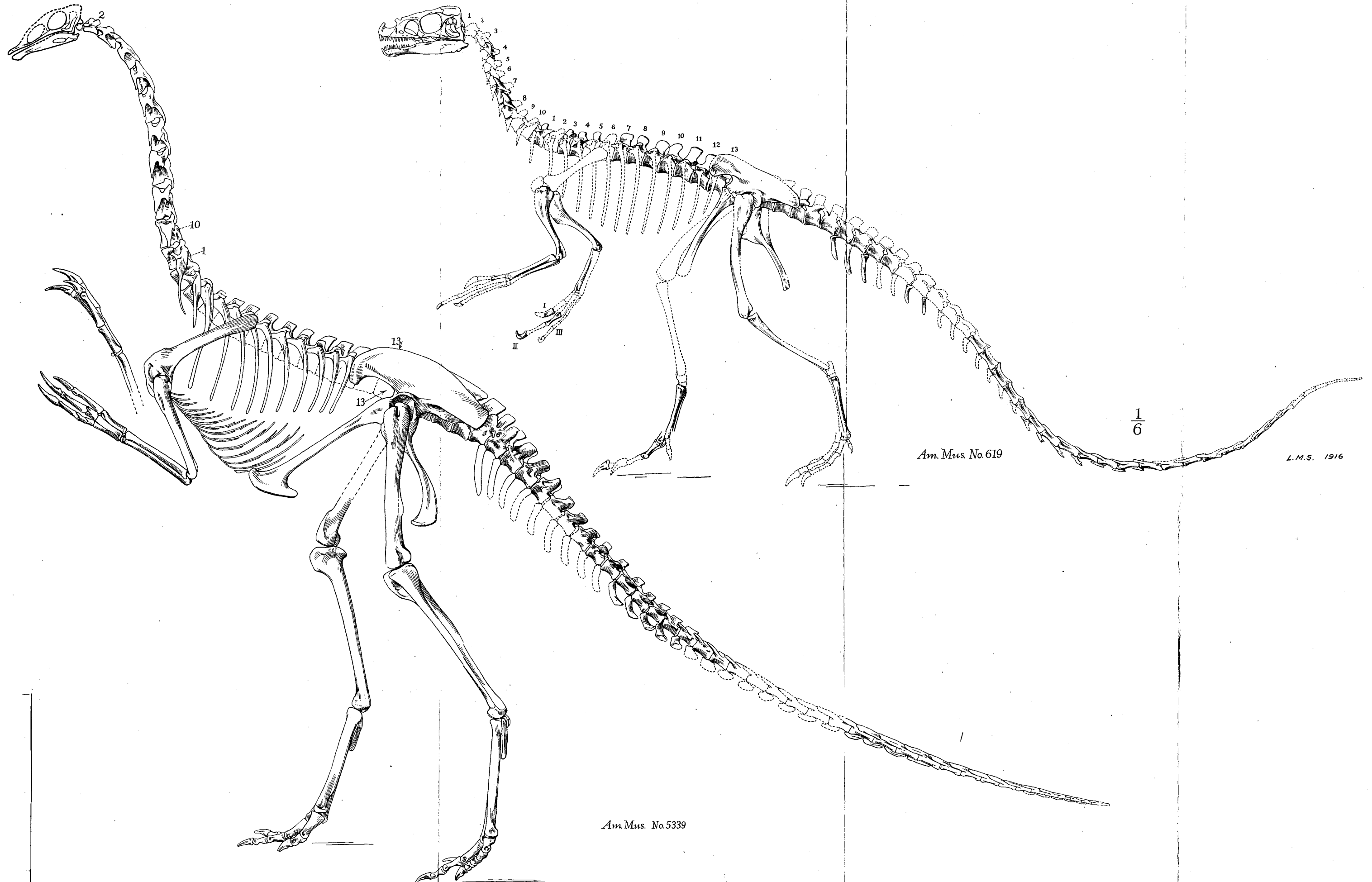
Skeleton of *Struthiomimus altus*. Genotype specimen, Amer. Mus. 5339. One-tenth natural size.  
In this panel mount the animal is placed approximately as found. The pollex is too closely appressed to the other digits, see Fig. 3.





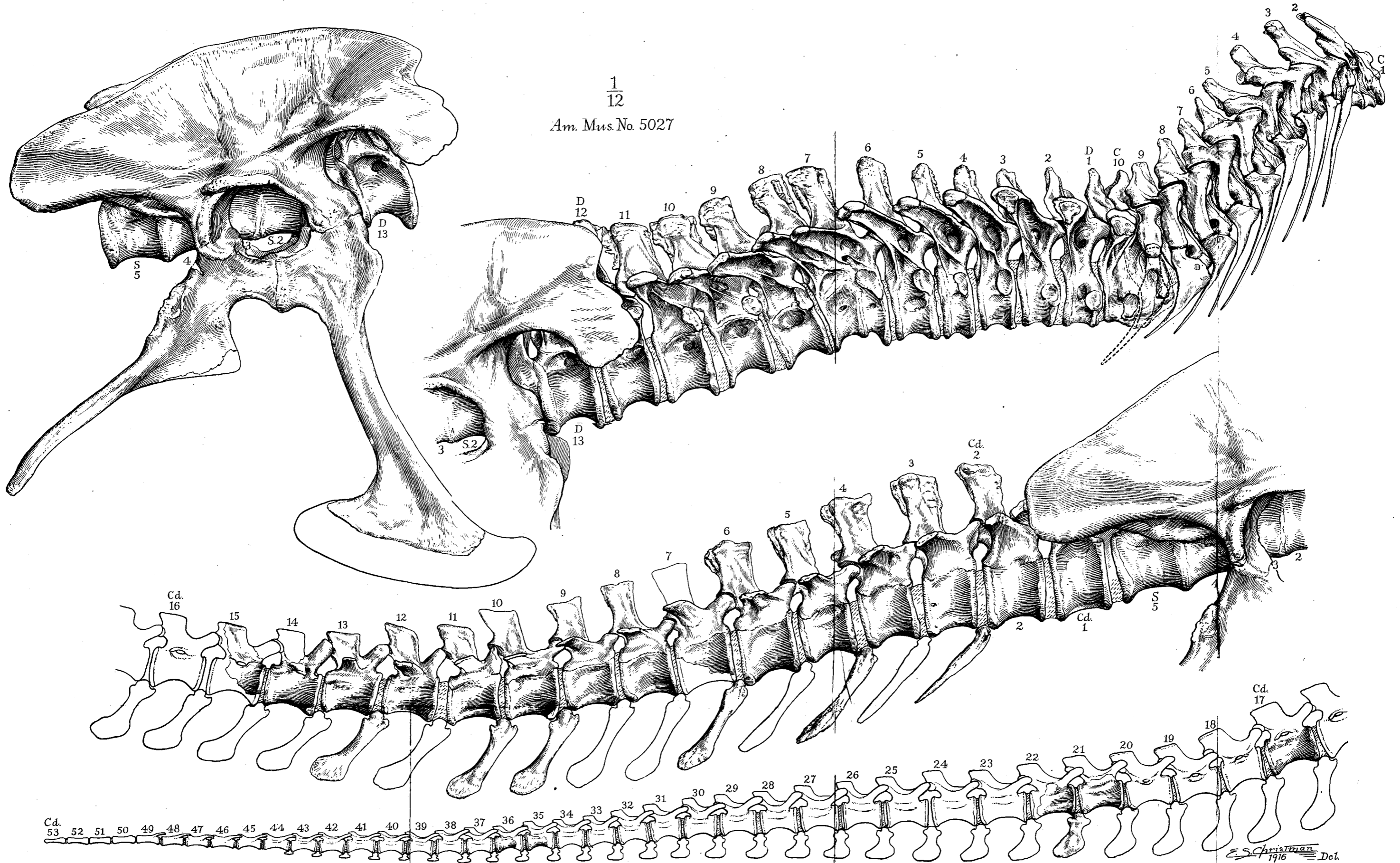
Anterior, lateral, and posterior aspects of the mounted skeleton of *Tyrannosaurus rex*, chiefly from Amer. Mus. 5027, partly from the type specimen Amer. Mus. 973. The sternal ribs are not restored. The structure of the manus is unknown as yet; the restoration of the digits is conjectural. About  $\frac{1}{5}$  natural size.





Reconstruction of the skeletons of *Struthiomimus altus* (left) and *Ornitholestes hermanni* (right). *Struthiomimus*  $\frac{1}{10}$ , *Ornitholestes*  $\frac{1}{6}$  natural size. The *Ornitholestes* restoration replaces the original restoration by Osborn in 1903 which is very faulty. The *Struthiomimus*, Amer. Mus. 5339, mount has the distal end of the tail restored from Amer. Mus. 5355; dotted vertebrae from Amer. Mus. 5262. In both restorations the pollex is too closely appressed to the other digits, see Fig. 3.

$\frac{1}{12}$   
Am. Mus. No. 5027



Pelvic arcade and vertebral structure of the second chief specimen of *Tyrannosaurus rex*, Amer. Mus. 5027, discovered in 1908. An orthogonal projection executed on a very large scale and reproduced one-twelfth natural size. C1-C10 cervical series, D1-D13 dorsal or thoracic series, S1-S5 sacral series, Cd 1-Cd 53 caudal series. The caudals actually preserved are shaded; those drawn in outline are conjectural and restored. The total number of caudals is conjectural.