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OF THE

American Museum of Natural History.

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I.—CRANIA OF TYRANNOSAURUS AND ALLOSAURUS.

II.—INTEGUMENT OF THE IGUANODONT DINOSAUR *TRACHODON*.

BY HENRY FAIRFIELD OSBORN.

June, 1912.

(*Continued from 3rd page of Cover.*)

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New Series, Volume I, Part I.

CRANIA OF TYRANNOSAURUS AND ALLOSAURUS.

PLATE I, WITH KEY (FIG. 1).

Tyrannosaurus skull, side view.

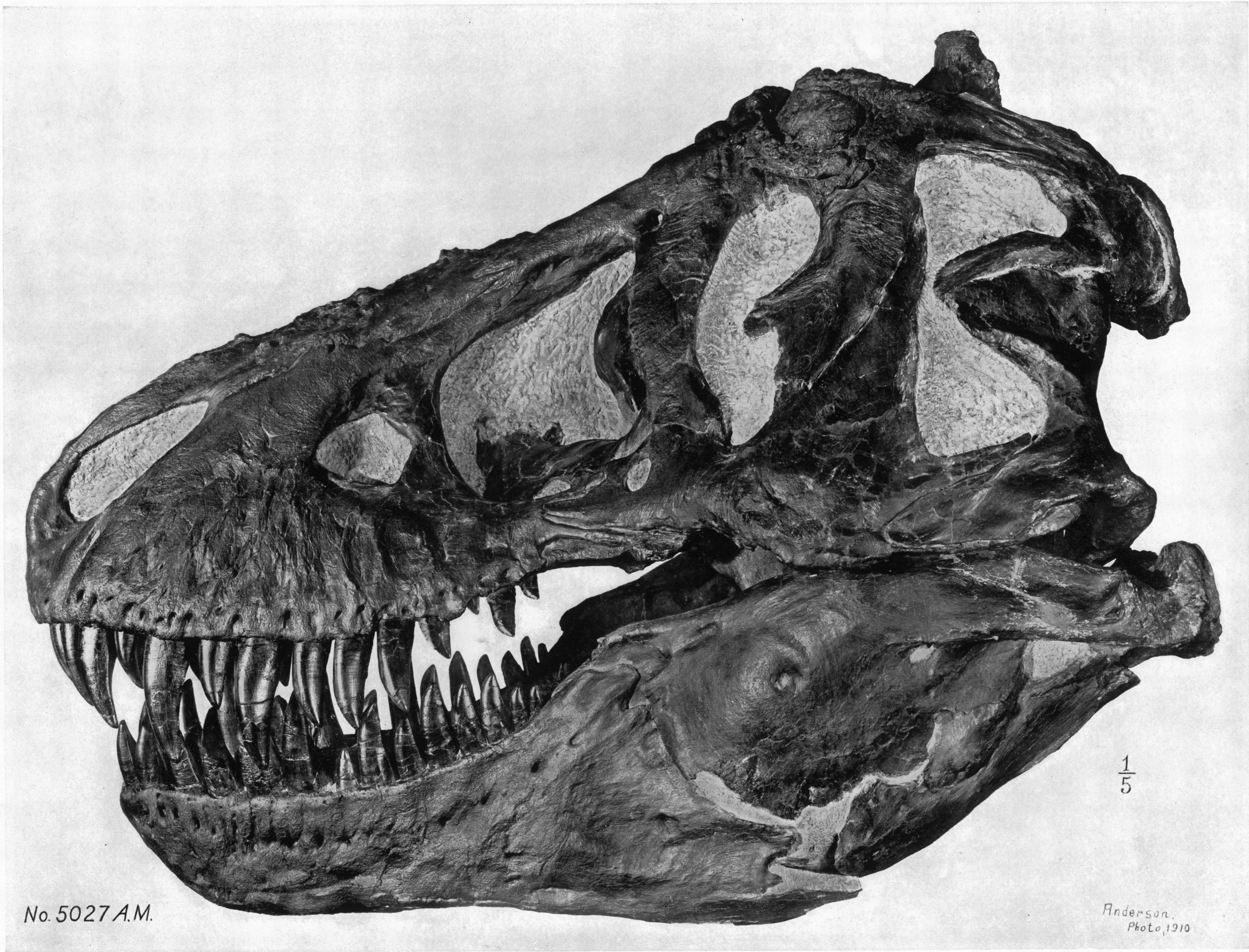

Plate I. Complete skull of *Tyrannosaurus rex* Osborn. Amer. Mus. No. 5027. One-fifth natural size.

The element shown in the upper posterior part of the first antorbital fenestra is the displaced ectopterygoid (transversum) of the opposite side.

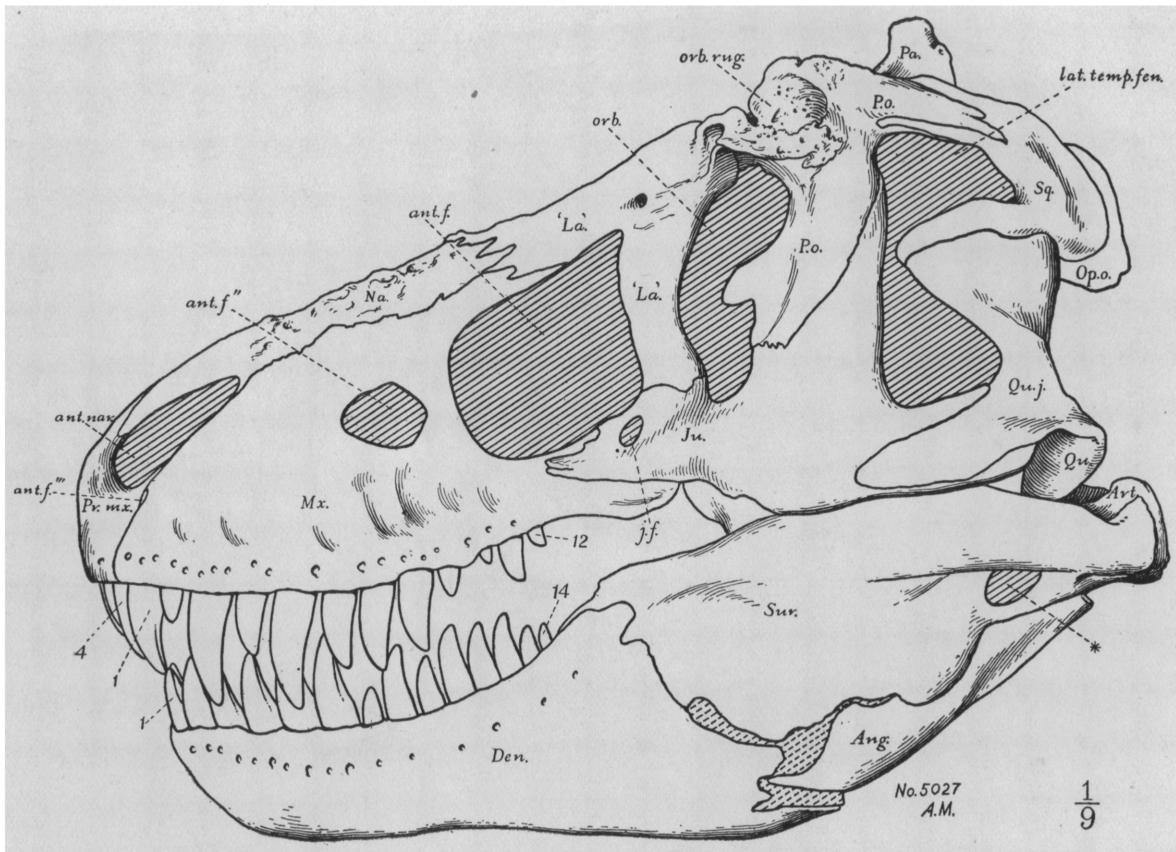

Fig. 1. *Tyrannosaurus rex.* Key to Plate I.

Abbreviations: *ant. f', f'', f'''*, first, second and third antorbital fenestræ.
'La.,' "lachrymal" (= adlachrymal Gaupp.)
j. f., jugal fenestra.
orb. rug., orbital rugosity.
Op. o., opisthotic (paroccipital process).
4, fourth premaxillary tooth.
1, first maxillary tooth.
*, fenestra in surangular.

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AMERICAN MUSEUM OF NATURAL HISTORY.

PART I.—CRANIA OF TYRANNOSAURUS AND ALLOSAURUS.

BY HENRY FAIRFIELD OSBORN.

PLATES I–IV.

(Tyrannosaurus Contributions No. 3.[1])

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Through comparison of the extensive series of specimens assembled by the American Museum of Natural History expeditions during a number of years past from the Upper Jurassic (Morrison) and Upper Cretaceous, we are enabled for the first time to give a nearly complete description of the crania of the Theropodous Dinosaurs known as *Allosaurus* and *Tyrannosaurus*.

In this description the author has been greatly assisted by the following persons: Mr. Barnum Brown, the discoverer of the greater part of the known remains of *Tyrannosaurus*; throughout the preparation of the text and illustrations by Dr. W. K. Gregory, who has made a special investigation of the homologies of the bones of the skull; also by Dr. F. von Huene, who spent a portion of the winter of the year 1911 studying the extinct reptiles in the American

[1] Osborn, H. F. 'Tyrannosaurus and other Cretaceous Carnivorous Dinosaurs'. Bull. Amer. Mus. Nat. Hist., Vol. XXI, Art. XIV, Oct. 4, 1905, pp. 259–266. Also 'Tyrannosaurus, Upper Cretaceous Carnivorous Dinosaur'. Bull. Amer. Mus. Nat. Hist., Vol. XXII, Art. XVI, July 30, 1906, pp. 281–296.

Museum collections. This paper is practically a joint contribution from the author and Messrs. Brown and Gregory. The drawings are the work of Mr. Erwin S. Christman; the photographs were made by Mr. Abram E. Anderson.

Summary of Materials.

The materials in the American Museum of Natural History are as follows:

1. *Allosaurus*, mounted with skeleton No. 5753 Cope Coll., Amer. Mus.
2. " " skull nearly complete, No. 666 Amer. Mus.
3. " " " partly " " 600 " "

1. *Tyrannosaurus rex*, skull (imperfect) and jaws, type, No. 973 Amer. Mus. (Brown).
2. " " " complete, with skeleton, No. 5027 Amer. Mus. (Brown).
3. " " " occiput and brain case, sectioned, No. 5029 Amer. Mus. (Brown).
4. " " " occiput and brain case, complete, No. 5117 Amer. Mus. (Sternberg).
5. " " " of *Dynamosaurus* (synonym), jaws and part of skeleton, No. 5866 Amer. Mus. (Brown).

The three *Allosaurus* crania from the Upper Jurassic, Morrison, or Como Horizon, include the imperfect skull found with the remarkably complete skeleton in the Cope Collection (No. 5753), also the two skulls (Nos. 666, 600), more perfect, found in the Bone Cabin Quarry.

The *Tyrannosaurus* series from the Upper Cretaceous of Hell Creek, northern Montana (Nos. 973, 5027, 5029, 5866), and from Converse County, Wyoming (No. 5117), include parts of five skulls and jaws.

The type skull of *Tyrannosaurus rex* (No. 973), also the type of the supposed genus *Dynamosaurus* (No. 5866), which proves to be a synonym of *Tyrannosaurus*, were the first to be described. Very valuable information is derived from the cranium (Amer. Mus. No. 5029) from which the brain cast has been obtained (Text Fig. 17 and Pl. III). Still more valuable information comes from the young *Tyrannosaurus* cranium (Amer. Mus. No. 5117) in which nearly all the sutures are open (Figs. 7, 8). There is also a fine occiput in the Carnegie Museum, Pittsburgh, which was not accessible for the present description although kindly loaned by Dr. W. J. Holland for a previous restoration of the type skull.

The crowning specimen is the superb skull Amer. Mus. No. 5027, associated with a second skeleton of *Tyrannosaurus* discovered in the Hell Creek region of Montana during the American Museum Expedition of 1907 by Mr. Barnum Brown. This specimen together with the type (Amer. Mus. No. 973) nearly completes our knowledge of the skeleton of this remarkable animal. These skeletons are now being mounted and will form the subject of a final memoir by the present writer.

The American Museum is indebted to Mr. Brown for the untiring exploration continued through a period of six years which resulted in the discovery of this superb material.

Elements of Theropod Skull.

Through the studies of Williston, Hay, von Huene, and especially Gaupp, much progress has been made in recent years in respect to the homologies of the elements in the reptilian, including the Theropod, skull. This has been accompanied by several changes in the nomenclature.

Gregory has brought these researches to bear on the present determination of the principal elements in the skulls of *Tyrannosaurus* and *Allosaurus* as set forth in the following notes.

The *adlachrymal* of Gaupp is the large bone in front of the orbits, marked '*La.*' This is the so-called "lachrymal" of authors, but is not homologous with the true lachrymal of mammals. The prefrontal ('*Pr. f*') above and behind the adlachrymal is a greatly reduced bone in Theropoda and Sauropoda; in Crocodilia it is equal in size to the adlachrymal. The prefrontal is homologous with the true lachrymal of mammals.

The *postorbital* (*P. o.*) is undoubtedly a complex of two separate elements, namely, the postfrontal and postorbital of more primitive reptiles. It is similar in its relations to those two bones in *Sphenodon* and the phytosaurs.

The *orbitosphenoids* (*O. s.*) of the figures correspond with the "alisphenoids" of previous descriptions of the reptile skull. This true orbitosphenoid is precisely homologous with that of *Crocodilus* (Fig. 14) as shown by its relations with the nerve exits and surrounding bones. It is believed by von Huene to be the homologue of the orbitosphenoid of the mammalian skull.

The *opisthotics* are equivalent to the paroccipitals of Owen.

The *prearticulars* are represented as a forward continuation of the articulars by Williston in the Mosasaurs. They are also present in Cotylosaurs. This element is not yet known to be separate in *Ceratosaurus*. The separation in *Tyrannosaurus* is apparently clear (Brown). The prearticular is probably the homologue of the dermal internal extension of the cartilaginous articular described in recent reptiles and homologized by Gaupp with the "goniale" (*processus anterior mallei*) in mammals (Gaupp, 1911).

The *supradentary* is a new term applied by Osborn to an anterior dermal extension of the splenials, which appears to be suturally separate from the splenials proper. The term "presplenial" is not applicable because it has been shown by Williston that the so-called "presplenial" of Baur is the true splenial while the "splenial" of Baur is the angular; this brings the Theropoda into harmony with the Crocodilia and Parasuchia. The bone termed "presplenial" by Lambe in *Albertosaurus* is part of the dentary (Gregory).

The known elements of the theropod skull are the following:

Angular	*Ang.*	Parietal	*Pa.*
Articular	*Art.*	Postorbital (fused with postfrontal)	*Po. o.*
Basioccipital	*B. oc.*	Postfrontal	*Po. f.*
Basisphenoid	*B. sp.*	Prefrontal	*Pr. f.*
Coronoid	*Cor.*	Premaxillary	*Pr. mx.*
Dentary	*Den.*	Prearticular	*Pr. art.*
Ectopterygoid (transpalatine, transverse)	*Ec. pt.*	Presphenoid	*Pr. sp.*
Ethmoid (including mesethmoid)	*Eth.*	Proötic	*Pr. ot.*
Exoccipital	*Ex. oc.*	Pterygoid	*Pt.*
Frontal	*Fr.*	Quadrate	*Qu.*
Jugal	*Ju.*	Quadrato-jugal	*Qu. j.*
'Lachrymal' (=adlachrymal)	*'La.'*	Splenial	*Spl.*
Maxillary	*Mx.*	Squamosal	*Sq.*
Nasal	*Na.*	Surangular	*Sur.*
Opisthotic (paroccipital)	*Op. ot.*	Supradentary	*S. d.*
Orbitosphenoid ('alisphenoid')	*O. sp.*	Supraoccipital	*S. oc.*
Palatine	*Pal.*	Vomer ('prevomer' Broom)	*Vo.*
Parasphenoid (=vomer of mammals, *fide* Broom)	*Pa. sp.*		

Skull of *Tyrannosaurus*.

Unless otherwise stated the following description refers to the most perfect skull No. 5027 Amer. Mus. Collection.

In general the skull is by far the most powerful and massive known among the reptiles. Among the living Reptilia it has remote resemblances with the skulls of *Sphenodon* (temporal region) and of *Crocodilus* (occipital and basisphenoidal region); among the extinct Reptilia its closest resemblances are with the skulls of other Theropoda and of the Sauropoda, especially in four points, namely:

(1) Abbreviation of the cranial region.
(2) Elongation of the facial region.
(3) Multiple fenestration of the facial region.
(4) Upward flexure of the brain case.

The palate displays one feature which is very important, namely, the union of the vomers into a single diamond-shaped plate articulating by a long, narrow process with the pterygoids posteriorly. This is a strong avian analogy as seen by comparison with the primitive ratite palate of *Dromæus* (Fig. 5). This resemblance was first pointed out to the author by his friend Mr. Pycraft of the British Museum.

Another striking feature is the deep downward prolongation of the basioccipital-basiphenoidal plate, in which these tyrannosaurs contrast widely with all recent reptiles, including the Crocodilia, but agree with the Sauropoda.

Chief Measurements of Skull (Amer. Mus. No. 5027).

1. Basilar length, premaxillaries to occipital condyles	1.210m.	48 in.
2. Total width across quadrato-jugals		
(a) As estimated from transverse measurements in the crushed condition	.835	33
(b) As estimated by doubling the width of the nearly normal right side	.904	35⅝
3. Total height, top of occipital crest to bottom of the quadrate bone	.635	25
4. Length along side of skull, premaxillaries to back of paroccipital processes	1.355	53½
5. Length of lower jaw, symphysis to back of articulars	1.205	48

Apparently the above measurements of No. 5027 are almost identical with those of the type skull (No. 973). The cranium No. 5117 belongs to a smaller and younger animal in which the sutures are more distinct.

It will simplify the description to consider the different aspects of the skull in consecutive order.

Lateral View, Skull No. 5027.

Text Fig. 1 and Pl. I.

The skull and jaw combined present deep and massive rather than elongate proportions. The areas of muscular attachment are heavily rugose. The rugose area extends also down the superior surface of the nasals.

Parietal, summit of crest only observed in lateral view.

Paroccipital (process) or opisthotic (*op. o.*), extreme lateral portion projecting behind the squamosal.

PLATE II, WITH KEY (FIG. 2).

Tyrannosaurus skull, top view.

Plate II. *Tyrannosaurus rex.* Superior view of skull. Amer. Mus. No. 5027. Scale about 1/6.

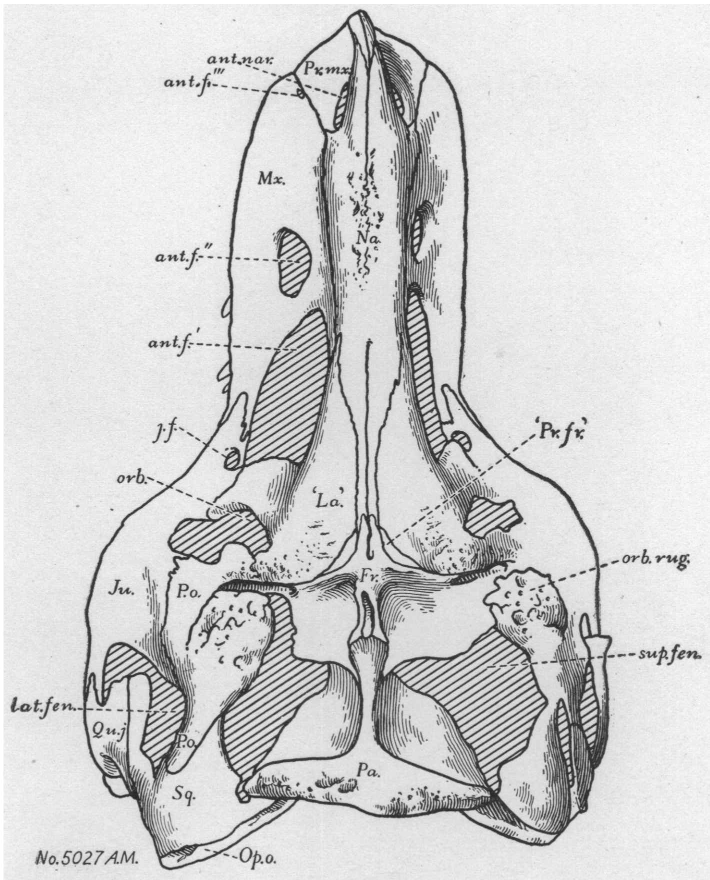

Fig. 2. *Tyrannosaurus rex.* Superior view of skull, Amer. Mus. No. 5027. Key to Plate II. Abbreviations as in preceding figures.

sup. fen., superior temporal fenestra.
lat. fen., lateral temporal fenestra.
'La.,' adlachrymal of Gaupp.
P. o., postorbital + postfrontal.
'Pr. fr.,' lachrymal of Gaupp, prefrontal of authors.

Squamosal, with forwardly projecting bars and uniting respectively with the postorbital and the superior surface of the quadrato-jugal.

Quadrato-jugal, with broad superior plate for inferior bar of squamosal, overlapping outer portion of quadrate and with an inferior bar overlapping the jugal.

Jugal of triradiate shape with anterior bar uniting with maxillaries and adlachrymals, perforated by a small fenestra (*jf.*); the superior bar uniting with the postorbitals, the posterior bar uniting with the quadrato-jugals.

Pterygoid, superior surface of palatal portion seen through the first antorbital fenestra (Pl. II).

Postorbital, probably a complex of postfrontals and postorbitals, with an inferior jugal and a posterior squamosal process. The orbital rugosity (*orb. rug.*) rises immediately behind a deep notch which separates this element from the adlachrymal. The orbit is partly bounded below by an anterior process of the postorbital.

Prefrontals and frontals visible only on top of skull.

Adlachrymal ('*La*'.) (= "lachrymals" of authors), greatly enlarged, with broad anterior process uniting with nasals and maxillaries, inferior process uniting with jugals. The supraorbital rugosity of the adlachrymal is separated by the deep notch from the rugosity of the supraorbital; the upward and backward growth of the adlachrymal has shut the frontal, pre- and postfrontal out of lateral view. No sutures remain between the adlachrymal and postorbital.

Nasal, uniting with adlachrymals, maxillaries, and premaxillaries.

Maxillary fenestrated, suturally uniting with premaxillaries, with nasals, but not with frontals.

Orbit, reduced in size, surrounded by adlachrymals, postorbitals, and partly enclosed below by anterior bar of postorbitals.

Nares, elongate, oval.

Fenestration.

Beside the orbital and narial openings, we observe five openings, on the side of the skull, namely:

(1) Latero-temporal fenestra, partially divided by the horizontal squamosal-quadrato-jugal bar.

(2) Infraorbital fenestra restricted off from the orbital fenestra proper.

(3) Small, round jugal fenestra (*j. f.*).

(4) Large antorbital fenestra (*ant. f.*).

(5) A smaller second antorbital fenestra (*ant. f.''*).

(6) Diminutive maxillo-premaxillary fenestra (*ant. f.'''*).

Superior View, Skull No. 5117.

Text Fig. 2 and Pl. II.

The superior view of the skull brings out with great clearness the relations of pairs of the same bony elements in the facial and cranial regions, especially the peculiar relations of the adlachrymals, postorbitals, and greatly reduced and constricted prefrontals, which are thrust in toward the median line of the skull instead of occupying the free lateral supraorbital position which is observed in *Allosaurus*.

Parietals, rising into an antero-posterior sagittal crest and a transverse supraoccipital crest.

Frontals, abbreviated, suturally separate from each other and from surrounding elements in young individuals; in adults closely united laterally with postorbitals. Anteriorly uniting with nasals, prefrontals, and adlachrymals. Suture between frontals and nasals not apparent in adult skull.

Postorbitals, with prominent rugosity (*orb. rug.*), immediately in front of which is the deep, narrow groove separating this element from the adlachrymal rugosity. This deep groove or fossa is apparently a vestige of the opening or cleft above the orbit in *Allosaurus* (Fig. 26), in which the prefrontals are displayed.

Prefrontals (*Pr. fr.*), with very limited, wedge-shaped exposure on top of the skull.

Adlachrymals ('*La*'.) greatly expanded.

Nasals narrow, median area coalesced into a single rugose plate, suturally separate anteriorly and posteriorly, uniting by very narrow sutural contact with frontals posteriorly, and with premaxillaries anteriorly.

No pineal opening is observed at the top of the skull; the sagittal crest, formed of the frontals and parietals, is solid.

Fenestration.

The following openings are observed:

(1) The large supratemporal fenestra (*sup. fen.*).

(2) The lateral temporal fenestra (*lat. fen.*).

(3) The orbito-infraorbital opening.

(4) The first antorbital fenestra (*ant. f.*).

(5) The second antorbital fenestra (*ant. f''.*).

(6) The third antorbital fenestra (*ant. f'''.*).

(7) The anterior nares (*ant. nar.*).

ANTERIOR VIEW, SKULL No. 5027.

Text Fig. 3.

The anterior views of skull shown in Fig. 3 serve to bring out still more clearly the relations of the same cranial elements. From behind forward the median line is seen to be composed in pairs of the *parietals, frontals, nasals,* and *premaxillaries.*

Prefrontals (*Pr. fr.*), wedged in between the frontals and adlachrymals.

Adlachrymals ('*La*'), form vertical buttresses between the orbital and antorbital openings.

Premaxillaries, suturally separate, each containing four teeth.

Dentaries, freely apposed, *i. e.*, not united in median line.

OCCIPITAL VIEW, SKULLS Nos. 5027, 5117.

Text Fig. 4.

The relations of pairs of bones of the occipital region are perfectly displayed in No. 5027 (Fig. 4) and in the younger specimen No. 5117.

Parietals, vertically and horizontally expanded, forming the entire upper portion of occiput,

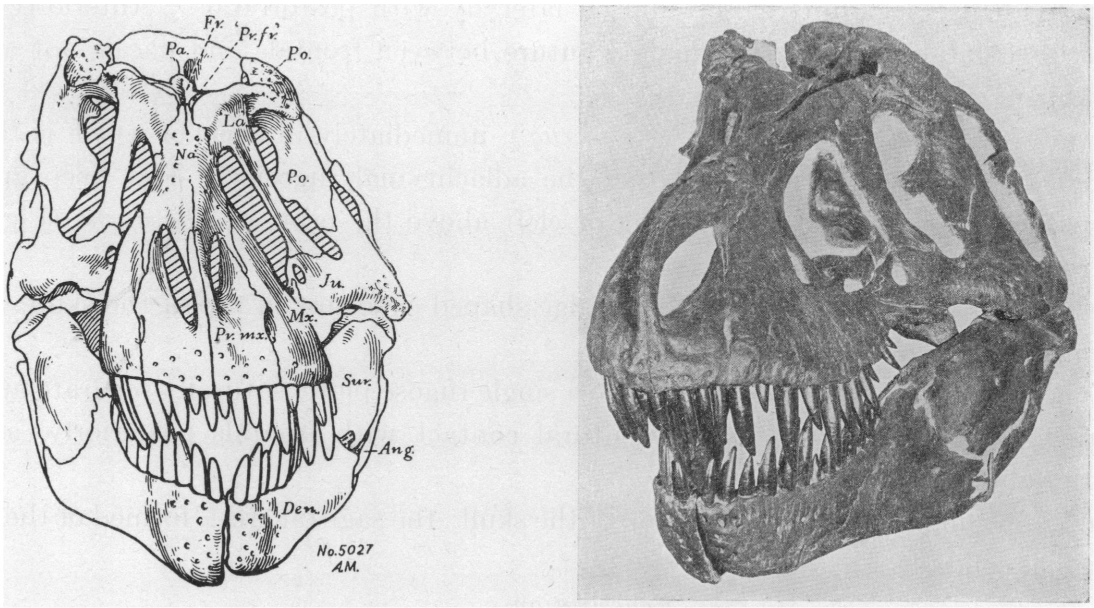

Fig. 3. *Tyrannosaurus rex*. Full front and oblique front view of skull. Amer. Mus. No. 5027. Greatly reduced.
'*Pr. fr.*,' prefrontal (= lachrymal of mammals, *fide* Gaupp).
'*La.*,' "lachrymal" of reptiles (= adlachrymal Gaupp).

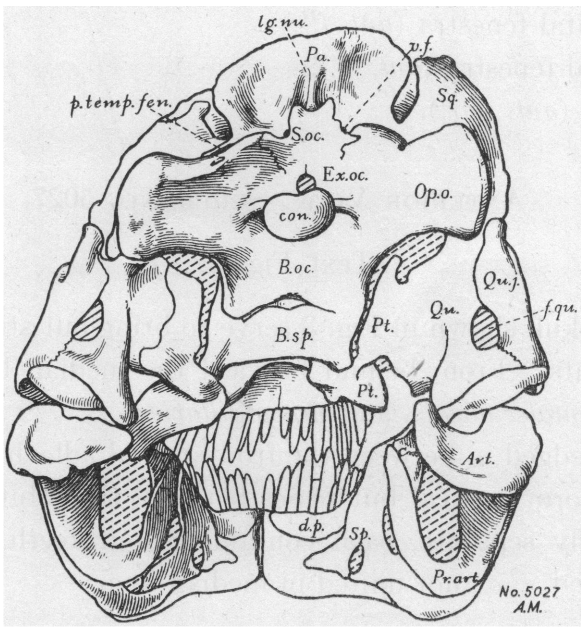

Fig. 4. *Tyrannosaurus rex*. Posterior view of skull. Amer. Mus. No. 5027.
lg. nu., pits for ligamentum nuchæ.
p. temp. fen., vestigial post-temporal fenestra.
v. f., venous foramen.
f. qu., quadrate foramen.
d. p., presplenial process or supradentary.
Pr. art., prearticular (dermarticular).

impressed posteriorly by median pits for the attachment of the *ligamentum nuchæ*, extending laterally over the paroccipital processes (*Op. o.*); between this parietal spur and the paroccipital process may be observed the vestigial posttemporal fenestra (*p. temp. fen.*).

Supraoccipitals, relatively reduced in size, coalesced inferiorly with exoccipitals, which probably bridge over the *foramen magnum* as in *Allosaurus*, coalesced laterally with paroccipital or opisthotic elements.

Basioccipital, composing the broadly oval condyle (*con.*), sending down a flange inferiorly into the basioccipital plate (*B. oc.*), spreading laterally to coalesce with the paroccipital processes (*Op. o.*) or opisthotics.

Paroccipitals, or opisthotics (*Op. o.*) coalescing toward median line with exoccipitals and basioccipitals, expanding laterally and articulating with squamosals.

Basisphenoids, projecting downward below level of basioccipitals (compare Pl. III and Text Figs. 7 and 16); presenting inferior lateral processes for articulation with the pterygoids; homologous with the "basipterygoid" processes of *Sphenodon* and lizards.

Pterygoids, uniting by movable joints with "basipterygoid" process of basisphenoid; uniting laterally by a broad suture with the quadrate. (This suture is shown on the left hand side of the occiput in Fig. 4 but not on the right side.)

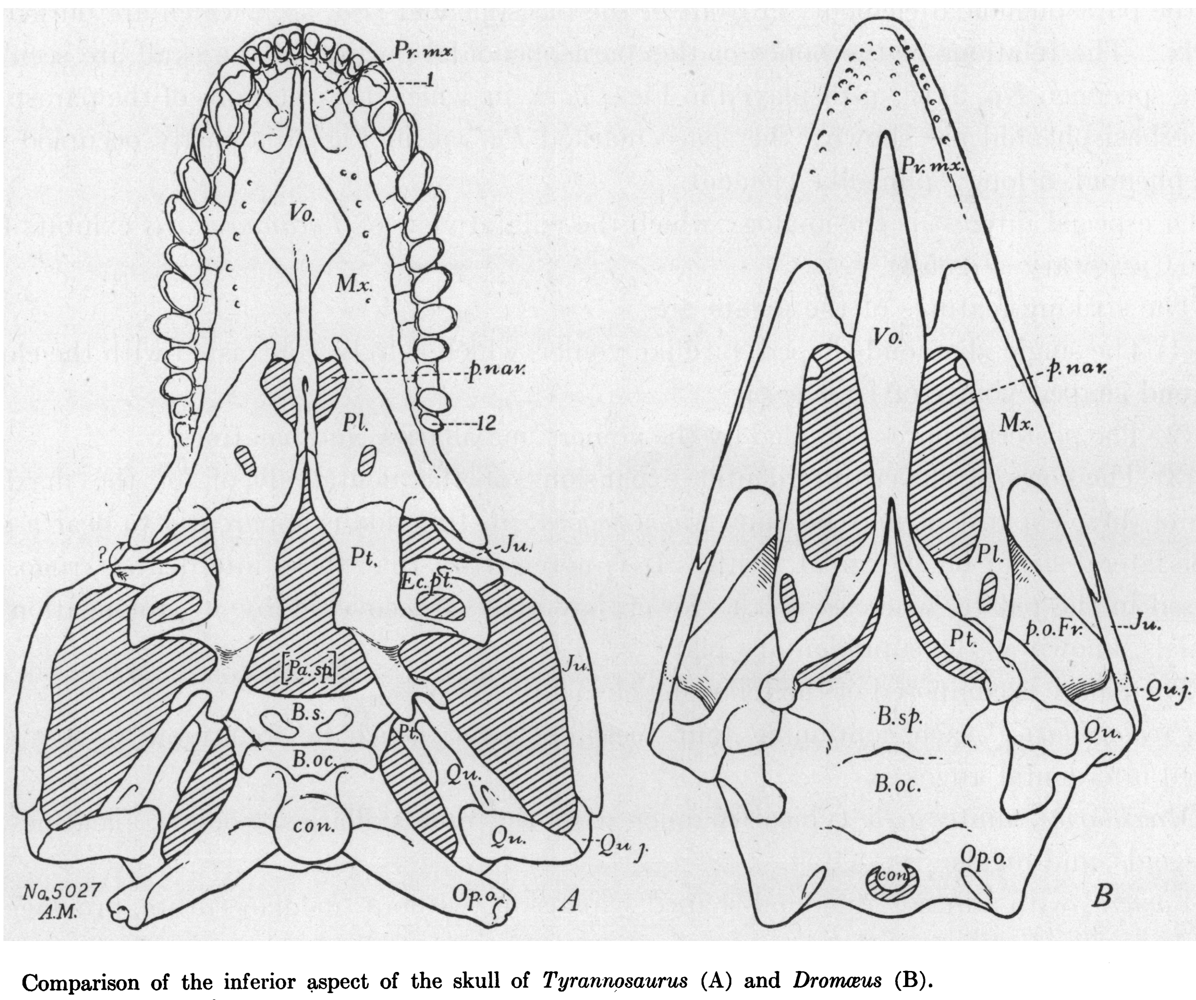

Fig. 5. Comparison of the inferior aspect of the skull of *Tyrannosaurus* (A) and *Dromæus* (B).
p. nar., posterior nares.
[*Pa. sp.*], position of parasphenoid.
Ec. pt., ectopterygoid.
The ectopterygoids (*Ec. pt.*) have slipped back from the normal contact with the posterior process of the maxilla, as indicated by the arrow.

Quadrates, broad posteriorly, firmly united by suture with pterygoids anteriorly; suturely united with quadrato-jugals exteriorly except at the point of the large quadrate foramen (*f. qu.*).

The most important feature of *Tyrannosaurus* as distinct from *Allosaurus* is that the quadrate is closely united with the squamosals above and by suture instead of presenting a ginglymoid, or hinge relation as in *Allosaurus*.

Fenestration.

Three pairs of fenestræ appear at the back of the skull, namely:

(1) vestigial posttemporal fenestræ,

(2) very constricted openings between the parietal crest and the squamosals leading into the supratemporal fenestræ.

(3) the fenestræ (*f. qu.*) between quadrate and quadrato-jugal.

Palatal View, Skull No. 5027.

Text Figs. 5, 6.

All the elements of the palate are clearly displayed in the natural position excepting the ectopterygoids, which are thrust backward from their natural junction with the maxillaries, and the parasphenoidal elements in front of the basisphenoid (*Pa. sp.*), which are buried in the matrix. The relations of the bones of this parasphenoidal portion of the skull are seen in the young specimen No. 5117, as displayed in Figs. 7, 8, in which the relations of the parasphenoid to the basisphenoid are shown; the space marked *Pa. sp.* in Fig. 6 is partly occupied by the parasphenoid, a long, splint-like element.

Of especial interest is the analogy which the palatal view of *Tyrannosaurus* exhibits to that of the Cassowary (Fig. 5B).

The striking features of the palate are:

(1) The single, diamond-shaped, birdlike vomer, which is to be contrasted with the elongate, diamond shaped vomer of *Dromæus*.

(2) The posterior nares bounded by the vomers, maxillaries, and palatines.

(3) The rows of eleven interdental expansions of the dental alveoli of the maxillaries. Each of these expansions may be known as a *rugosa*; its function is apparently to bear a portion of the lateral strain on the great teeth. It is noteworthy that these interdental 'rugosæ' are exposed in the palate, whereas in the lower jaw they are covered by a prolongation of the splenials, known as the supradentary plate.

The palate is composed of the following elements:

Premaxillaries, each containing four teeth, between which lie four more or less sharply defined interdental rugosæ.

Maxillaries, unite in a typical manner with the premaxillaries, vomers, palatines, ectopterygoids, and jugals.

Vomers, with anterior diamond-shaped expansion, without median suture, prolonged posteriorly to divide the posterior nares (*p. nar.*) and unite with slender anterior spurs of the pterygoids.

Palatines, bounding the posterior nares laterally, uniting with maxillaries, pterygoids, vomers, and jugals.

Pterygoids, very large and complex, laterally uniting with the ectopterygoids (displaced in

No. 5027), anteriorly with the vomers and palatines, posteriorly with the basisphenoids and with the quadrates by broad pterygo-quadrate sutures.

Ectopterygoids, suturally uniting with pterygoids and loosely united externally with maxillaries and possibly in contact with the jugals. The ectopterygoid of the right side is seen displaced within the upper part of the left antorbital fenestra (Plate I).

Occiput and Brain Case with Temporal Arches Removed, No. 5117.

Text Figs. 7, 8; and Pll. III, IV.

The outer structure of the brain case proper is best shown in the cranium of the relatively young tyrannosaur (No. 5117), collected and presented to the Museum by Charles H. Sternberg. The absence of the temporal arches freely displays the component elements of the cranium and the exits for the various cranial nerves. The homologizing of these elements and identification

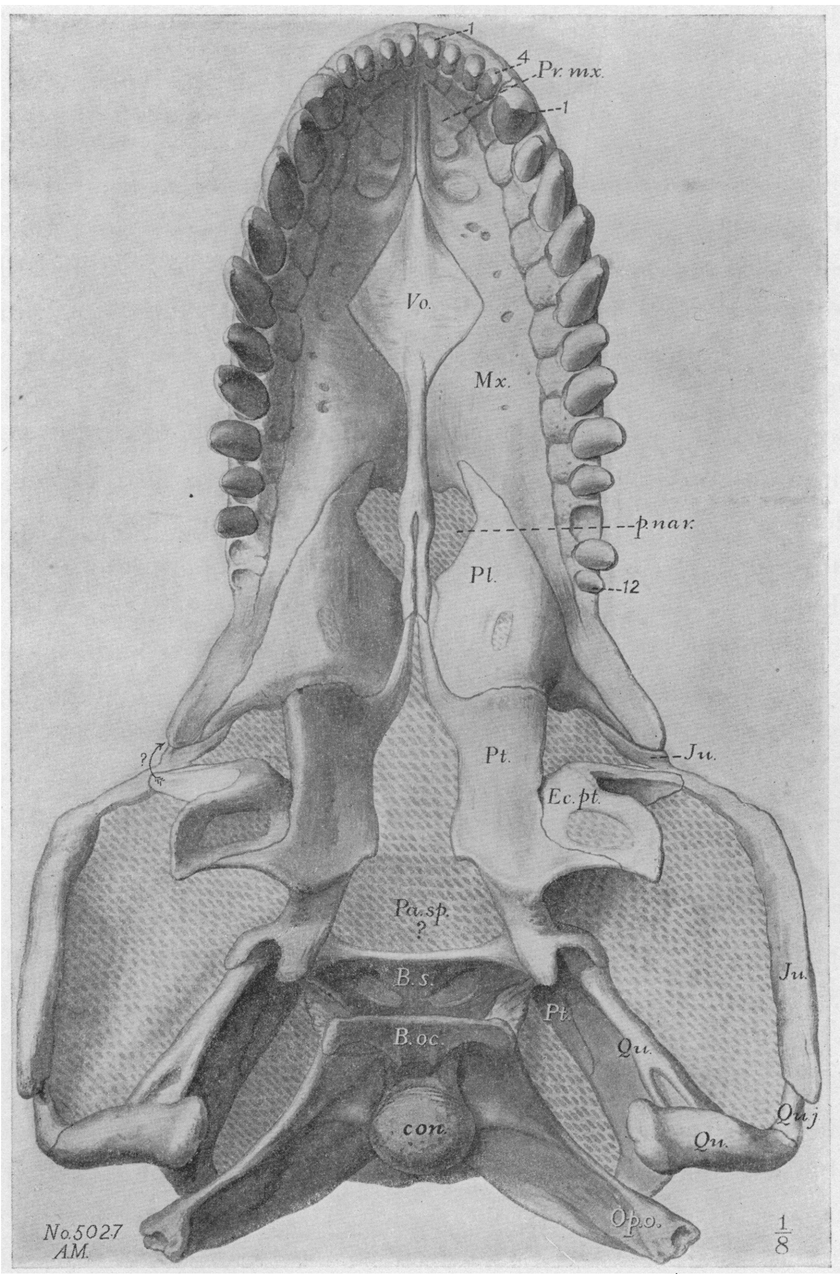

Fig. 6. *Tyrannosaurus rex.* Inferior aspect of the skull, slightly corrected for distortion. Amer. Mus. No. 5027. Scale $\frac{1}{8}$. The ectopterygoids, *Ec. pt.*, have slipped back from the normal connection with the maxillaries.

of the nerve exits has been a very difficult undertaking, for which Mr. Barnum Brown, Dr. W. K. Gregory, and Dr. F. von Huene are chiefly to be credited.

Parietals, with broadly expanding posterior plate, narrow and depressed median crest.

Frontals, abbreviate, suturally separate from parietals and from prefrontals.

Prefrontals (*Pr. f.*) greatly reduced, wedged in between frontals and nasals (*Na.*), only the posterior part of which are shown.

Ethmoid complex uniting suturally above and laterally with prefrontals and frontals, posteriorly with (?) presphenoids (*P. sp.*); in anterior view ethmoid complex (Fig. 7) with a median septum dividing olfactory lobes (Fig. 8).

? *Presphenoids* (*P. sp.*) imperfectly separated from parasphenoids, or parasphenoid region, below; bounded anteriorly by ethmoids, superiorly by frontals, posteriorly by orbitosphenoids (see obscure sutures in Fig. 7).

Parasphenoids (*Pa. sp.*), supporting ethmoid above, coalescing with ?presphenoids posteriorly and descending as a vertical plate (Figs. 7, 8) to bifurcate on the anterior surface of orbitosphenoids and basisphenoids.

Orbitosphenoids (*O. sp.*) (= alisphenoids of authors), very large elements, uniting above with ?presphenoids, frontals, parietals, posteriorly with proötics, exoccipitals, inferiorly overlapping basisphenoids; perforated by the following cranial nerves, ii, iii, iv, v_1, v_2, v_3; anterior border of the orbitosphenoids (compare Pl. III, IV) invaginated by the pituitary fossa (*pit. fos.*).

The relations of the orbitosphenoids of *Tyrannosaurus* (Figs. 7, 8 and Pll. III, IV) are similar to those of *Crocodilus* (Figs. 14, 15) which have been worked out for comparison and drawn under the direction of Dr. W. K. Gregory.

Basisphenoids (*B. sp.*), extending down below the level of the basioccipital (Figs. 7, 8), unlike the condition in the Crocodilia (Figs. 14, 15).

The antero-inferior border is indented by the internal carotid foramen (*Car. in.*).

Proötics, widely exposed, bounding auditory fenestra (*fen. ov.*), superiorly, uniting with orbitosphenoids anteriorly, with parietals superiorly, with opisthotics laterally, with exoccipitals posteriorly (Figs. 7, 8 and Pll. III, IV).

Paroccipitals, or opisthotics (*Op. o.*), perforated by external auditory opening, or *fenestra ovalis.* Near the *fenestra ovalis* is a minute opening for the transmission of the seventh nerve (vii).

Mid-cranial Section, Skull No. 5029.

Pll. III, IV.

Taken with the previous description of the external elements of the cranium, the mid-cranial section of another skull, Amer. Mus. No. 5029, as represented in the beautiful drawings of Mr. Christman in Pll. III, IV, completes the anatomy of the brain case, and presents the brain cavity and exits of the cranial nerves from within.

This specimen displaying the very massive roof of the brain case composed of the supraoccipitals, parietals and frontals, and massive floor of the *medulla oblongata* composed of the orbitosphenoids, basisphenoids and basioccipitals, may be compared with the similar parts in the skull of *Crocodilus* (Figs. 14, 15), from which it appears that the anterior portion of the brain-case is relatively weak and possibly in part membranous, *e. g.*, anterior wall of pituitary fossa (*pit. fos.*).

(Continued on page 20.)

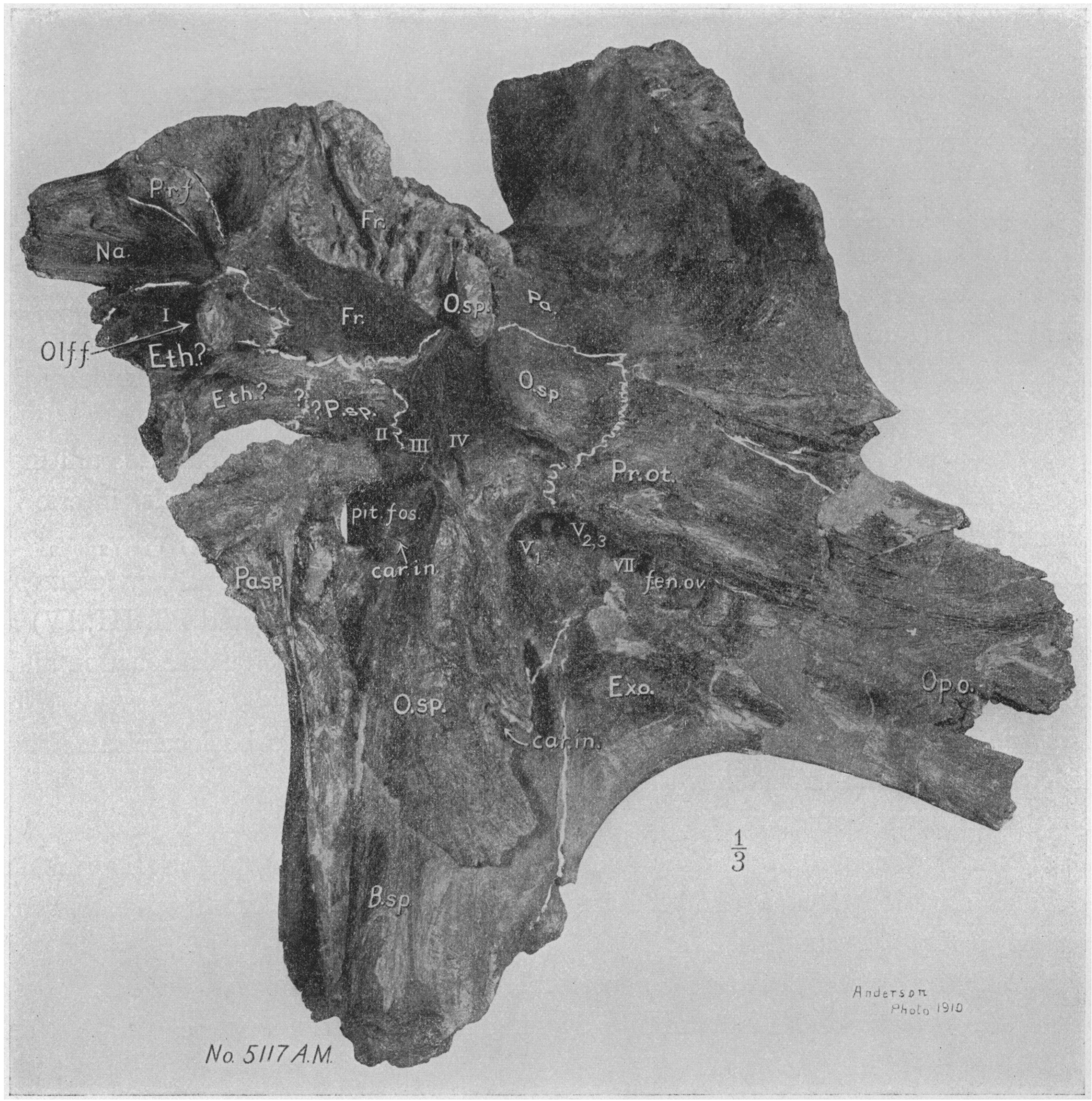

Fig. 7. *Tyrannosaurus rex.* Immature cranium with temporal arches removed, oblique view of left side. Amer. Mus. No. 5117. Scale ⅓.

?*P. sp.*, supposed presphenoid.
Pa. sp., parasphenoid.
?, Marks supposed suture between ethmoid and presphenoid.
Pr. f., prefrontal of authors (lachrymal of Gaupp).
Pa. sp., parasphenoid.
O. sp., orbitosphenoid (Gaupp), "alisphenoid" of authors.
car. in., lower and upper entrance for internal carotid.
fen. ov., fenestra ovalis (for stapes).
i–vii, exits of cranial nerves i–vii.

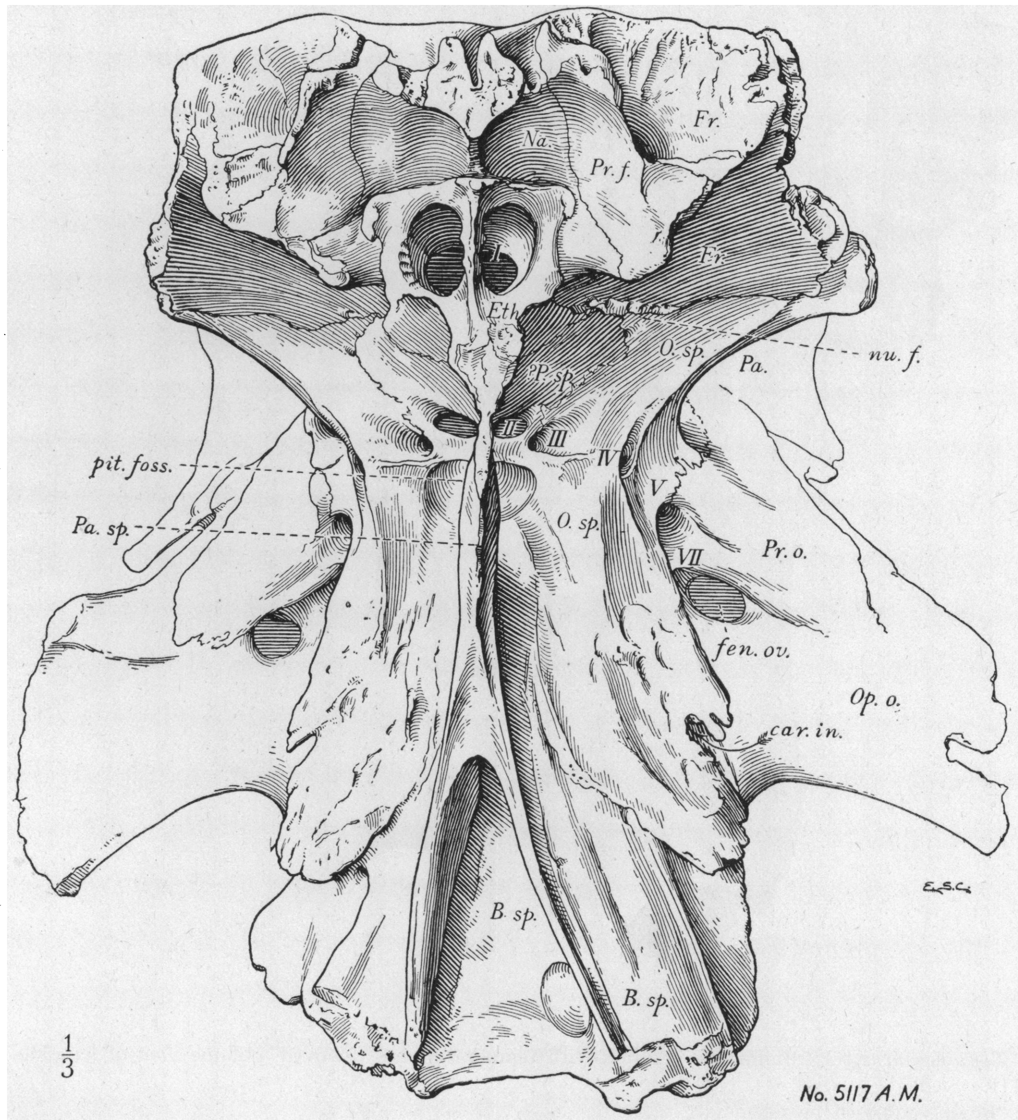

Fig. 8. *Tyrannosaurus rex*. Immature cranium, same as in Fig. 7, full front view. Amer. Mus. No. 5117. Scale ⅓.

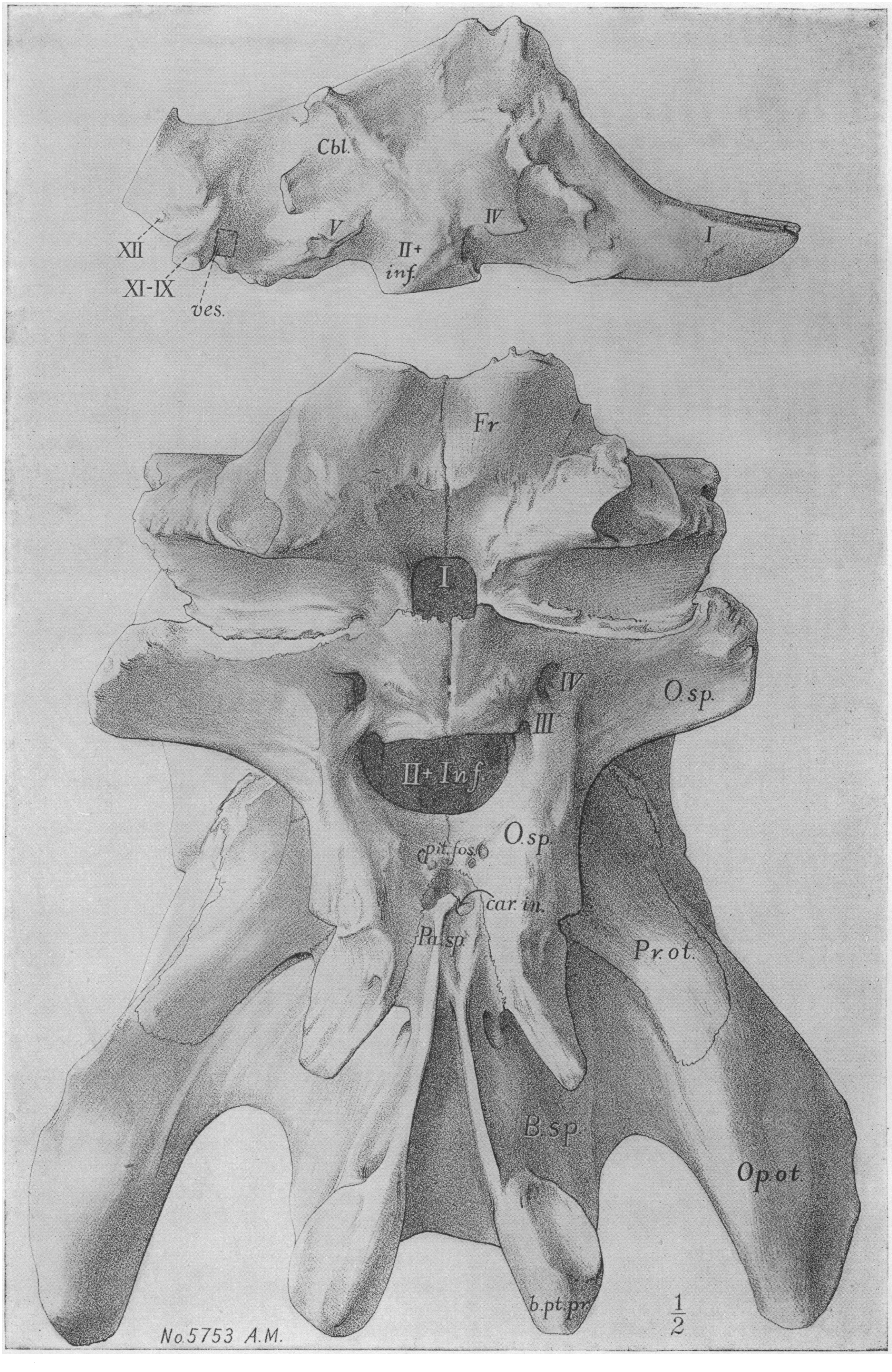

Fig. 9. *Allosaurus agilis.* Dura mater cast (right side) and cranium viewed from in front and below. Amer. Mus. No. 5753. Scale ½.

car in., point where the carotid canal opens into the pituitary fossa.
ves., region of vestibulum.

PLATES III AND IV.

Tyrannosaurus skull, brain cavity.

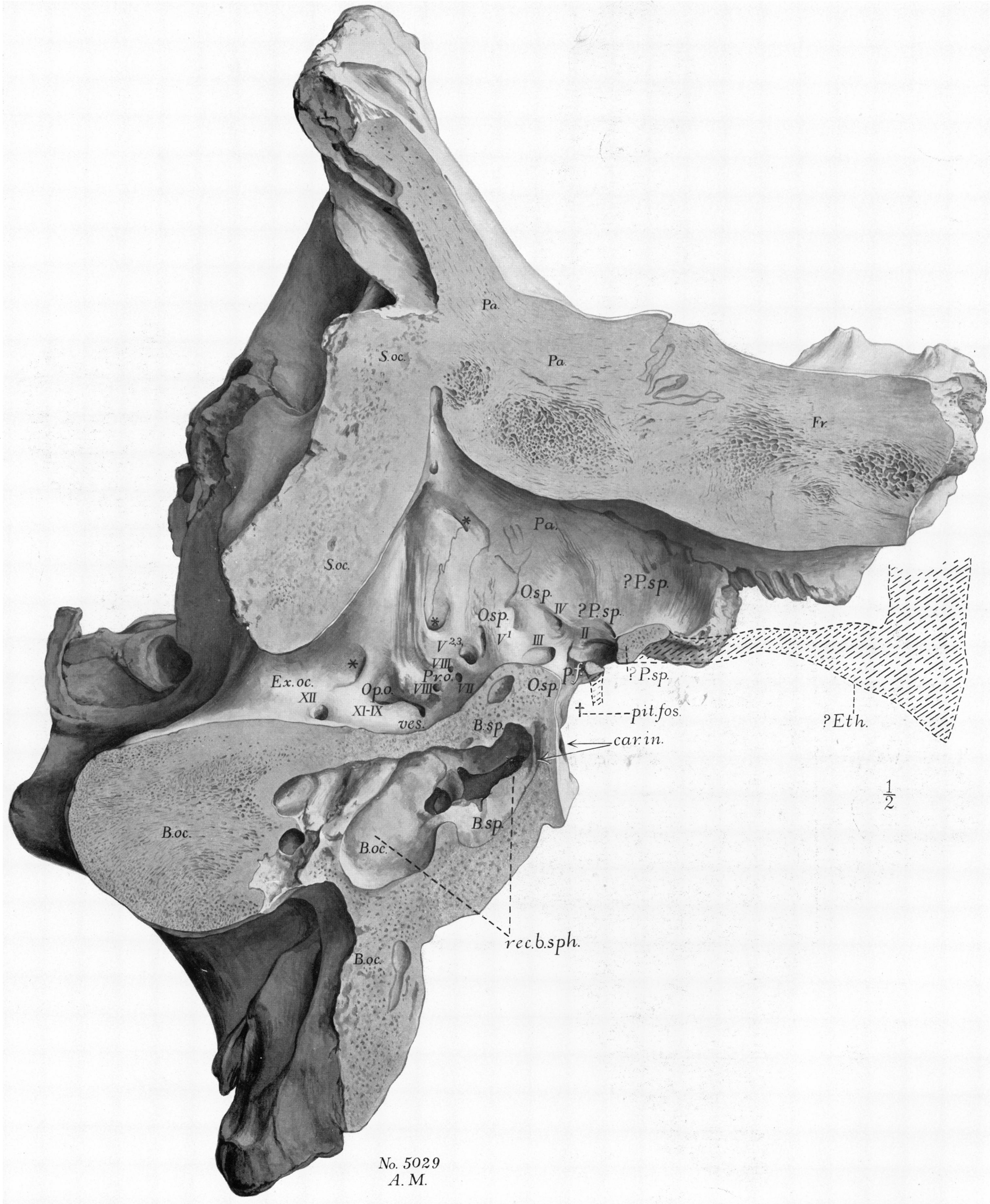

Plate III. *Tyrannosaurus rex.* Section of skull showing brain cavity. Amer. Mus. No. 5029. Scale ½.

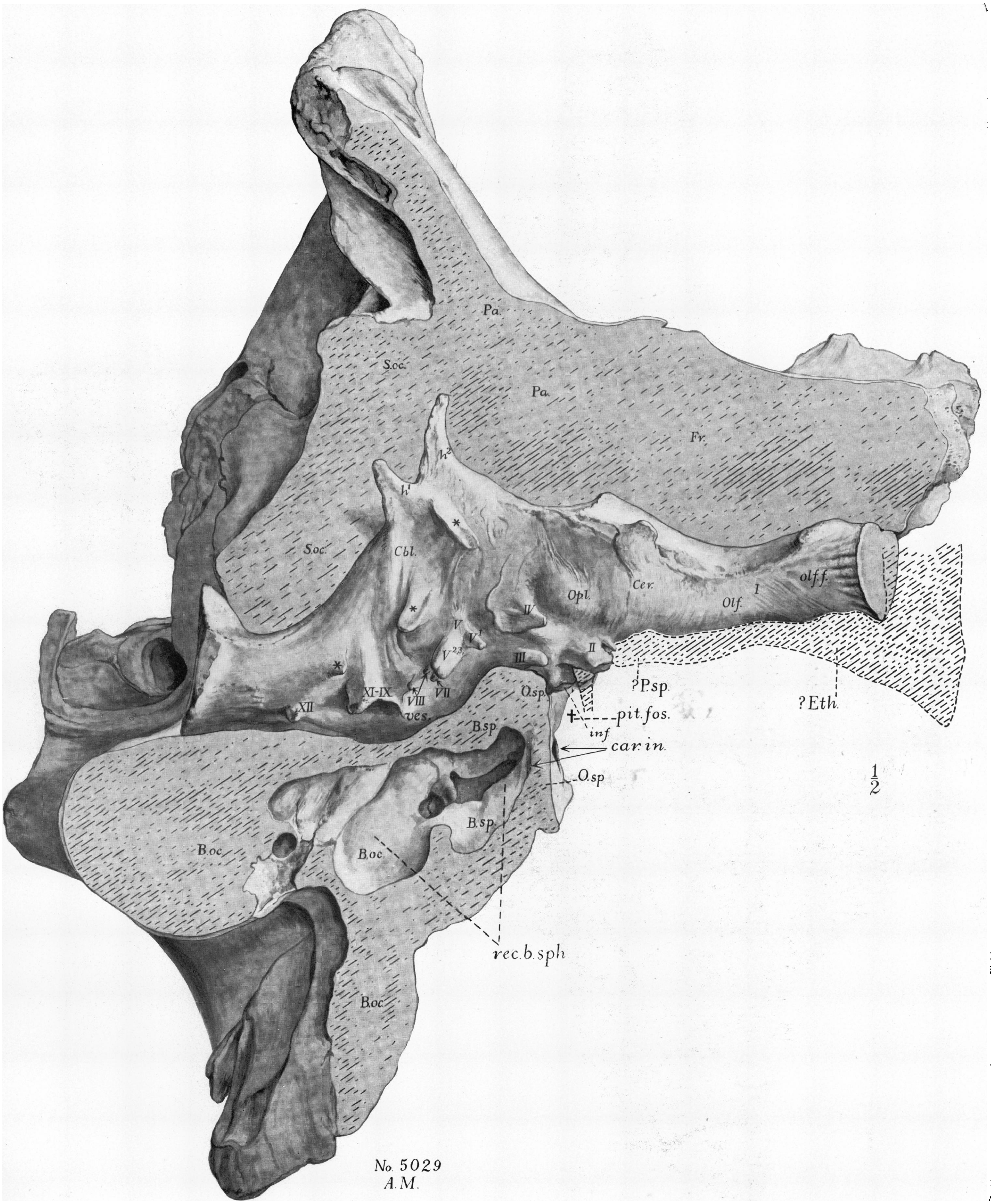

Plate IV. *Tyrannosaurus rex.* Section of skull showing cast of brain in situ. Amer. Mus. No. 5029. Scale ½.

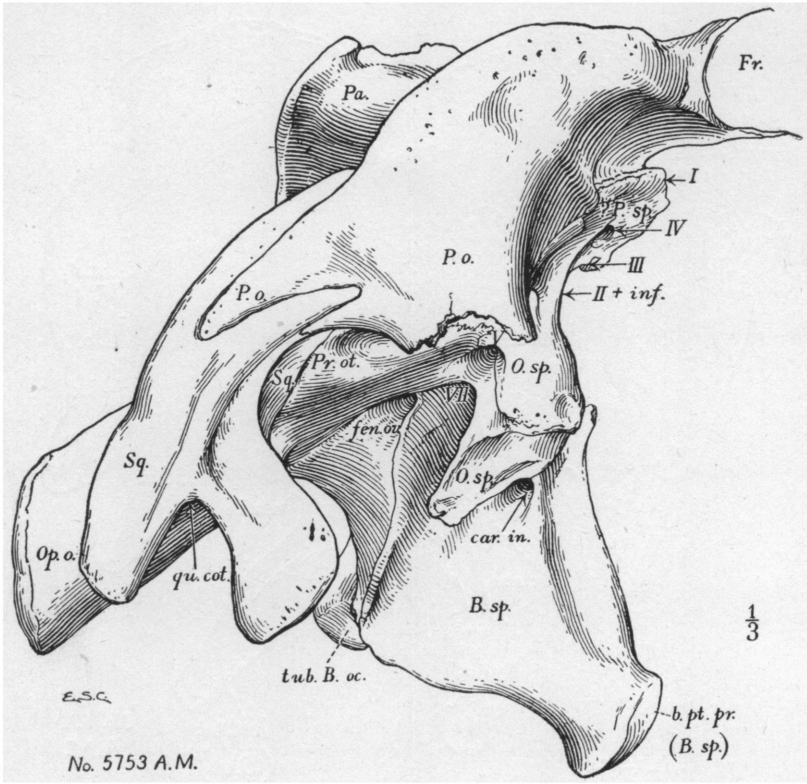

Fig. 10. *Allosaurus agilis*. Amer. Mus. No. 5753. Scale $\frac{1}{3}$. Oblique side view of brain case partly concealed by the postorbital (*P. o.*) and squamosal (*Sq.*), showing relations of nerve foramina I–VII.
qu. cot., articular socket for quadrate; *tub. B. oc.*, tuber basioccipitale.

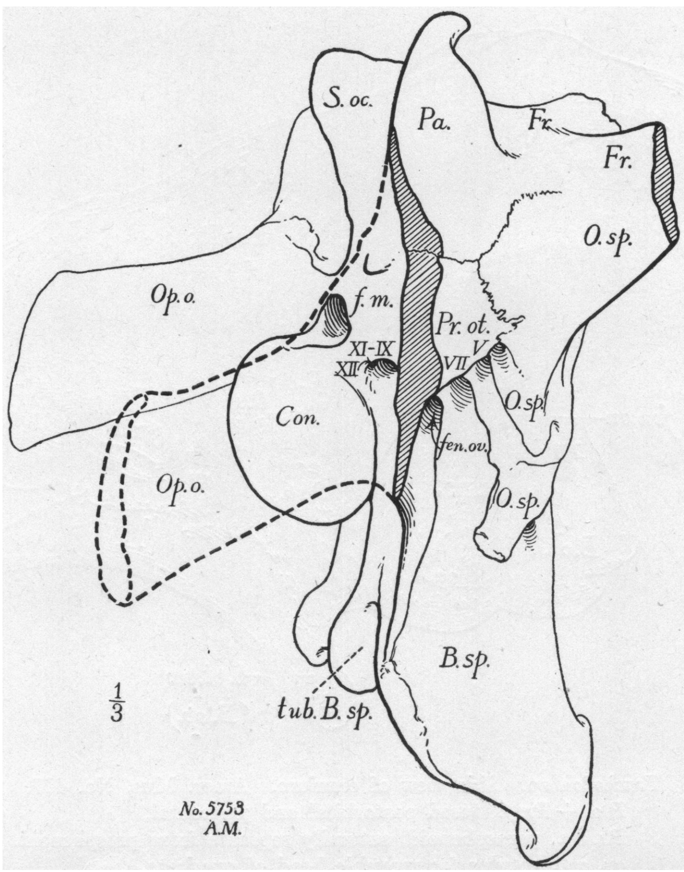

Fig. 11. *Allosaurus agilis* (same specimen as in Fig. 10). Amer. Mus. No. 5753. Viewed more from the rear, oblique; the postorbital and squamosal removed; left opisthotic (dotted lines) represented as transparent in order to show foramina V–XII.

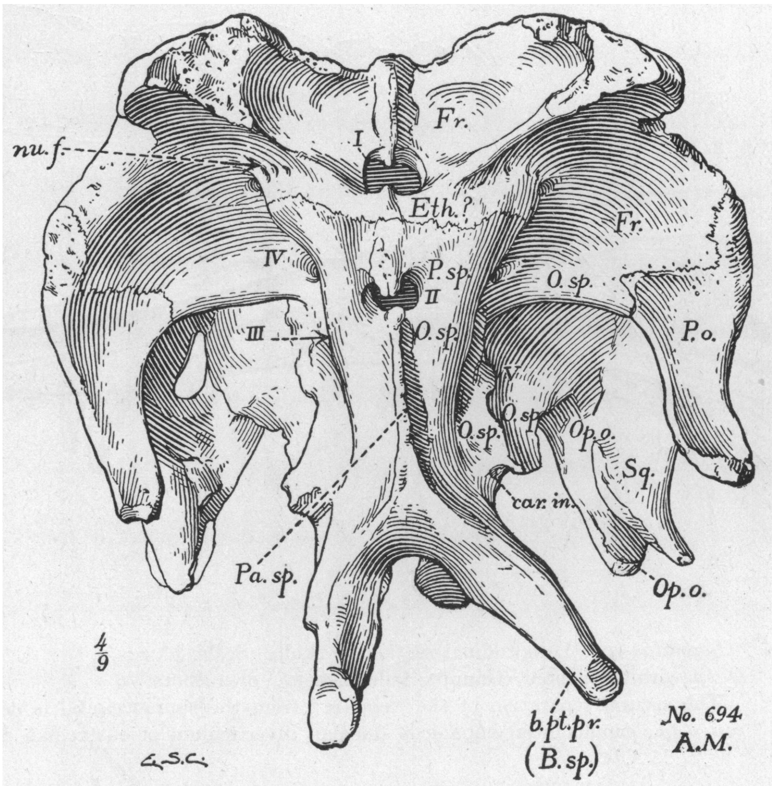

Fig. 12. *Diplodocus longus*. Cranium, full front view. Amer. Mus. No. 694. Scale 4/9.
b. pt. pr., "basipterygoid" process of basisphenoid.
nu. f., nutrient foramina.
P. o., postorbital.

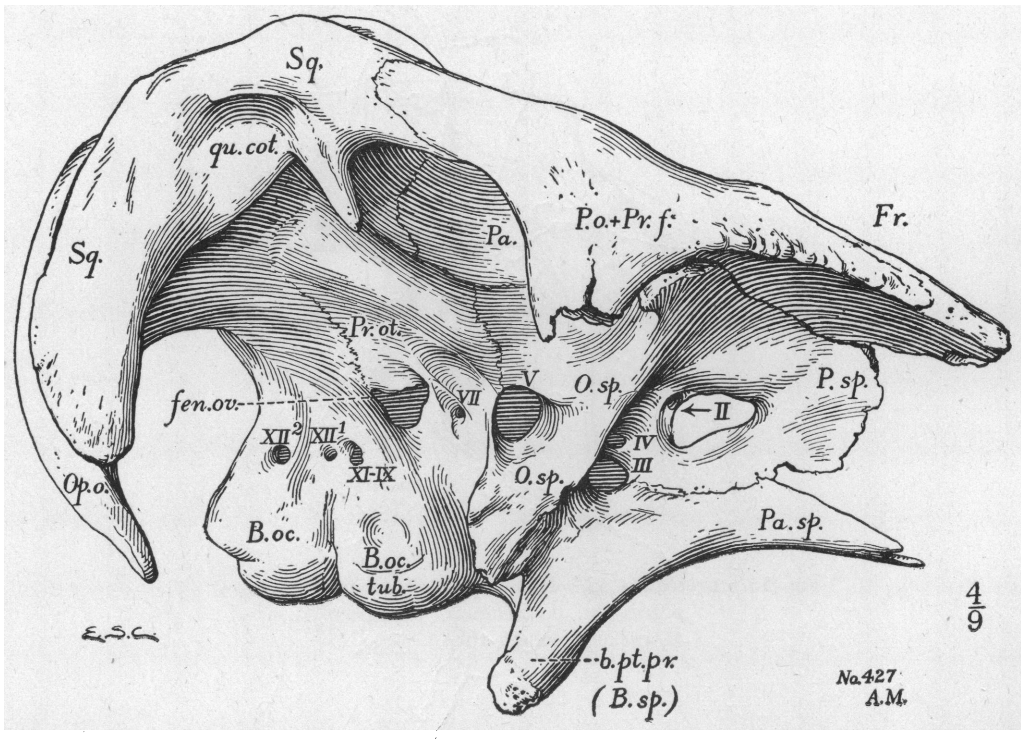

Fig. 13. *Trachodon* sp. Side view of cranium. Amer. Mus. No. 427. Scale 4/9.
P o. + Pr. f., fused postorbital and prefrontal.
Pa. sp., parasphenoid, suturally separate from presphenoid.
qu. cot., cotylus for movable head of quadrate.
i–xii, nerve foramina.

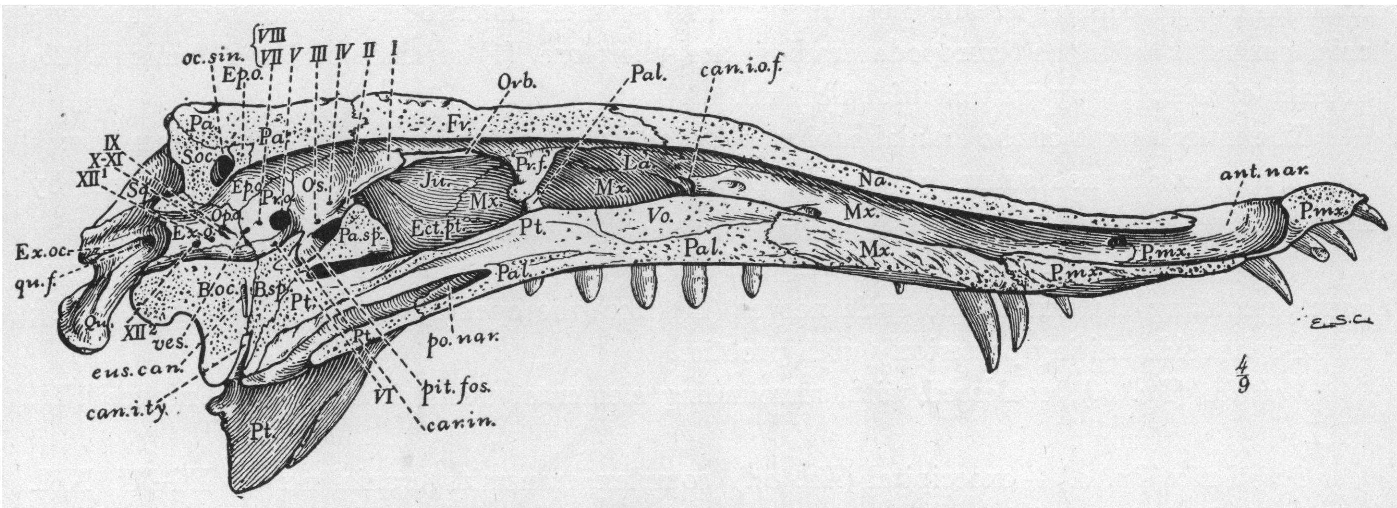

Fig. 14. *Crocodilus* sp. Longitudinal section of skull. Scale 4/9.
O. sp., orbitosphenoid (Gaupp), "alisphenoid" of authors.
The sutural separation of the "epiotic" from the supraoccipital is doubtful.
can. i. ty., canalis intertympanicus (median diverticulum of eustachian canal).

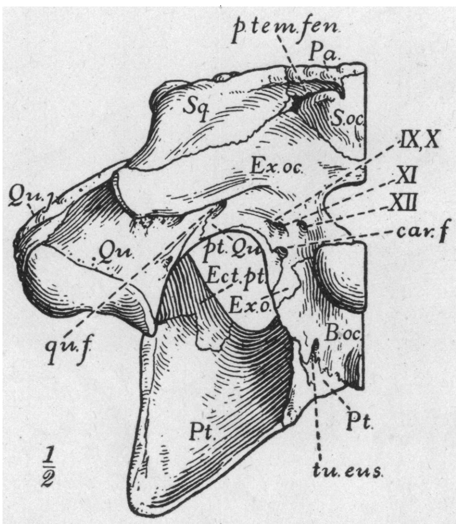

Fig. 15. *Crocodilus* sp. Half section of occiput. Scale ½.
p. tem. fen., posttemporal fenestra.
tu. eus., eustachian tube.

The latter contrasts with the solid boundaries of the pituitary fossa in the cranium of Sauropoda (Fig. 16, *Diplodocus*). The large (?)pineal fenestra (*f. pin.*) in the roof of the *Diplodocus* cranium has no counterpart in the massive parieto-frontal union of *Tyrannosaurus*. The two chief contrasts with the Sauropoda cranium are, therefore, (1) absence of pineal fenestra, (2) absence of heavy bony wall of infundibulum.

The inner aspect of the cranial cavity of *Tyrannosaurus* displays the following elements:

?*Presphenoids* not suturally distinct posteriorly from orbito-sphenoids. Perforated by nerve II.

Orbitosphenoids perforated by openings of III, IV, V^1, V^2, V^3; inferiorly there is a bridge of bone separating the exit of the optic nerves (II) from the opening of the infundibulum (*p. f.*); orbito-sphenoids uniting posteriorly with proötics.

Proötics (*Pr. o.*), coalesced with surrounding elements, transmitting cranial nerves VII, VIII.

Opisthotic (*Op. o.*) + exoccipital (*Ex. oc.*) complex, transmits cranial nerves IX–XI, XII.

Basisphenoid containing a large cavity or *recessus basisphenoideus*; at first mistakenly regarded as lodging the pituitary body. No opening is found for the abducens nerve (VI), which probably pierced the floor of the basisphenoid near the midline, as in *Crocodilus*.

Brain Cavity, Skull No. 5029.

Pll. III, IV.

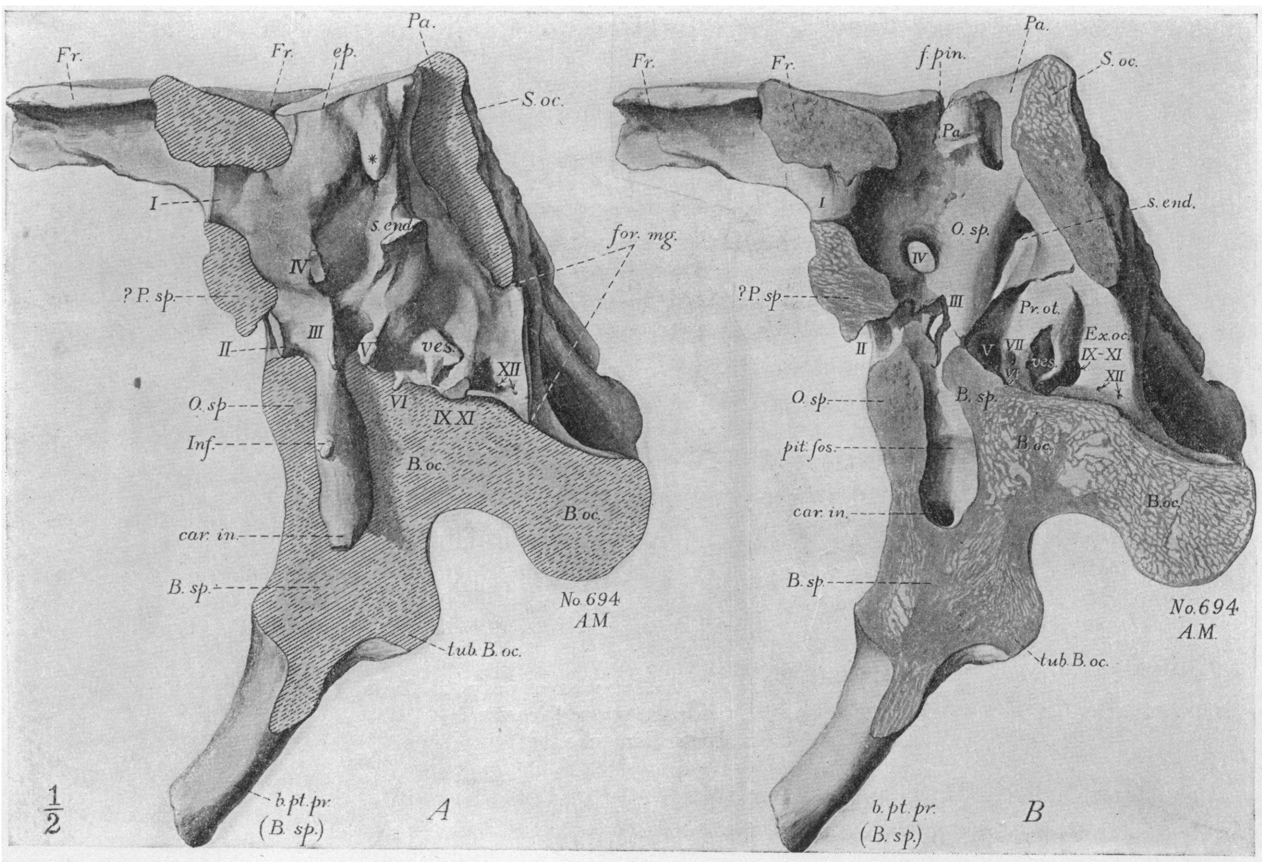

Fig. 16. *Diplodocus longus* Marsh. Amer. Mus. No. 694. Scale ½.
A, sagittal section with "brain cast" in place.
B, " " " " " removed.
S. end., saccus endolymphaticus.
ves., region of vestibulum (recessus vestibuli).

Comparison of the intracranial cavity of *Tyrannosaurus* with the mid-section of the skull of *Sphenodon* and brain *in situ* as figured by Dendy[1] (1910, pl. xix, fig. 1), shows that the intracranial cavity in *Tyrannosaurus* corresponds with the outer surface and foldings of the *dura mater* and is thus merely a cast of the outer envelope of the brain, which gives us little idea either of the form or the size of the brain itself. The reasonable inference is that the intracranial cast of *Tyrannosaurus* greatly exceeds and possibly doubles in cubic capacity the actual brain which was formerly contained within it.

In *Sphenodon* the cubic capacity of the *dura mater* envelope appears to be double that of the brain itself. Thus the cast of *Tyrannosaurus* (Fig. 17; Pl. III) gives us a means of measuring the size of the *dura mater* envelope. It displaces 530 cubic centimeters of water. If the brain proper bore the same proportion to the *dura mater* envelope as that of *Sphenodon*, the bulk of the brain of *Tyrannosaurus* may be estimated at 250 cubic centimeters. The brain proper was extremely small in comparison with the enormous size of the body.

Dendy observes (*op. cit.*, pp. 236): "Hence it comes about that the brain occupies not nearly the whole of the cranial cavity, being suspended in it by innumerable thin strands of connective tissue which extends radially across the sub-dural space and connect the *dura mater* with the *pia*, which latter closely invests the brain. . . . I may be allowed to lay stress on the extraordinary disparity between the size of the brain and that of the cranial cavity. It follows that the shape of the latter can afford no reliable indication of that of the former. The same is probably true of many fossil reptiles, so that the greatest caution should be exercised in drawing conclusions from the study of casts of the cranial cavity."

Dura mater cast. The protrusions (h^1, h^2, *, *, *), observed in the superior (Fig. 17) and lateral views (Pl. III) of the *dura mater* cast extend into corresponding invaginations of the intracranial surface (Pl. IV).

The *dura mater* cast enables us, however, to distinguish the actual exits of cranial nerves I, II, III, IV, V, VII, VIII, IX–XI, XII, which have been traced by Mr. Brown into openings which (with the exception of VIII) lead through to the outer surface of the cranium, as displayed in Figs. 7, 8. As above noted, VI has not been observed.

The cast indicates that the brain within was long and narrow. Successive swellings which are observed in the superior (Fig. 17) and lateral (Pl. III) views indicate the location of the olfactory

(*Continued on page 24.*)

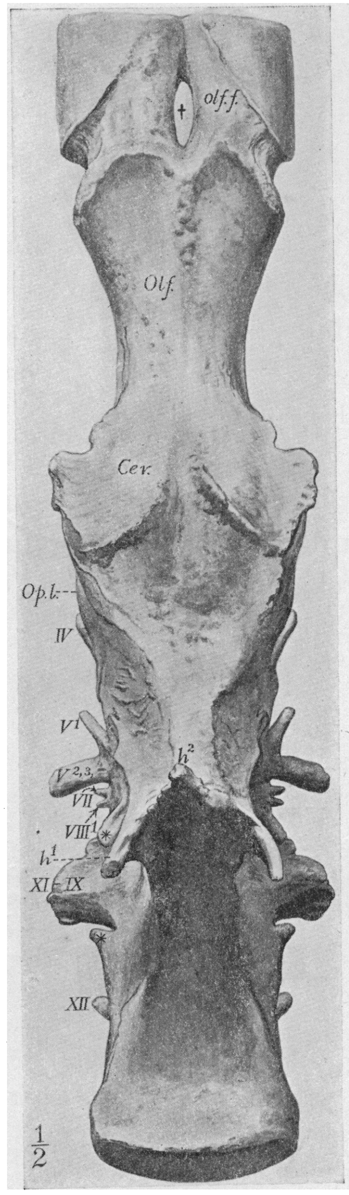

Fig. 17. *Tyrannosaurus rex.* Superior aspect of brain cast, from skull no. 5029 Amer. Mus. (cf. Pl. III). Scale ½.
h^1, h^2., membranous prolongations of dura mater.
*, marks the position of the saccus vasculosus.
†, marks the position of the ethmoid septum.
Olf., olfactory peduncles.
Op. l., optic lobes.
V^1, Ramus ophthalmicus trigemini.
$V^{2,3}$, Rami maxillaris et mandibularis trigemini.

[1] Dendy, Arthur. 'On the Structure, Development and Morphological Interpretation of the Pineal Organs and Adjacent Parts of the Brain in the Tuatara (Sphenodon Punctatus).' Philos. Trans. Roy. Soc. London, Ser. B, Vol. 201, 1911, pp. 227–331.

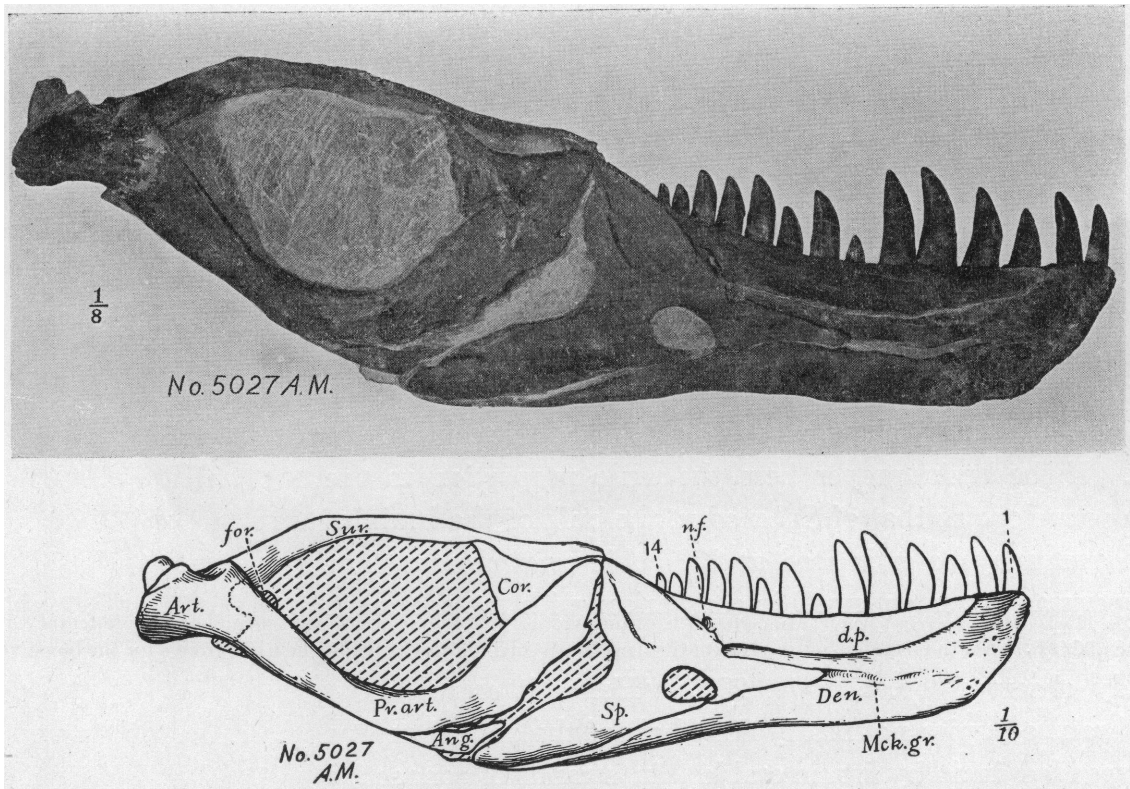

Fig. 18. *Tyrannosaurus rex.* Inner view of left lower jaw, with the splenial and supradentary (*d. p.*) plate present. Amer. Mus. No. 5027.

for., foramen in surangular.
n. f., nutrient foramen.
Mck. g., groove for Meckelian cartilage.
d. p., supradentary plate (may be an outgrowth of the splenial).

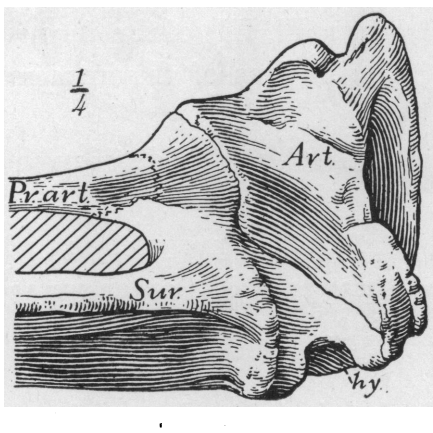

Fig. 19. *Tyrannosaurus rex.* Superior view of articular region of lower jaw. Amer. Mus. No. 5027.
hy., groove for hyoid bone.

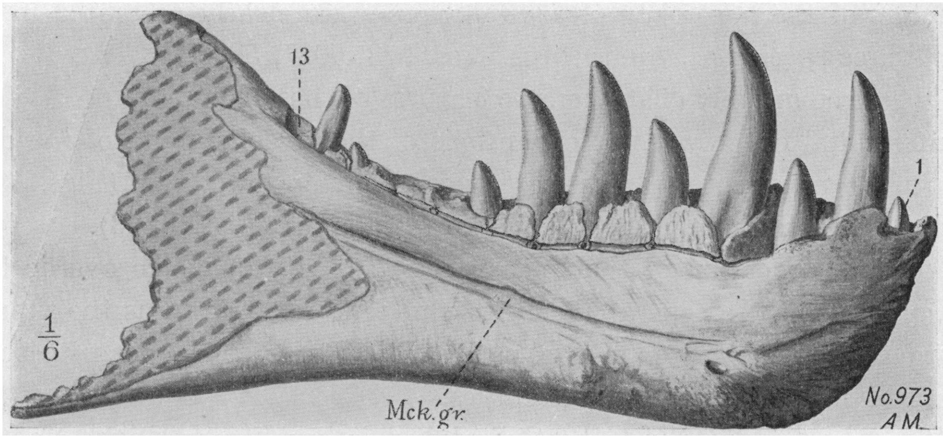

Fig. 20. *Tyrannosaurus rex*. Amer. Mus. No. 973. Inner view of left dentary, with the splenial and supradentary absent. The small rugose plates between the teeth are outgrowths of the dentary alveolar borders. Below them is a groove for the blood vessel supplying the roots of the teeth (see Fig. 13).

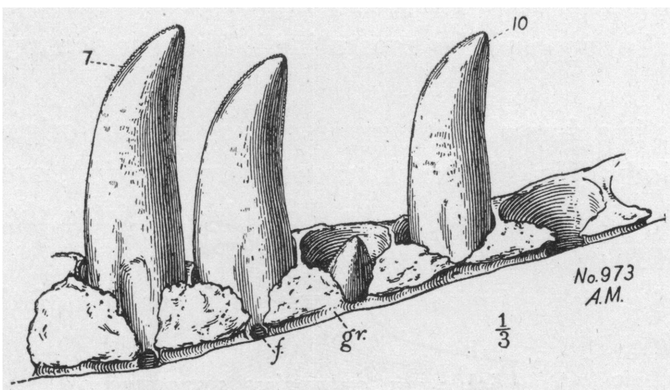

Fig. 21. *Tyrannosaurus rex*. Inner view of dentary between exposed alveoli of 7th to 10th teeth. Amer. Mus. No. 973. Relations of the nutrient groove (*gr.*) and foramina (*f*) to the interdental plates (rugosæ) and teeth.

nerves, separated by the ethmoidal septum (†), of the olfactory lobes (*Olf.*), of the cerebral hemispheres (*cer.*), of the optic lobes (*Opt.*), of the cerebellum (*cbl.*) and of the medulla oblongata.

Lower Jaws.

Text Figs. 18, 19, 20, 21.

The characters of the lower jaw of *Tyrannosaurus* are clearly presented in the inner and outer aspects of three specimens, Amer. Mus. Nos. 973, 5027, 5866.

There are three remarkably characteristic features of these jaws.

1. The interdental outgrowths or expansions of the alveolar septa of the dentary constitute a row of rugose interdental plates or "rugosæ" in the lower jaw (Figs. 18, 20, 21) corresponding with the interdental "rugosæ" of the maxillaries (Figs. 6, 23).

2. The broad prolongation of the splenials (Fig. 18, *d. p.*) which overlie the interdental rugosæ. This appears to be a separate element which may be known as the supradentary.

3. Forward and downward extension of the articular, which appears to correspond with the prearticulars of Mosasaurs and other reptiles.

Dentary. The dentary proper is best displayed in jaw Amer. Mus. No. 973 (Fig. 20); this contains alveoli for thirteen mandibular teeth. In Amer. Mus. No. 5027 there are fourteen teeth.

Between the alveoli (Fig. 21) are thin alveolar septa which expand internally into the interdental "rugosæ." Along the base of these rugosæ runs a longitudinal groove (*gr.*) for the dental artery which gives off side branches (*f.*) to the lower portion of the teeth; between the thirteen teeth may be reckoned twelve more or less prominent interdental "rugosæ."

The middle portion of the ramus is traversed by the horizontal Meckelian groove (*Mk. gr.*). The union with the opposite jaw was merely membranous, there being no indication of symphysial borders. The relations of the dentary, partly obscured by the overlying splenial and supradentary, is shown in Fig. 18. The bone termed presplenial by Lambe in *Albertosaurus* is a part of the dentary, the supposed line separating it from the dentary below being the Meckelian groove (Gregory).

Supradentary. This is a dermal plate apparently of splenial origin but suturally separated from the splenial posteriorly (Fig. 18) which extends forward (*dp.*), overlapping the basis of the teeth and dermal complex of the dentary. As shown by Williston the 'presplenial' is the true splenial; the 'splenial' of Baur is the true angular.[1]

Angular (Figs. 1, 18), with a limited exposure on inner side of the jaw and an extensive exposure on the outer side.

Surangular (Figs. 1, 18, 19), with very extensive exposure on the outer side, forming the entire upper border of the inner side of the jaw above the pterygoid fossa; perforated by a fenestra (*, Fig. 1) or foramen (*for.*, Fig. 18).

Coronoid (Fig. 18), small, triangular, restricted to anterior border of pterygoid fossa.

Articular (Figs. 1, 18, 19), forming the posterior portion of the ramus and broadly uniting on the upper surface (Fig. 19) with the surangulars and supposed prearticulars. Relations to the quadrate are shown in Figs. 4, 1. The broad groove on the outer side of the articulars (Fig. 19 *hy*) possibly served for the passage of the *hyoid cartilage* which in *Sphenodon* passes around the outer border of the articular, thence passing upward and inward (Gregory.)

[1] Williston, S. W. 'Some Osteological Terms.' Science, N. S., Vol. XVIII, No. 469, Dec. 25, 1903, pp. 829–830. For a full discussion of this subject, see Gaupp, 1911.

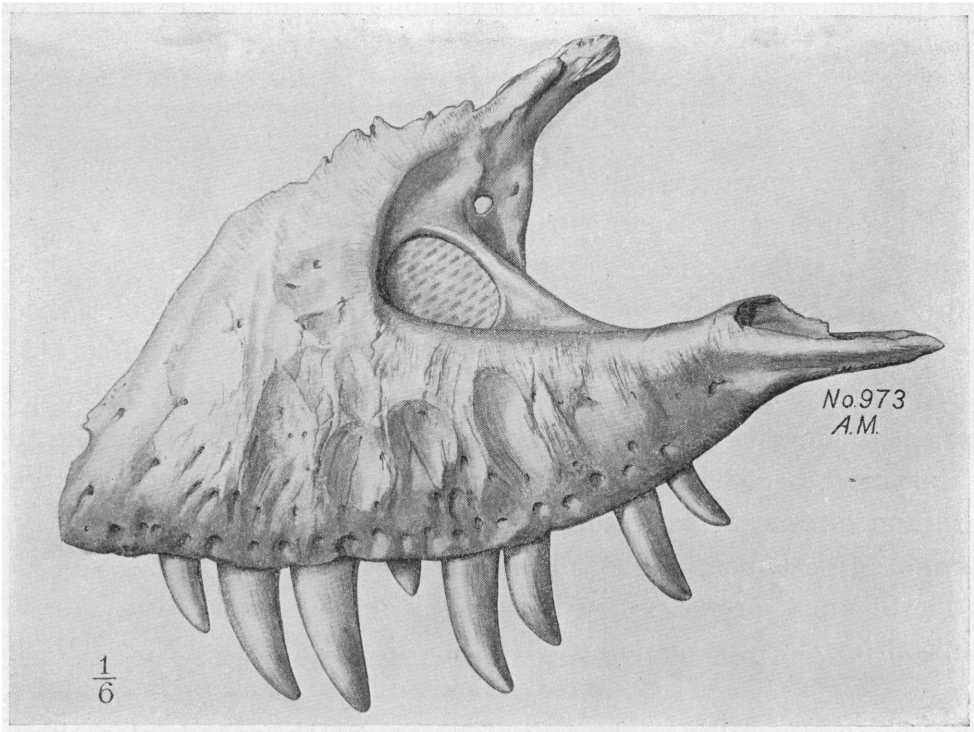

Fig. 22. *Tyrannosaurus rex.* Left maxilla, outer view. Amer. Mus. No. 973. (Type.) Scale $\frac{1}{6}$.

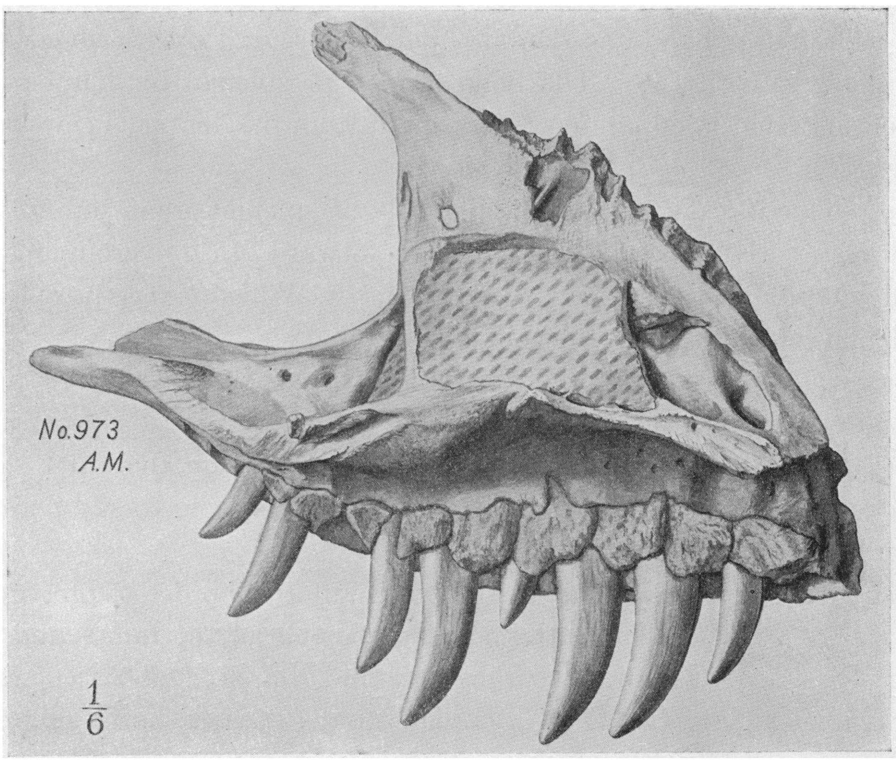

Fig. 23. *Tyrannosaurus rex.* Left maxilla, inner view of the same specimen, Amer. Mus. No. 973. Exhibiting eight of the maxillary teeth, four vacant alveoli, and nine interdental plates of the maxilla.

TEETH OF *Tyrannosaurus*.

Text Figs. 1, 3, 18, 20–24 and Pl. I.

The maxillary teeth are completely preserved in skull No. 5027 (Pl. I) and in the maxillary fragment No. 973 (Figs. 22, 23). The mandibular teeth are shown in Nos. 5027, 973, and 5866.

The dental formulæ are as follows:

UPPER JAW: { Premaxillary teeth, 4; Maxillary " 12 } total 16.

LOWER JAW: Inferior maxillary teeth, 13 to 14.

All the teeth in the upper jaw display the serrate edges characteristic of the Sauropoda, but the proportions of the crowns and of the external and internal or buccal and lingual surfaces, as defined by the positions of the serrate edges, are widely modified as we pass backwards from the extreme anterior to the extreme posterior members of the series.

Superior Teeth.

The four *premaxillary* teeth present a strong anterior convexity and lateral compression, the serrate edges being confined to the posterior lateral or lingual surfaces which are slightly convex. This type of tooth is adapted (Pl. I) for a tearing action.

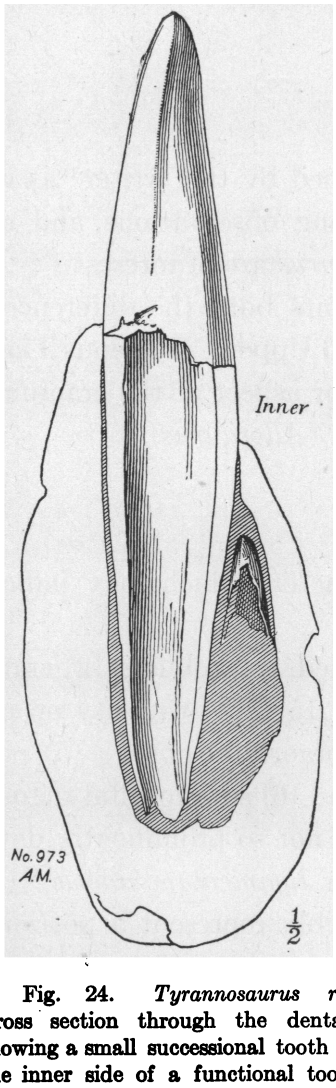

Fig. 24. *Tyrannosaurus rex.* Cross section through the dentary showing a small successional tooth on the inner side of a functional tooth. Amer. Mus. No. 973. Scale ½.

The twelve *maxillary* teeth mark the graduated transition from the laterally compressed form with the serrate margins somewhat obliquely placed (Pl. I) to oval, lance-shape form, in which the teeth are laterally compressed and the serrated edges form the anterior and posterior borders of the crown. As the sections of the teeth change, the outer or buccal surface becomes reduced, the inner, or lingual surface is expanded until finally on the eighth maxillary tooth (Pl. I) the outer and inner surfaces of the crown are subequal. The first maxillary tooth is sharply demarcated from the lateral premaxillary tooth by its much greater size. The apparent irregularities of size in the adjoining teeth of the maxillary series are due to the different degrees of the extrusion of the teeth. There is also (Pl. I) a gradual decrease in size from the first to the tenth maxillary tooth. The eleventh and twelfth maxillary teeth, however, are both of relatively diminutive size; the twelfth tooth is especially small.

Mandibular Teeth.

The mandibular teeth vary numerically in two specimens from fourteen teeth in each side (No. 5027) to thirteen teeth on each side (No. 973). It is not known whether this is a matter of individual variation or of specific difference. As in the maxillary teeth, the outer surfaces are generally more convex than the inner surfaces. The crowns are gently concave on the inner surface near the base

(Fig. 21), which is perforated for a branch of the dental artery (*f.*). The successional teeth (Fig. 24) arise on the inner side. There are always a double pair of small posterior teeth on each side which correspond with the single diminished teeth in the upper series.

The four anterior teeth of the mandibular series do not correspond in form and proportions with the four compressed premaxillary teeth in the upper series; only two, namely, the first and second mandibular teeth, are laterally compressed with deep sections and serrated edges on the posterior or lingual borders.

Of these two the second mandibular tooth is intermediate in form while the third is more like the teeth which follow.

The third to the thirteenth or fourteenth mandibular teeth are of sub-oval transverse section; the anterior and posterior serrated edges are placed somewhat obliquely in the third to the fifth mandibular teeth; in the sixth to the thirteenth the serrated edges are placed directly on the anterior and posterior borders of the tooth so as to be observable in the lateral or outer view of the jaw (Fig. 18).

There seems to be considerable variation in different individuals in the size of the mandibular teeth. In No. 973 the first mandibular tooth is much smaller than the second; in No. 5027 the first tooth while inferior in size to the second is a relatively larger tooth than the first, No. 973.

Comparison with Skull of *Allosaurus*.

Text Figs. 9–11, 26, 27.

In addition to the descriptions of the skull of *Allosaurus* published by the writer[1] as well as to the description by Hay of the skull of *Creosaurus*,[2] the following observations and new characters brought out in the comparison with the skull of *Tyrannosaurus* are of interest.

Comparison of Figs. 25, 26, 27 all reproduced to $\frac{1}{8}$ scale, exhibits both the difference in size and in proportion of the Upper Jurassic (or Lower Cretaceous) and Upper Cretaceous Theropoda. The substantial resemblance in the morphology of the anterior aspect of the cranium is shown in the comparison of Figs. 7, 8 (*Tyrannosaurus*), and Figs. 9–11 (*Allosaurus*).

1. *Skull of Allosaurus.*

Allosaurus surely has a more primitive skull, with some characters which may indicate that it is not in the direct line of ancestry of *Tyrannosaurus*.

Primitive characters of *Allosaurus*: (1) *Allosaurus* is slender-skulled, less robust; (2) cranial region longer and lower; (3) larger number of maxillary teeth (*circa* 15); (4) rugosity on posterior border of lachrymal separated from postorbital by a deep supraorbital notch; (5) postfrontals loosely articulated, forming upper border of supraorbital notch; (6) supraorbital rugosity not developed; (7) nasal rugosity not pronounced; (8) parietal crest not so prominently developed; (9) supraoccipitals narrow, rectangular, bearing large keel for *ligamentum nuchæ*; (10) above the occipitals a pair of pits lodging rounded prominences possibly represent a portion of the periotic mass; (11) quadrates movably articulated with squamosals; (12) postorbitals without an infraorbital process leaving a very large, widely open orbital fenestra; (13) exoccipi-

[1] Osborn, H. F. 'The Skull of Creosaurus.' Bull. Amer. Mus. Nat. Hist., Vol. XIX, Art. XXXI, Dec. 24, 1903, pp. 697–701.
[2] Hay, O. P., *op. cit.*, 1909.

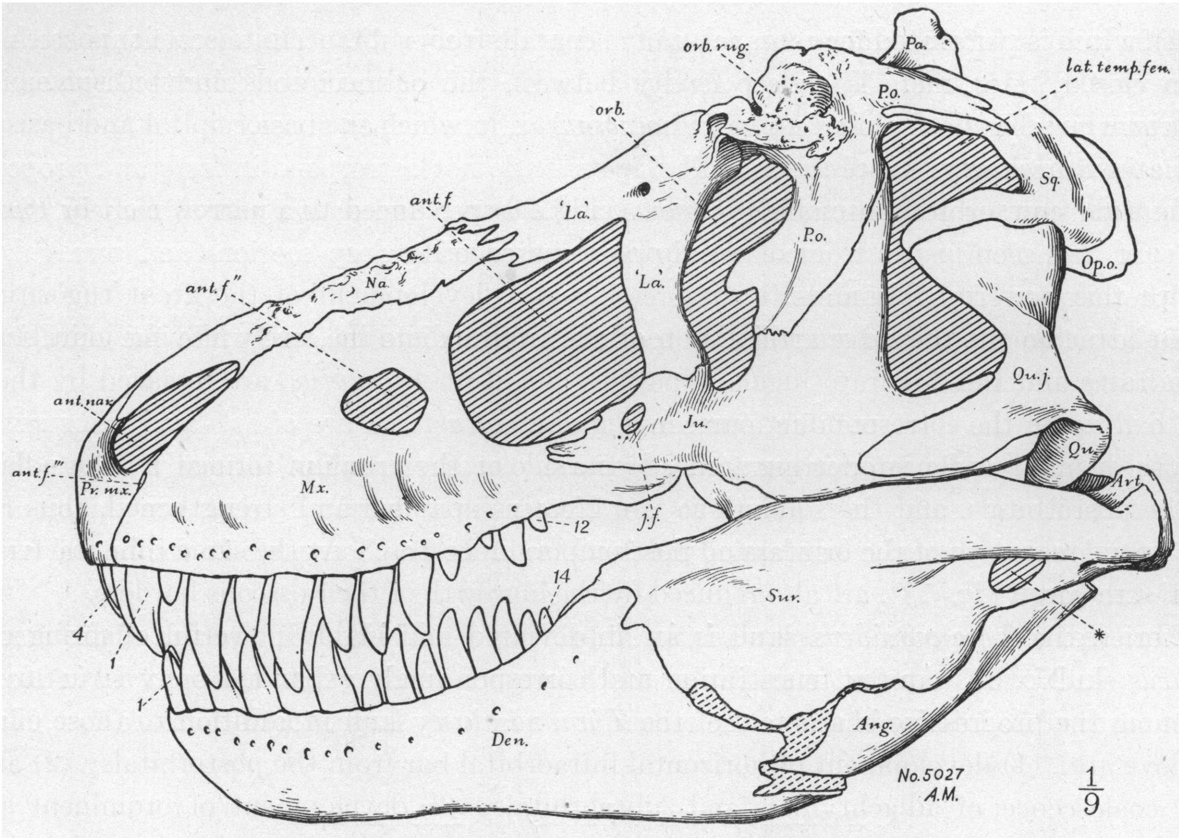

Fig. 25. *Tyrannosaurus rex.* Lateral view of cranium and lower jaw.

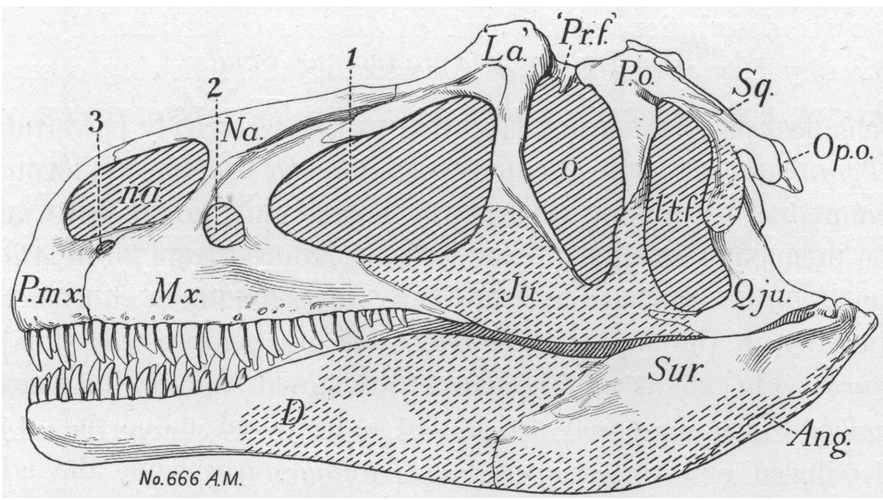

Fig. 26. *Allosaurus agilis* Marsh. Lateral view of cranium and lower jaw. Amer. Mus. No. 666. Scale $\frac{1}{9}$.
1, 2, 3, antorbital fenestræ.
La., lachrymal (adlachrymal) rugosity.
Pr. f., prefrontals (separate, movable).

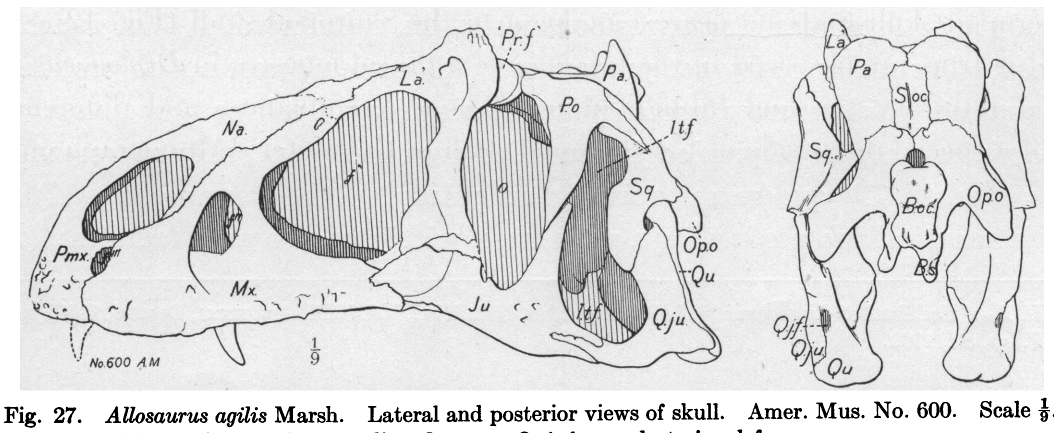

Fig. 27. *Allosaurus agilis* Marsh. Lateral and posterior views of skull. Amer. Mus. No. 600. Scale $\frac{1}{9}$.
Abbreviations as in preceding figures. *Q. j. f.*, quadrato-jugal foramen.

tals closing in over foramen magnum, suturally separate from supraoccipitals; (14) posttemporal fenestra closed; (15) there is a deep cavity between the basioccipitals and basisphenoids in *Allosaurus* which has been closed up in *Tyrannosaurus*, in which the basioccipital and basisphenoidal plates are closely compressed.

The wide supraorbital notch in *Allosaurus* (Fig. 26) is reduced to a narrow cleft in *Tyrannosaurus* (Fig. 25), seen just in front of the supraorbital rugosity.

With this powerful fore-and-aft compression and development of the great rugosities for muscular attachment, the loose articulation of the frontals and the freely moving joint between the quadrates and the quadrato-jugals, especially noted in *Allosaurus*, are replaced by the firm sutural fixation of the corresponding parts in *Tyrannosaurus*.

At the same time the supporting arches of the side of the cranium formed by the adlachrymals, the postorbitals, and the squamosals are greatly expanded and strengthened, thus reducing the open areas both of the orbital and posttemporal fenestræ. At the same time the fenestræ in front of the orbit (f^1, f^2, f^3) are also reduced by the ingrowth of their osseous borders.

In brief, the *Tyrannosaurus* skull is an abbreviated and highly powerful offspring of the *Allosaurus* skull, with reduced fenestration and correspondingly expanded bony structure.

Among the progressive characters of the *Tyrannosaurus* skull in addition to those enumerated above are: (1) development of horizontal infraorbital bar from the postorbitals; (2) anchylosis or coalescence, of adlachrymals and supraorbitals; (3) development of prominent supraorbital rugosity; (4) development of nasal rugosities; (5) coalescence of supraoccipitals and exoccipitals in median line; (6) vertical reduction of supraoccipitals and corresponding expansion of parietals.

2. *Abbreviation of Tyrannosaur Skull.*

The chief mechanical progression in adaptation to the excessively powerful and destructive functions of the *Tyrannosaurus* skull is antero-posterior *abbreviation*, analogous to that in the more powerful mammalian Carnivora, such as the Felidæ and short-faced Canidæ. Thus the dental series of the premaxillo-maxillary is numerically reduced from 20 in *Allosaurus* to 16 on each side in *Tyrannosaurus*; the face and jaws are correspondingly shortened and deepened. The cranium, especially in the supraorbital region, is also compressed; thus the adlachrymal rugosity of *Allosaurus* (Fig. 26) is approximated to the great supraorbital rugosity in *Tyrannosaurus*; the *prefrontals*, which are loosely articulated and exposed above the orbits in *Allosaurus* (Figs. 26, 27) are reduced and thrust inward in *Tyrannosaurus* while the adlachrymals and postorbitals are brought together.

The *Albertosaurus* skull, which will shortly be redescribed by Mr. Barnum Brown, will show many transitional characters between those of *Allosaurus* and *Tyrannosaurus*.

The Theropod skull finds its nearest analogue in the Sauropod skull (Fig. 12). Important differences, it is true, are observed in the presence of a pineal fenestra in *Diplodocus* and a completely closed pituitary sac and infundibulum. These resemblances and differences will be the subject of a special discussion of the theropod skull in the writer's Monograph on the Sauropoda.

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NEW SERIES, VOLUME I, PART II.

INTEGUMENT OF THE IGUANODONT DINOSAUR *TRACHODON*.

PLATE V.

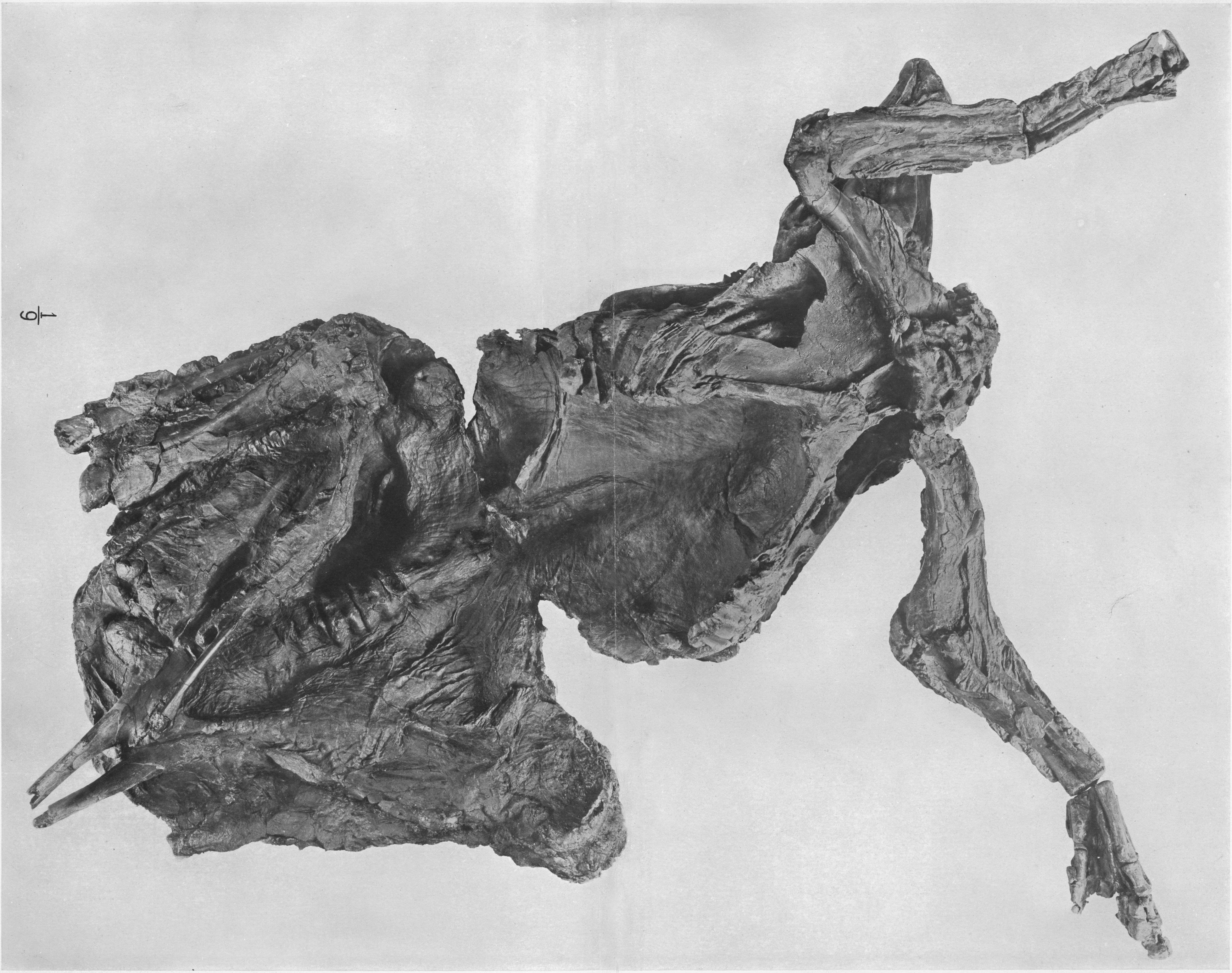

Plate V. *Trachodon annectens.* Ventral view of mummy. Amer. Mus. No. 5060. Scale 1/9.

MEMOIRS

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PART II. INTEGUMENT OF THE IGUANODONT DINOSAUR *TRACHODON*.

BY HENRY FAIRFIELD OSBORN.

PLATES V–X.

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INTRODUCTION.

In recent years the nature of the superficial epidermal pattern or markings of the integument of the Upper Cretaceous trachodonts has been gradually revealed through a number of discoveries which, added to the new light thrown upon the skeleton, afford a knowledge of this terrestrial type of reptilian life that is unique in completeness. The only parallel among the extinct Reptilia in general is that of the aquatic ichthyosaurs of Holzmäden, in which the epidermal and skeletal characters are alike known.

At least seven individuals of *Trachodon* have been found with associated epidermal impressions, more or less completely preserved, from various parts of the body, as follows:

Summary of Complete or Partial Epidermal Casts.

1.	Skeleton of *Trachodon mirabilis,*	Am. Mus. No. 5730,	Discovered	by	Wortman, 1884.
2.	Fragment, *Trachodon* ? sp.	Am. Mus. No. 5730,	"	"	?
3.	" " " "	Am. Mus. No. 5863	"	"	Barnum Brown.
4.	Tail region, *Trachodon* ? sp.	Am. Mus. No. 5894	"	"	" " in 1906.
5.	Skeleton, *Trachodon annectens,*	Am. Mus. No. 5060	"	"	Sternberg in 1908.
6.	" *Trachodon* ? sp.	Senckenberg Mus.	"	"	" "
7.	" *Trachodon* ? sp.[1]	Am. Mus. No. 5058	"	"	Barnum Brown in 1911.

[1] To be described by Mr. Barnum Brown in a forthcoming paper.

The specimen here described (Amer. Mus. No. 5060) far surpasses all those previously discovered, and yields a nearly complete picture of the epidermal markings of the species *Trachodon annectens* except in the tail region. It was discovered by Charles H. Sternberg in 1908. It is said to be approached or rivalled by a second specimen discovered in 1910 by the same indefatigable explorer and now in preparation in the Senckenberg Museum of Frankfurt.

First among these integument specimens to be discovered was the famous type of *Trachodon mirabilis* Cope (Amer. Mus. No. 5730), found by Dr. J. L. Wortman in 1884 and now mounted in the American Museum of Natural History as part of the Cope Collection. This animal is said by Dr. Wortman to have been surrounded by a natural cast of its epidermal impressions, which unfortunately were largely destroyed or lost in the removal of the skeleton from its surroundings. There are only three patches of epidermis remaining from the tail of this specimen.

The tail impressions of another *Trachodon* (Amer. Mus. No. 5894) probably belonging also to the species *T. mirabilis*, are described in this article.

In general it appears from the above materials that all of the trachodonts of Upper Cretaceous times were covered with flattened or rounded epidermal tubercles of relatively small size, which varied in shape in different species, and that not improbably associated with this varied epidermal pattern there was developed a varied color pattern.

It is to be recalled, however, that these river- or shore-frequenting iguanodonts (Trachodontidæ) of the New World were very distinct in structure and habits and, therefore, probably distinct in epidermal covering from the terrestrial iguanodonts (Iguanodontidæ) of the Lower Cretaceous of Europe and the Jurassic of North America.

It is probable also that specific characters were well marked or differentiated in the epidermis of the trachodonts.

Summary of Illustrations.

Plate V,	*Trachodon annectens*, Amer. Mus. No. 5060	Ventral view of mummy	opposite p. 32
Text Fig. 1,	" " "	" " " "	p. 36
" Fig. 1*a*,	" " "	Key to Pl. V and Fig. 1	p. 37
" Fig. 2,	" " "	Lateral view of mummy	p. 38
" Fig. 3,	" " "	Restoration of integument	p. 39
" Fig. 4,	" " "	Integument of jugular region	p. 40
" Fig. 4*a*,		Key to same	p. 41
" Fig. 5,	" " "	Cervical frill region	p. 42
" Fig. 5*a*,	" " "	Key to same	p. 43
" Fig. 6,	" " "	Chest region	p. 44
" Fig. 6*a*,	" " "	Key to same	p. 44
Plate VI,	" " "	Pectoral integument	opposite p. 44
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Plate VII,	" " "	Abdominal integument	opposite p. 45
Text Fig. 8,	" " "	Key to same	p. 45
" Fig. 9,	" " "	Pelvic integument	p. 47
" Fig. 10,	" " "	Integument on forearm	p. 49
" Fig. 11,	" " "	Integument on right manus	p. 50
Plate VIII,	" " "	Right manus, dorsal view. Key to same	opposite p. 51
Plate IX,	" " "	Right manus, palmer view. Key to same	opposite p. 51
Text Fig. 12,	Genus and species undetermined (Amer. Mus. No. 5894.)	Tail region of another Trachodont	p. 51
Plate X,	*Trachodon mirabilis*, etc.	Fragments of integumentary casts	opposite p. 52
Text Fig. 13,	*Trachodon mirabilis*	Restoration	p. 52

Discovery of the Trachodon 'Mummy'.

In August, 1908, the veteran explorer Charles H. Sternberg and his son George F. Sternberg were working in the Upper Cretaceous deposits of Converse County, Wyoming, which had been rendered famous by the prolonged and successful explorations of Hatcher (1889–1892) for remains of Ceratopsia. This region, like the Hell Creek Beds of Montana, is divided into successive "basal", "middle", and "upper" layers of sandstones and intermediate clays, which mark the close of the Cretaceous and terminate above in the Basal Eocene of the Fort Union.

It was in the lowest levels, or "basal sandstones" of this series that the younger Sternberg made the welcome discovery of a specimen of *Trachodon annectens* almost complete, encased in the 'impression-cast' of its integument. Fortunately, before the removal of the matrix from the bones had progressed very far the delicate epidermal markings were observed, and the subsequent quarrying and packing was done with the greatest care under the direction of the elder Sternberg, so that this precious record of the outer covering of an iguanodont dinosaur is preserved to a large extent. To his already long series Mr. Sternberg thus added another most important contribution to palæontology.

The specimen was offered by him to the Department of Vertebrate Palæontology and secured by the writer for the American Museum of Natural History through the Jesup Endowment Fund.

Position of the Skeleton.

Pl. V and Text Figs. 1, 1*a*.

When the skeleton was found the hind feet as well as the posterior portion of the pelvis and the entire tail had been eroded away, but undoubtedly all these missing parts were present when the animal was originally deposited. The remainder of the animal as discovered and as now prepared in the American Museum (Pl. I, Figs. 1, 2) lies on its back with all the bones connected; the knees are drawn up, the chest is open and upturned; the fore limbs are outspread; the neck and skull are sharply twisted downward and backward to the right side; the dorsal frill of the neck is turned to the left.

This position is that of an animal which died a natural death, or at least of one not dismembered by being preyed upon. The scapulæ (Fig. 6) are closely appressed to the sides of the ribs and probably lie in normal position, while the sternal bones are slightly drawn away from the coracoids (Fig. 1*a*) by the partial insinking of the chest.

There is reason to believe that when first discovered the fossilized skeleton, including the skull, was completely encased in impressions of its integument, but many portions of the impression area were destroyed because, as above noted, of the quite natural failure of the discoverer to recognize the extremely thin "impression layer" before certain of the bones had been cleaned up. Such an oversight of the epidermal impressions of trachodonts has probably occurred repeatedly before, but now that the attention of collectors is directed to this point other discoveries will doubtless be made and all parts will be most carefully preserved.

(*Continued on page 41.*)

Fig. 1. Ventral aspect of the *Trachodon annectens* 'mummy.' Same as Plate I. Scale $\frac{1}{13}$.

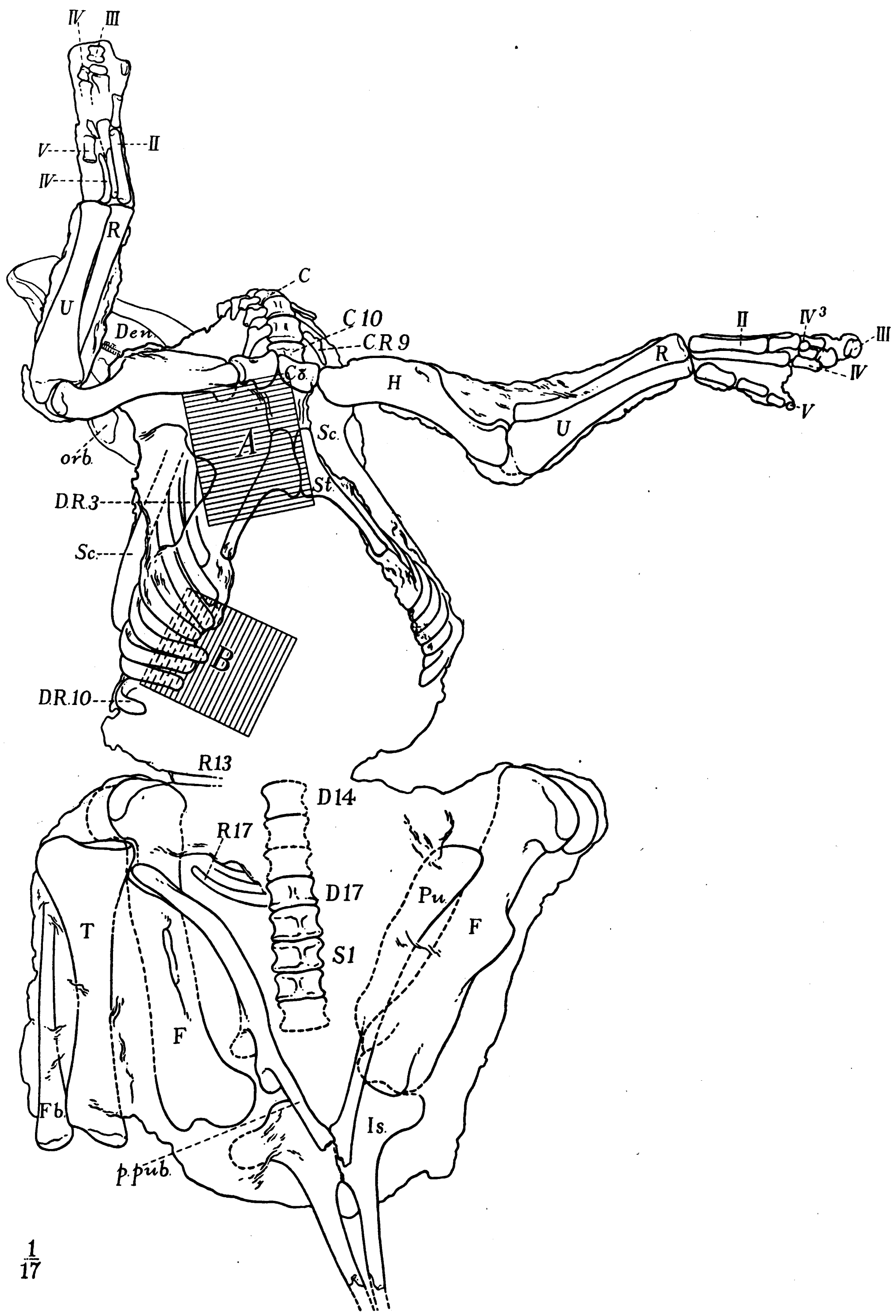

Fig. 1*a*. Outline of the ventral aspect of the *Trachodon annectens* 'mummy.' Designed as a key to drawings and plates. Scale $\frac{1}{17}$.
A, location of the epidermal impression area shown in Pl. VI.
B, location of epidermal impression area shown in Pl. VII.

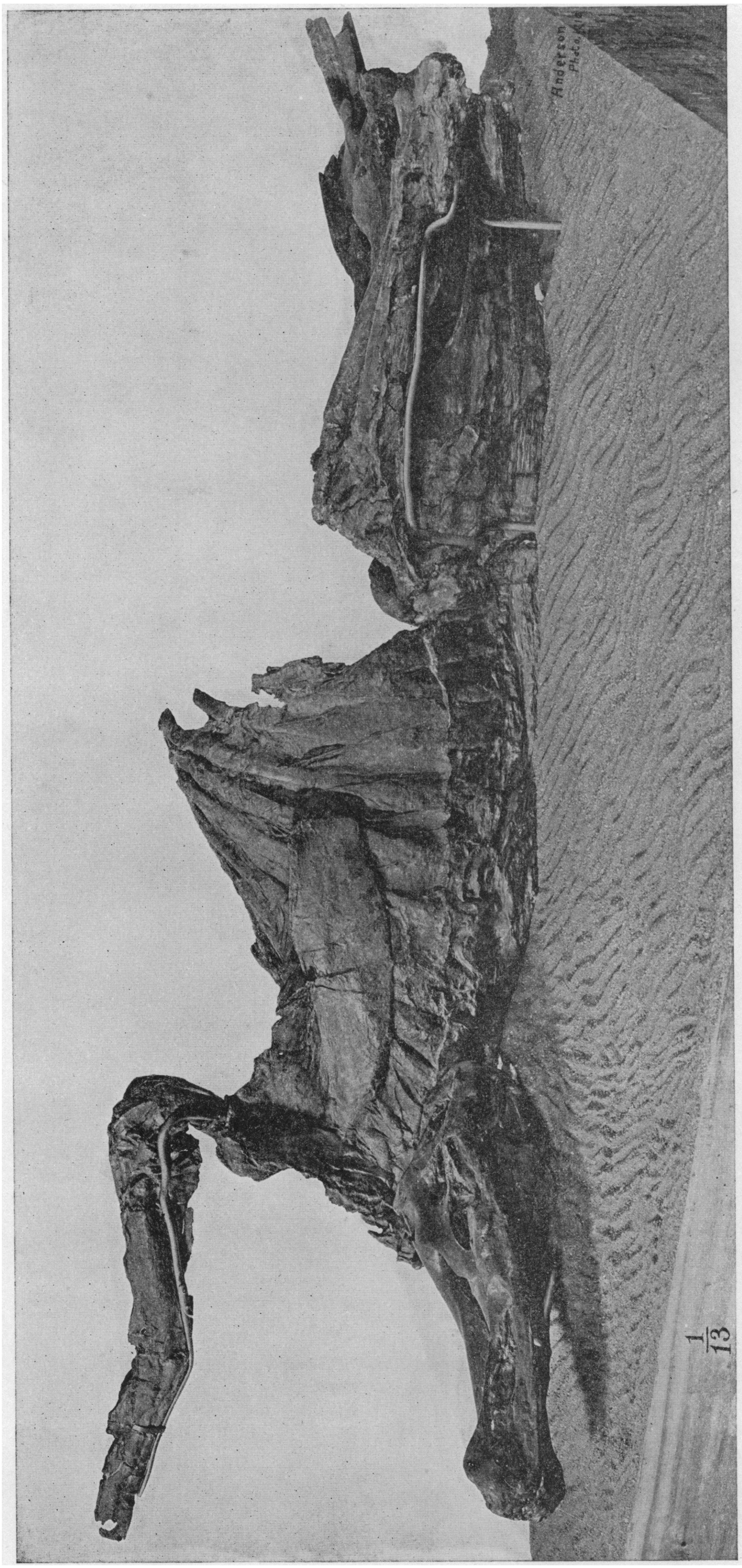

Fig. 2. View of the right side of the *Trachodon annectens* 'mummy.' Photograph by A. E. Anderson. Scale, $\frac{1}{13}$.

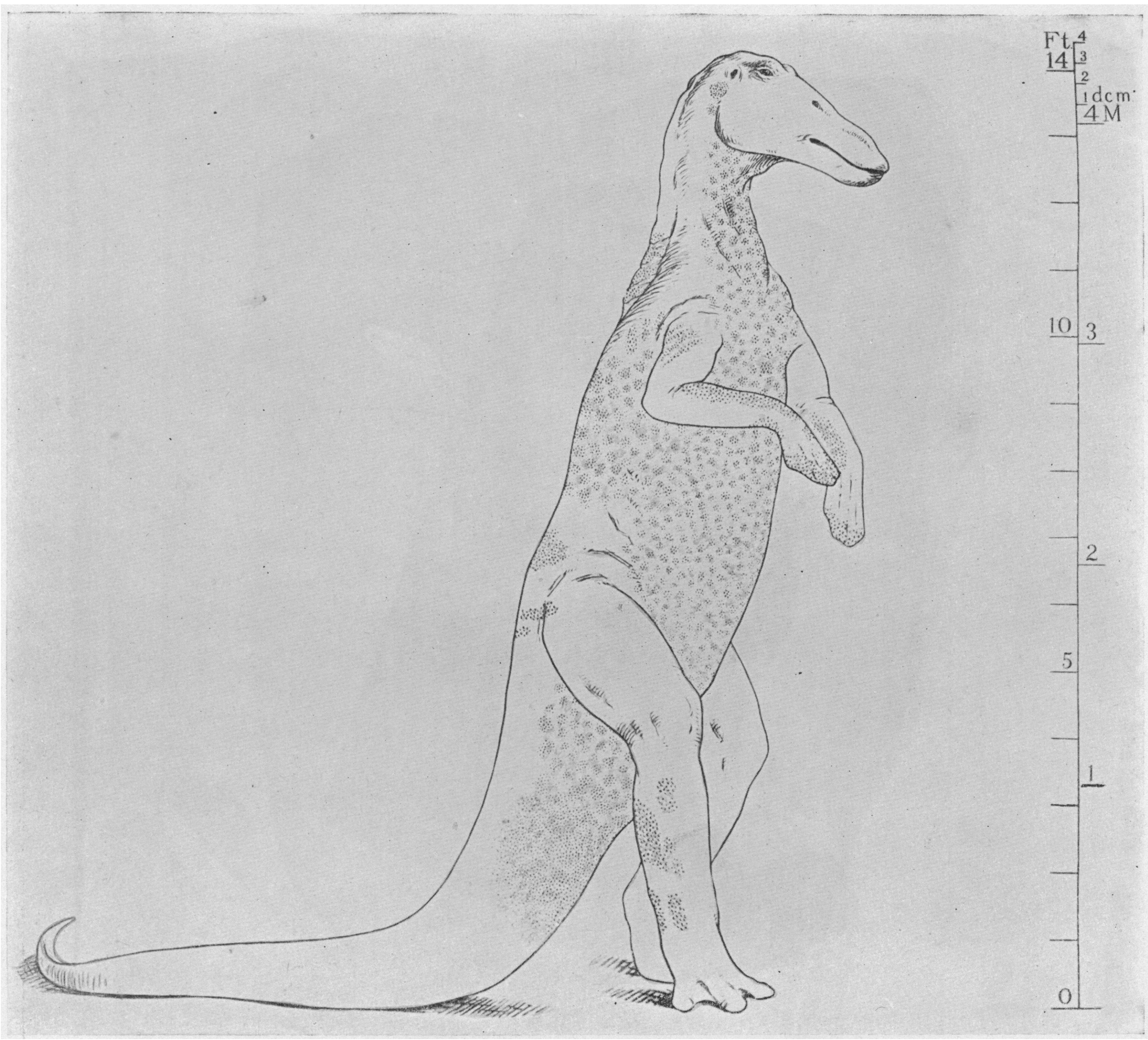

Fig. 3. Diagrammatic restoration of the body contours, integumentary outlines, and epidermal markings of *Trachodon annectens*, including the neck frill and the borders of the integument in the manus and pes. For details of the associated portions of the 'neck frill' compare Fig. 5. The 'pavement tubercle clusters' are greatly exaggerated in size and conspicuousness.

Fig. 4. Integument of the right jugular region and of the cheek over the quadrate bone, showing the clusters of large pavement tubercles interspersed with small rounded tubercles. *Trachodon annectens* 'mummy,' Amer. Mus. No. 5060.

Theory of Fossilization.

Mr. Sternberg's theory [1] of the fossilization was that the animal had floated for some time in water and then become entombed, covered with sand, and fossilized in its present position.

The writer suggested [2] a contrary theory, namely: that after a natural death the body lay exposed to the sun for a long time undisturbed, perhaps upon the sand flat of a stream in the low water stage; that the muscles and viscera had thus become completely dehydrated or desiccated by the sun, and that the epidermis, hardened and leathery, shrank around the limbs and was tightly drawn down along the bony surfaces. In this way a "dinosaur mummy" may have been formed. On the abdominal surfaces the epidermis was certainly drawn within the body cavity, while it was thrown into creases and folds along the sides of the body and on the arms, apparently owing to the shrinkage of the tissues within.

At the termination of the low water season during which this process of desiccation took place, the "mummy" may have been caught in a sudden flood, carried down the stream, and rapidly buried in a bed of fine river sand intermingled with sufficient clayey elements to take a perfect cast of all the epidermal markings before the epidermal tissues became softened under the solvent action of the water.

(*Continued on page 46.*)

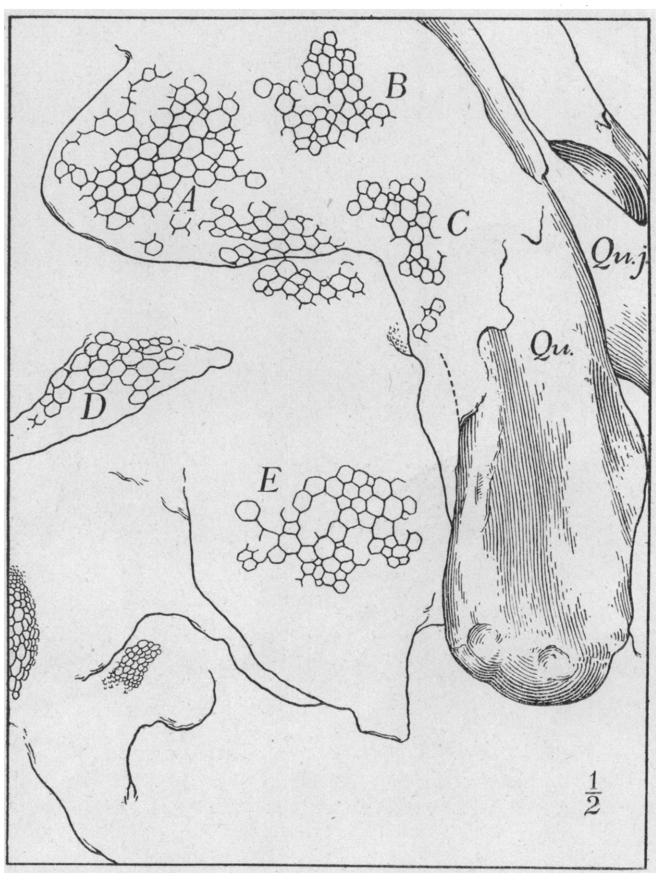

Fig. 4*a*. Key to Fig. 4.
A, B, C, D, E, groups of larger or pavement tubercles, *Qu*, quadrate; *Qu. j.*, quadrato-jugal.

[1] Sternberg, Charles H. 'A New Trachodon.' The Lawrence [Kas.] 'Daily World', Sept. 22, 1908.
Sternberg, Charles H. 'Expedition to the Laramie Beds of Converse County, Wyoming.' Proc. Kans. Acad. of Sci., Geol. Papers, 1908, pp. 113–116. 'Laramie Beds of Wyoming.' Guide to Nature, Vol. II, No. 4, July 1909, pp. 123–129.
[2] Osborn, H. F. 'The Epidermis of an Iguanodont Dinosaur.' Science, N. S., Vol. XXIX, No. 750, May 14, 1909, pp. 793–795.
Osborn, H. F. 'The Upper Cretaceous Iguanodont Dinosaurs.' Nature, Vol. 81, No. 2075, Aug. 5, 1909, pp. 160–162.

Fig. 5. Median neck frill of the *Trachodon annectens* 'mummy,' above the 8th, 9th, and 10th cervical vertebræ, showing the pattern formed by the larger pavement tubercles and smaller rounded tubercles. The integument extends into a frill above the spines, which are very short at this point. Amer. Mus. No. 5060.

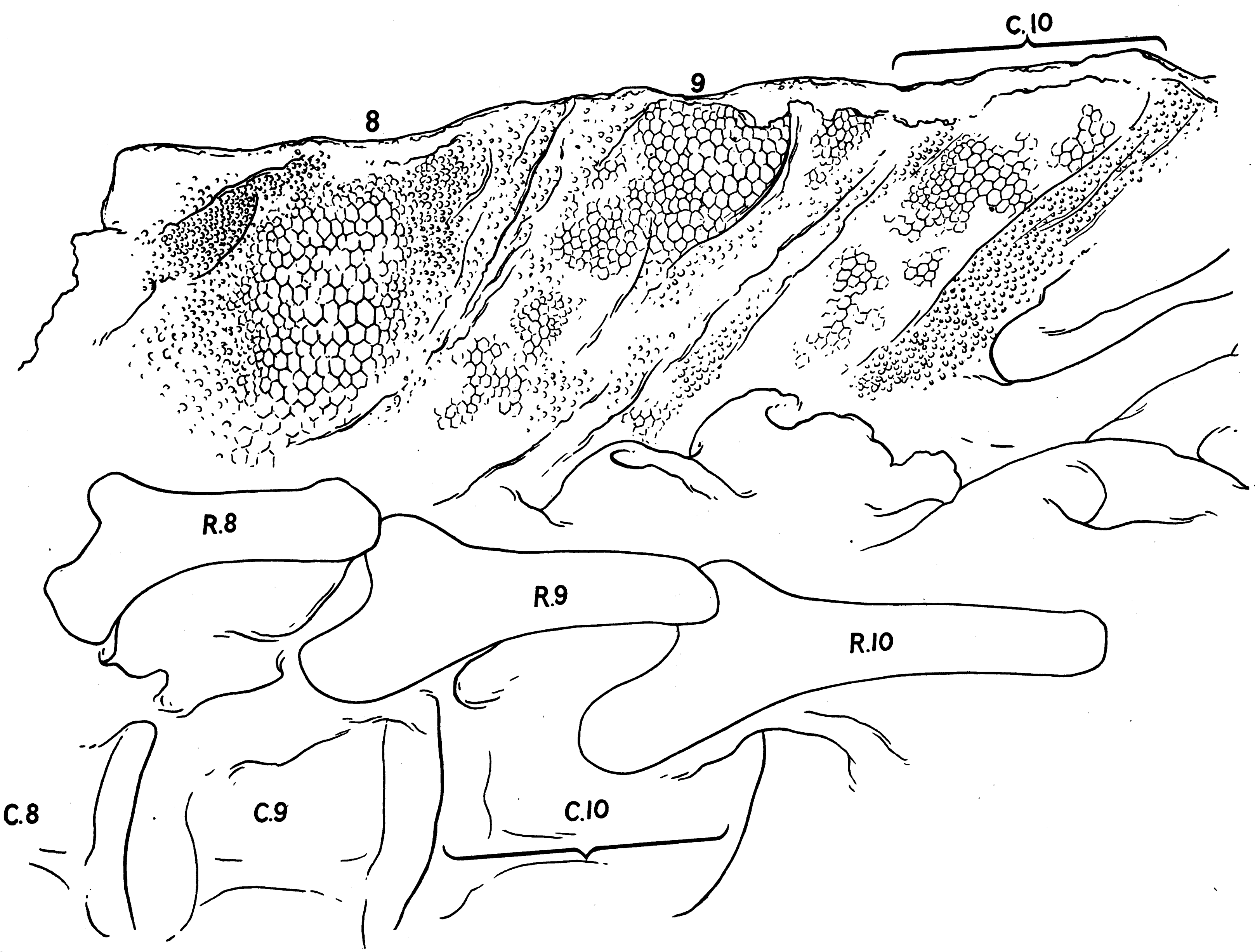

Fig. 5*a*. Key to Fig. 5, showing the distribution of pavement and rounded tubercles on the frill.
C. 8, C.9, C. 10, centra of cervical vertebræ 8–10.
R. 8, R. 9, R.10, cervical ribs 8–10.
8, 9, 10, epidermal 'pavement' and 'rounded' tubercle areas. Segmented vertebral (supraspinous) and intervertebral (interspinous) arrangement of the 'pavement' tubercle areas.

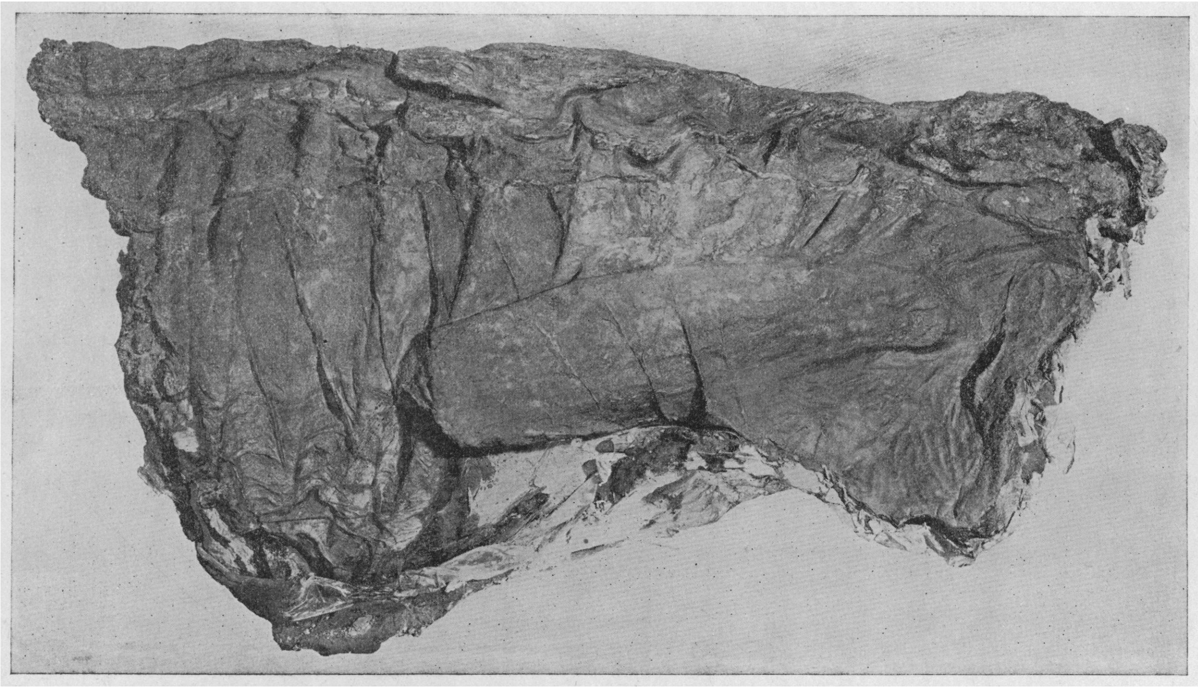

Fig. 6. Natural cast of foldings of the integument on the right side of the thorax of the *Trachodon annectens* 'mummy,' showing close appression to the ribs and scapula. Amer. Mus. No. 5060.

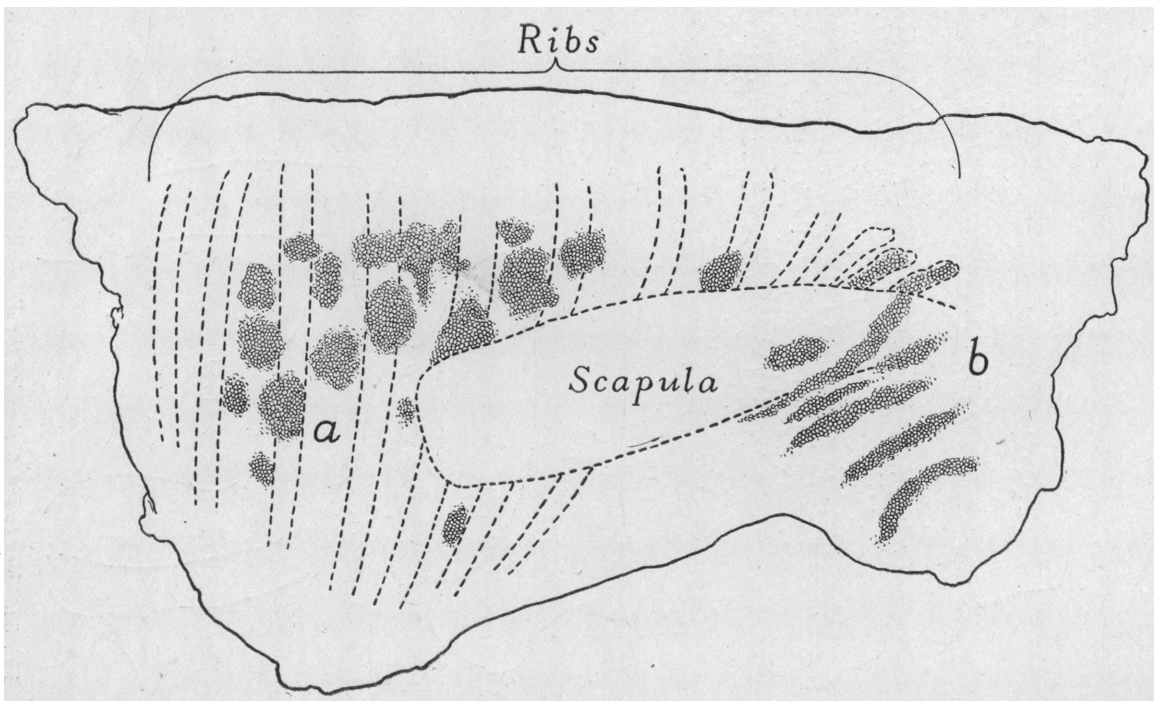

Fig. 6*a*. Key to Fig. 6. Showing distribution of large areas of rounded tubercles on the sides of the thorax: (*a*) rounded areas of pavement tubercles; (*b*) elongate areas of pavement tubercles above and in front of the anterior portion of the scapula.

Plate VI. Pectoral integument. Natural size photograph of the epidermal impression area on the right side of the pectoral region immediately over the union of the sternal plates. See area marked *A* in Fig. 1*a*. This shows the patches of larger pavement tubercles shading off into the smaller rounded tubercles of the ground pattern. Photograph by A. E. Anderson.

Plate VII. Abdominal integument. Natural size photograph of the epidermal area marked *B* in Fig. 1*a*. This shows the alternating arrangement of the large pavement tubercle clusters surrounded by the smaller rounded tubercles and more or less diamond-shaped areas. Photograph by A. E. Anderson.

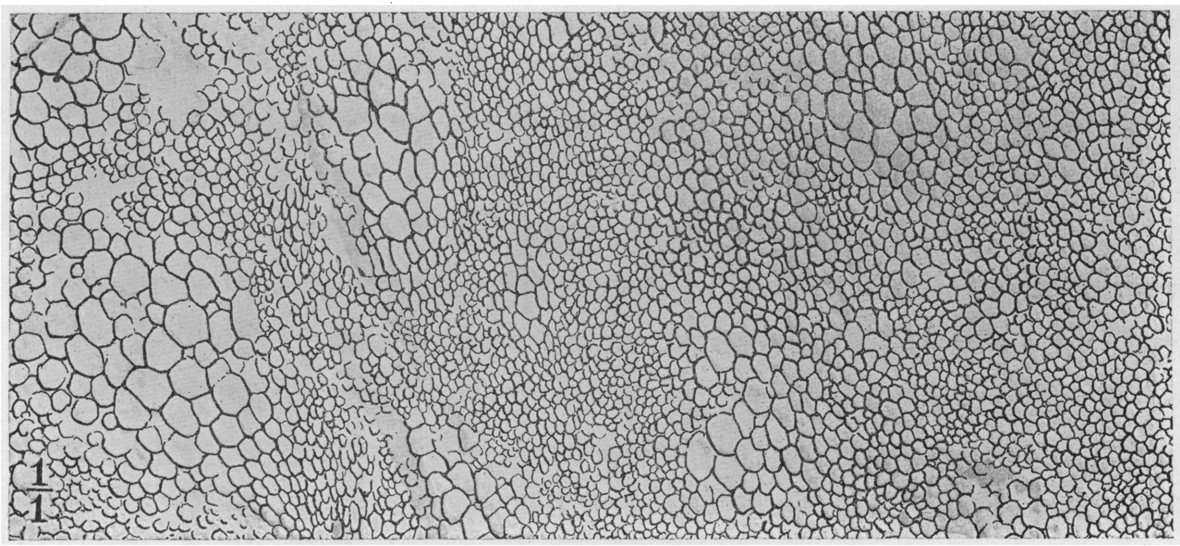

Fig. 7. Diagram showing details of the arrangement of the larger and smaller epidermal tubercles of the pectoral region; from the lower part of the area marked *A* in Fig. 1. Natural size.

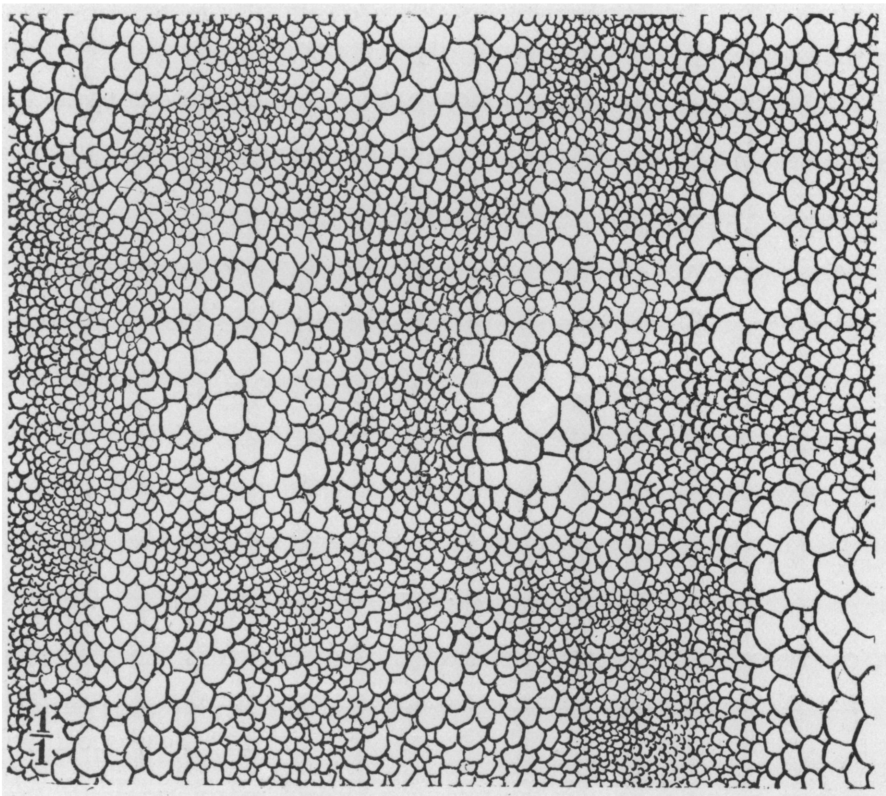

Fig. 8. Key to epidermal impressions in the abdominal region taken from the lower portion of the integument photographed in Pl. VII, showing more clearly the alternating arrangement of the clusters of large pavement tubercles upon the abdominal integument. It is possible that the pavement tubercles clusters are unnaturally elongated in this area by the longitudinal stretching of the integument.

Preservation of the Epidermal Area.

Fortunately nearly two-thirds of the total epidermal-impression area of the present specimen are preserved. They have been delicately and successfully exposed by one of the American Museum preparators, Otto Falkenbach, under the direction of Mr. Adam Hermann, preparator-in-chief.

Everywhere they present sharply defined and in many regions truly brilliant impressions of the epidermal pattern. This is invariably an impression cast, for there is no indication of the preservation of the epidermis itself.

Altogether we observe (Pl. V) in this 'impression-cast' the following regions of the upper parts of the body: (1) the right fore foot; (2) extensive portions of the fore limbs, both on the upper and lower sides; (3) the lateral portions of the neck and highly ornamented dorsal frill in the region of the neck; (4) the distinct ornamentation of the side of the throat and angle of the jaws; (5) the upper portion of the chest region, and the entire right side of the chest almost to the back. (6) Broad and thin folds, which are composed of the two cutaneous and epidermal impression-layers in contact, connect the left arm with the front part of the scapula, as well as with the side of the neck. These thin and closely appressed skin folds may be construed either as evidence of the looseness of the skin during life, or as evidence of the desiccation of the subjacent muscular and connective tissues after death.

(7) On the sides of the chest (Pl. V; Figs. 2, 6) the skin is tightly drawn in around the scapula and thrown up into ridges, precisely as we observe it in existing lizards after exposure and desiccation by the action of the sun.

(8) Most remarkable is the great concave sheet of unbroken epidermal covering (Pl. V) which falls like a curtain from the lower ends of the ribs down to the pubes. This curtain is uniformly concave in the suspended portions, but where it comes into contact with the vertebral column it rises and falls over the outlines of the dorsal and lumbar vertebræ and is deeply folded back into the pelvic cavity.

The extended areas of epidermal impression, taken altogether, enable us to give a tentative diagrammatic restoration (Fig. 3) of the greater part of the epidermal surface. The restoration of the tail is omitted because it is not preserved in this specimen; it was probably covered with large uniform pavement scales.

Characters of the Epidermis.

Pl. V–IX.

In no part of the epidermal impressions of this specimen is there evidence of the existence either of bony plates, of coarse tubercles or of overlapping scales. Properly speaking the skin is not squamate, or imbricating, as in the lizards, but is rather tuberculate. There is no evidence of a squamous overlapping, or of an imbricating arrangement of the scales anywhere.

Considering the very large size of the animal perhaps the most surprising feature is that the integument is extremely thin and that the tubercular markings are excessively fine and delicate. Even the largest of the separate tubercles on the body are relatively diminutive in comparison with those on the head of the Gila Monster (*Heloderma*), for example (Pl. X), an animal one-fifteenth of the linear diameter of *Trachodon*.

In all parts of the body where the impressions are preserved, the epidermis was evidently covered with a pattern composed solely of tubercles, which were mainly of two kinds: (1) Small, rounded tubercles = ground plan, uniformly distributed. (2) Large 'pavement' tubercles, irregularly pentagonal in outline = raised pattern, diversely distributed.

Rounded tubercles. Of the small, rounded tubercles, which form the ground plan, we observe that they are relatively more apical, or convex than the pavement tubercles. The smaller tubercles are mostly very minute, varying from 1 to 2 or even 3 millimeters in diameter, accord-

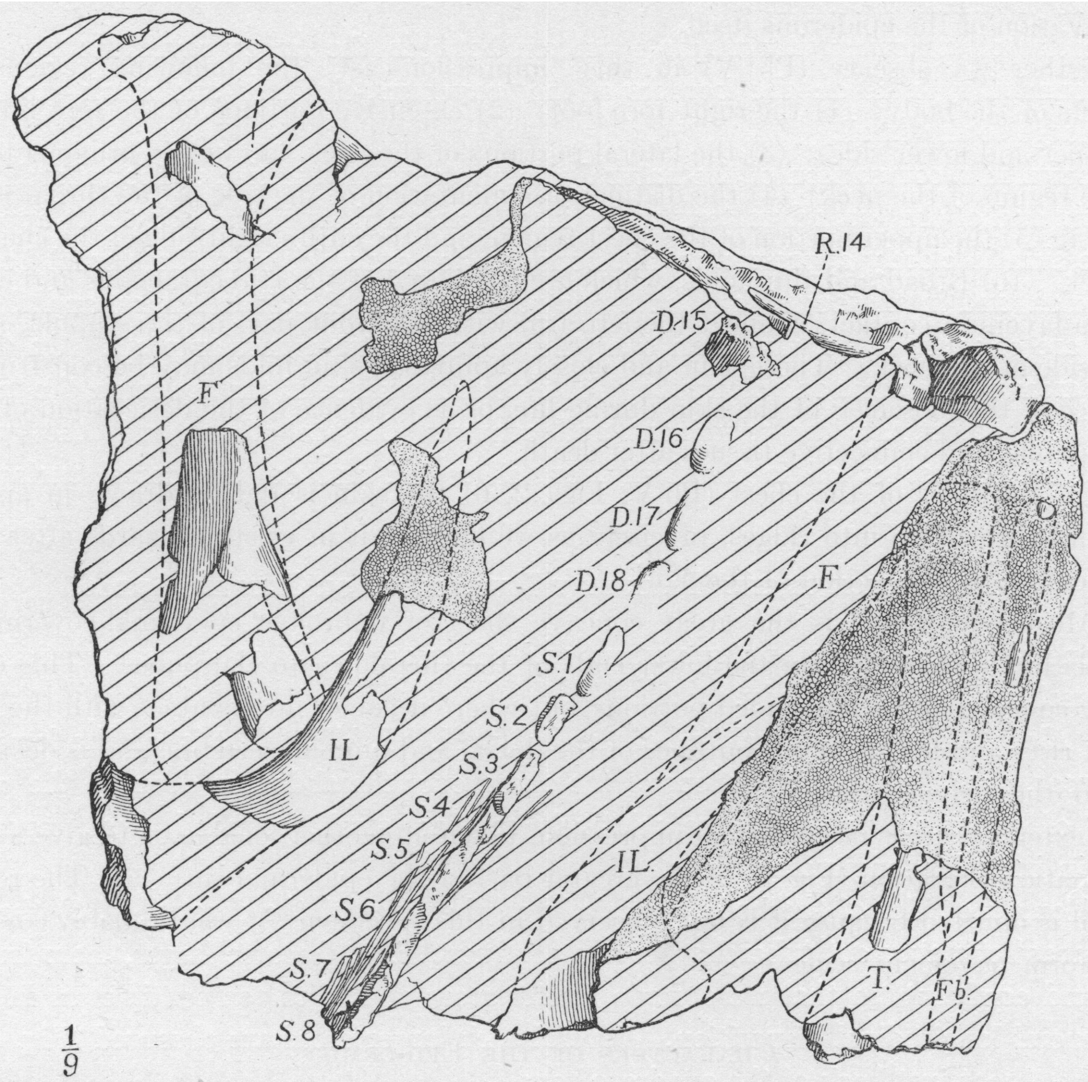

Fig. 9. Integument over the sacral and pelvic region of the *Trochodon annectens* 'mummy' showing the large and more or less confluent clusters of pavement tubercles in the dorsal region contrasted with the small and regular clusters in the abdominal integument. The darker shading indicates the areas of larger pavement tubercles; the dots represent smaller, rounded tubercles. Amer. Mus. No. 5060.

Il, anterior process of the left ilium; *Fb,* right fibula;
F, right and left femur; *D. 15–18,* posterior dorsals;
T, right tibia; *S. 1–8,* sacrals.

ing to the part of the body on which they occur; that is, both the smaller and the larger tubercles vary in size in different regions.

Pavement tubercles. The large, flat, or tesselated tubercles, with irregular angular borders, form the *raised pattern,* and from their relatively smooth, flattened surfaces, may be spoken of as 'pavement tubercles.' In this species at least, they generally do not exceed 5 mm. in diameter. On the outer side of the arm and probably on the tail they attain a centimeter in diameter.

They are grouped into circular or oval clusters, or 'cluster-areas,' which vary in breadth from one-half an inch to two inches. These are scattered in irregular longitudinal lines over the entire ventral surface of the body. As shown in figures 7, 8, the larger and more typical 'pavement tubercles' are in the centres of the groups, while those on the borders shade off gradually in size and in surface character into the smaller tubercles of the ground plan. The contours of these tubercles are irregularly rounded or angular where they impinge against each other. According to its size, a 'cluster area' may be composed of from twenty to one hundred, or even hundreds of pavement tubercles.

Tubercles of somewhat intermediate pattern between the larger pavement type and the smaller rounded type lie on the borders of the 'pavement-clusters,' and mark the transition from the large to the small.

As shown in a comparison of the natural size photographs the size of the tubercles both of the clusters and of the ground pattern varies in different regions of the body. It appears that where the skin is closely appressed to the bone, as, for example, over the sternal bones, over the coracoids, and in the dorsal frill, both the pavement, or cluster tubercles, and the ground tubercles are of much larger size than over the ventral softer muscular parts. On the entire muscular areas of the arms and along the pliable ventral surface of the abdomen the 'pavement tubercles' are somewhat less prominent and convex. On the other hand, the 'pavement tubercles' are largest of all in the fleshy, or tail region and on the dorsal surface of the forearm.

Distribution of the 'Pavement Tubercles,' or Cluster Areas.

In general the cluster areas of pavement scales increase in size as we pass from the ventral to the dorsal surfaces of the body.

(1). Along the entire ventral line of the body (Pl. VI, VII), that is, on the lower surface of the throat, over the ventral portions of the chest, over the abdomen down to the pelvis, the 'clusters' of pavement tubercles are relatively regular, small, rounded, oval, separate, and disposed in irregular longitudinal lines.

(2) Along the sides of the body, especially on the sides of the chest (Fig. 6) the rounded 'cluster areas' of pavement tubercles become confluent, *i. e.*, become larger, more irregular in contour and confluent, so that we observe cluster areas of five to ten centimeters in diameter with a general longitudinal disposition. Several such larger areas are observed (Fig. 4) on the sides of the throat just back of the quadrate bone.

(3) Still larger 'cluster areas,' fifty centimeters, or twenty inches in length, are observed in the particularly large impression-area above the left ilium (Fig. 9), showing that in this region of the back and probably along the entire dorsal surface there were great irregular 'cluster areas' of pavement scales of a general longitudinal disposition, but very irregular in arrangement. Thus the outer side of the right forearm is covered with one great 'pavement scale' cluster at least thirty-three centimeters in length and fourteen centimeters broad. The ventral cluster areas are very regularly disposed and patterned.

(4) As we descend from the shoulder to the arm the 'pavement-areas' become smaller and less numerous on the entire ventral side so that the *inner*, or axillary surface of the forearm was apparently entirely covered with the small tubercles.

(5) On the contrary, the *outer*, or dorsal surface of the arm, as well as the anterior borders

of the arm were mainly covered with the largest pavement tubercles which have been preserved (Fig. 10). The diameters of these separate pavement tubercles appear to increase in size to a centimeter.

(6) It is not probable that the upper portions of the hind limbs, or thighs, which are found to be similarly covered on the *inner* sides with the smaller 'ground tubercles,' were, like the

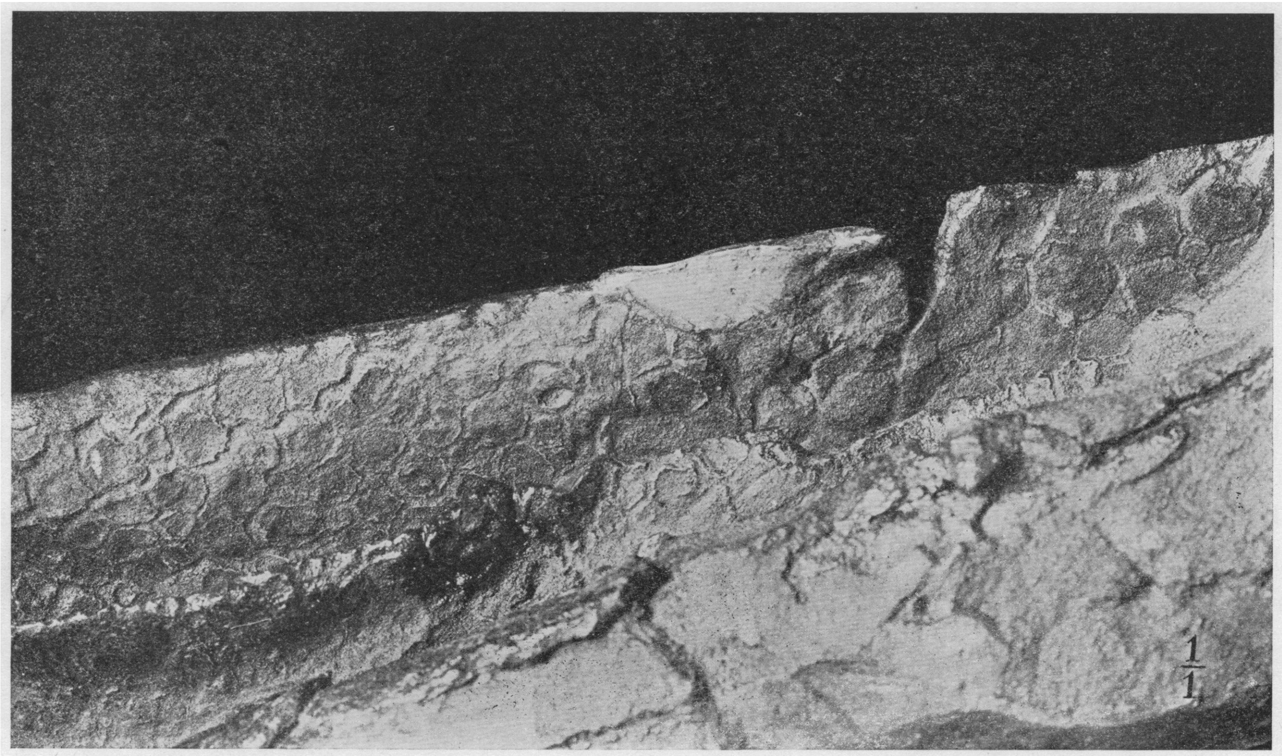

Fig. 10. Forearm integument. Natural size photograph of the large pavement scales on the outer and upper side of the left fore-arm of the *Trachodon annectens* 'mummy,' showing the continuous area of large irregular polygonal scales. Amer. Mus. No. 5060. Scale $\frac{1}{1}$.

fore limbs, also covered on the *outer* sides with the large pavement tubercles. These portions unfortunately are not preserved, yet indications of the outer sheathing of the leg by the larger pavement tubercles are shown upon the lower portion of the right fibula.

The Neck and Anterior Back Frill.

Figs. 4, 5, 5*a*.

The most elaborate epidermal ornamentation is that of a median integumentary fold or cervico-dorsal frill, portions of which are fortunately preserved opposite the abbreviated spines of the 8th, 9th, 10th, and 11th cervical vertebræ.

The pattern is repetitive, or segmental, to conform with the vertebral segments.

The total area of the 'frill' preserved is about fourteen inches or about twenty-five centimeters in length, and seven to eight centimeters in depth. Unfortunately the superior border of this ornamented frill was destroyed by the discoverer of the specimen before its presence was detected, so that the height of the frill, or vertical extent of its free border, is not known.

The frill pattern (Fig. 5) consists of oval lobes of pavement tubercles which were apparently appressed to the regions above the neural spinous processes of the cervico-dorsal vertebræ; they are raised on a ground pattern of the small rounded tubercles.

Corresponding with the intervertebral, or interspinous spaces of the cervical region, above the intervals between the short neural spines, the epidermis was raised into folds and creases which gave freedom to the movements of the neck and also apparently had a more or less definitely patterned arrangement.

There is reason to suppose that above these interspinous folds there was a vertical extension of the frill on which were displayed one or more upper rows of large pavement tubercles which gave the frill a still more elaborate pattern. Thus there were certainly two rows of these pavement tubercle areas, a lower and an upper.

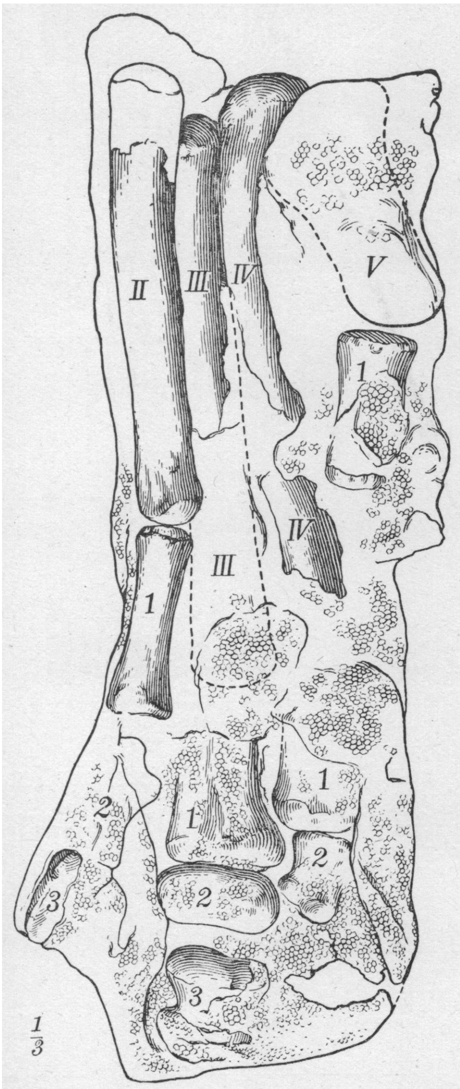

Fig. 11. Integument of the palmar surface of the right manus of the *Trachodon annectens* 'mummy,' Amer. Mus. No. 5060, showing the continuous distribution of the small pavement tubercles and apparent absence of the rounded tubercles. II–V, 2nd to 5th metapodials. Below the terminal phalanges of Mtc. III–IV the integumentary border seems to be complete, representing the terminal border of the web. The border seems to be broken below Mtc. II, also on the outer side of the manus. Scale $\frac{1}{3}$.

Epidermal Sheathing of the Manus.

Pls. VIII, IX, Fig. 11.

The impression areas of the right manus (Fig. 11) are most fortunately preserved, and they are peculiarly interesting and significant for two reasons, both of which bear upon our theories as to the habits of the iguanodonts in this Upper Cretaceous stage of evolution. The actual dorsal and ventral aspects of the manus is represented (Pls. VIII–IX) as closely as possible in the sepia drawings by E. S. Christman.

First, these epidermal impressions appear to show that the phalanges, or digits did not terminate in exposed nails or hoofs, and were not freely movable and independent. It is possible that this appearance is deceptive, that the integument was loose and drawn over the extremities of the phalanges, that there were nails or hoofs present which have been mechanically removed. This theory is tenable but it is not supported by the condition of the manus as presented.

As the manus is preserved the digits were *apparently* connected by an *integumentary web* which was developed even more prominently than in the swimming birds, because it extended beyond the terminal phalanges into a paddle-like thickening and free integumental border, which is especially well preserved on the outer side of the right fore foot in this specimen below metapodials III, IV. This thickened border, which in a desiccated condition at least, is apparently indented by a terminal groove, but which in life may have been convex, not only completely encases the foot and digits but like a mitten extends $5\frac{1}{2}$ centimeters beyond the terminal phalanx of the fourth digit (Pl. IX, III*a*).

If the manus had been partly used in terrestrial locomotion we should expect to find on its palmar, or ventral surface traces of callous pads or thickenings and a differentiation of the tubercles. There is evidence of the existence of at least two rather delicate callosities. These callosities may

PLATES VIII, IX, WITH KEYS.

Manus of *Trachodon annectens.*

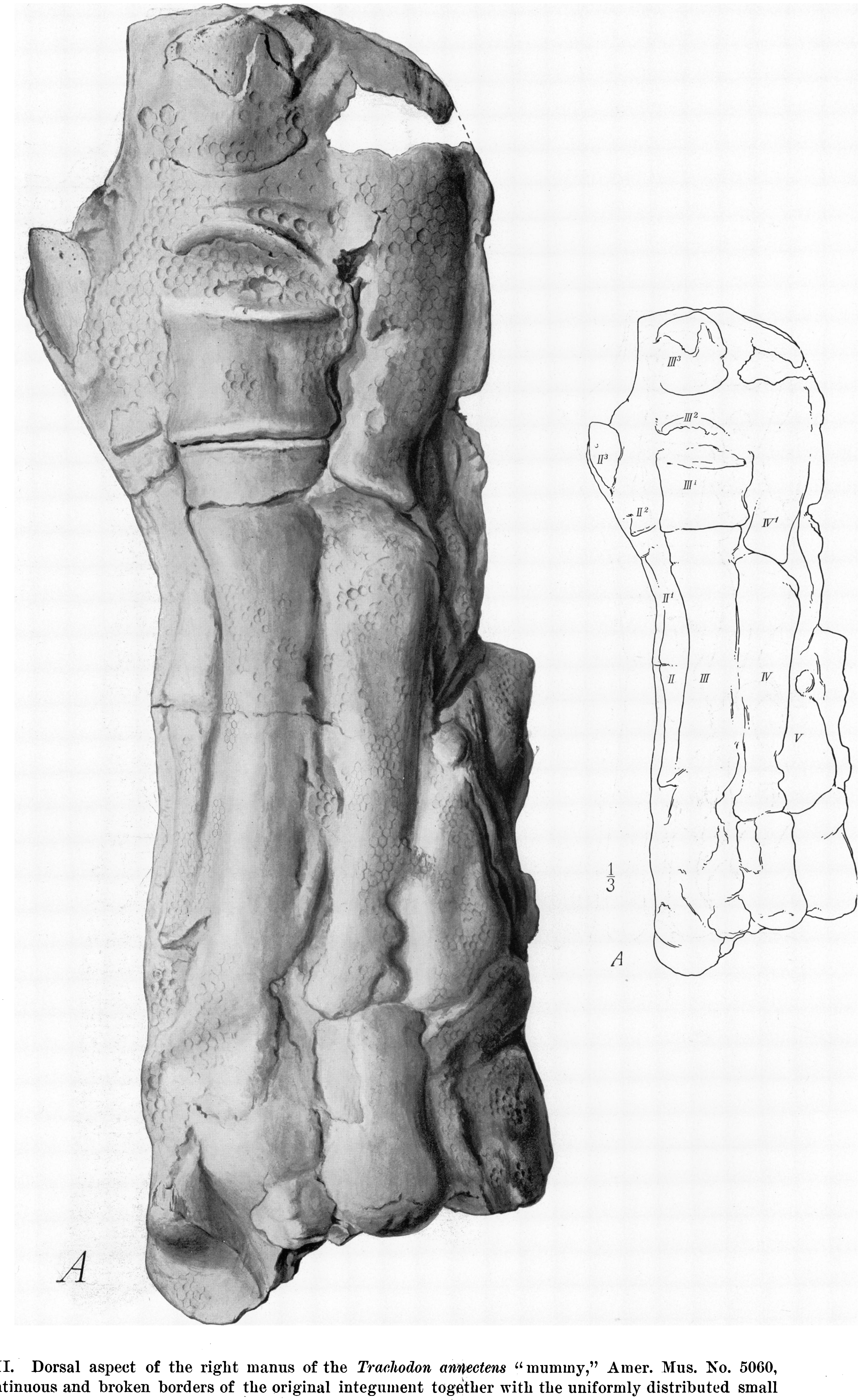

Plate VIII. Dorsal aspect of the right manus of the *Trachodon annectens* "mummy," Amer. Mus. No. 5060, showing the continuous and broken borders of the original integument together with the uniformly distributed small pavement tubercles covering the integument. This represents the dorsal aspect of the manus shown in Fig. 11 and in Plate IX. Scale 2/3.

Plate IX. Palmar surface of the integument of the right manus of the *Trachodon annectens* "mummy," Amer. Mus. No. 5060, showing the continuous fold of integument extending beyond Mtc. III–IV, also the continuous and evenly distributed small polygonal pavement scales. Scale 2/3.

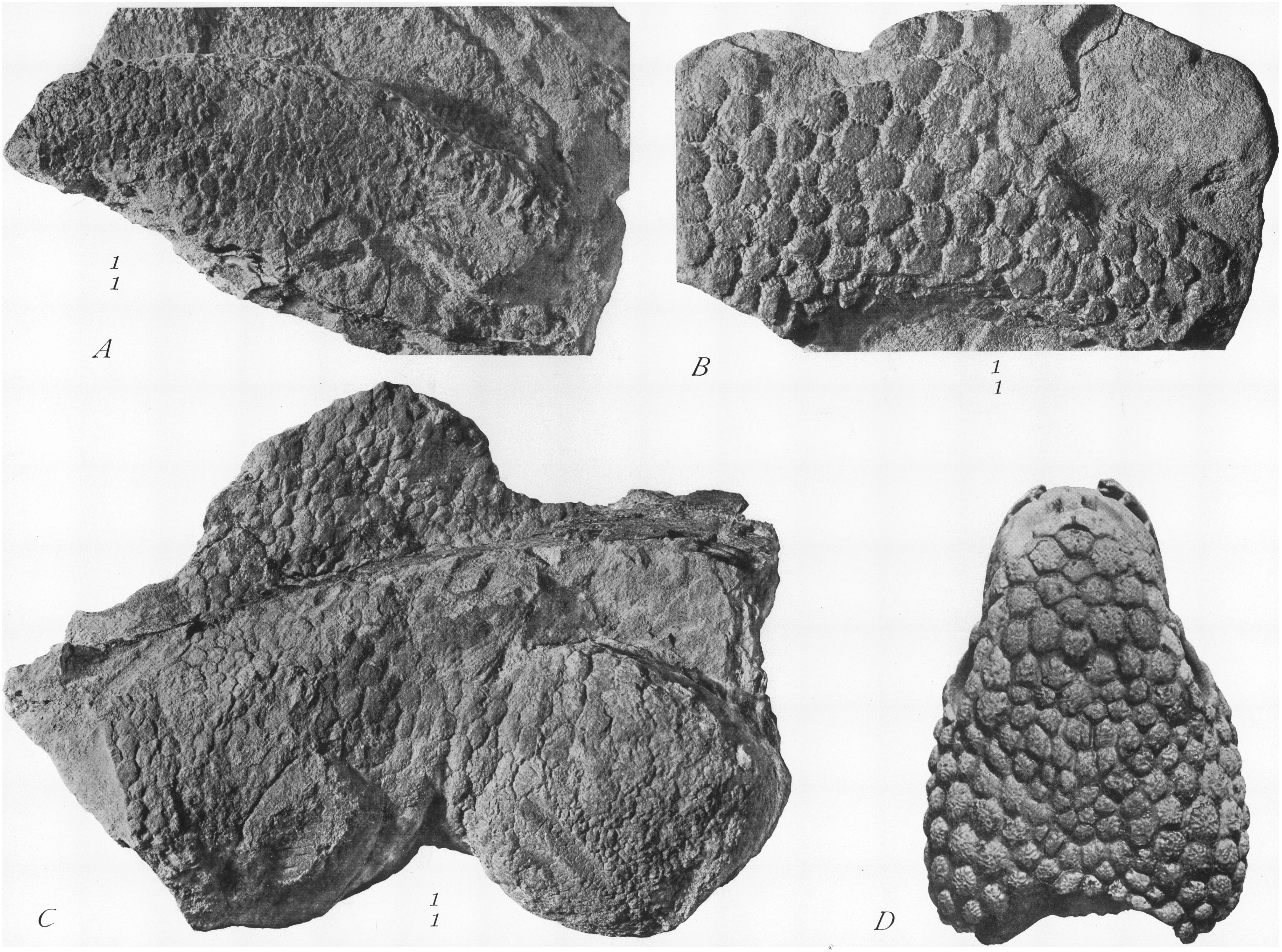

Plate X. Epidermal markings in various specimens of Trachodonts (*A–C*); also (*D*), for comparison with the tuberculated upper surface of the head of *Heloderma suspectum*, the Gila Monster.

A. Trachodon mirabilis. Amer. Mus. No. 5730. *B. Trachodon mirabilis.* Amer. Mus. No. 5730. *C. Trachodon sp.* Amer. Mus. No. 5863. *D. Heloderma suspectum.*

be observed in Plate IX, on the ventral side of the extremities of Metacarpal III and of Metacarpal IV.

The ventral surface (Pl. IX) is entirely covered with small pavement or gently convex tubercles of uniform size, two or three millimeters in diameter. These tubercles appear to be chiefly of the small 'pavement' type, that is, flattened and polygonal rather than convex and rounded.

The dorsal (Pl. VIII), or plantar surface of the manus was chiefly invested with the small 'pavement tubercles.' These are the same polygonal shape but about twice as large as those on the palmar surface, or about four or five millimeters in diameter, as best displayed in the impressions which may be observed over the phalanges.

The inferences which may be drawn from this relatively delicate sheathing of the manus are set forth below.

Covering of the Tail.

Text Fig. 12.

It appears probable that the larger pavement tubercles not only covered the outer sides of the limbs and the dorsal region of the body, but extended down to form the entire epidermal

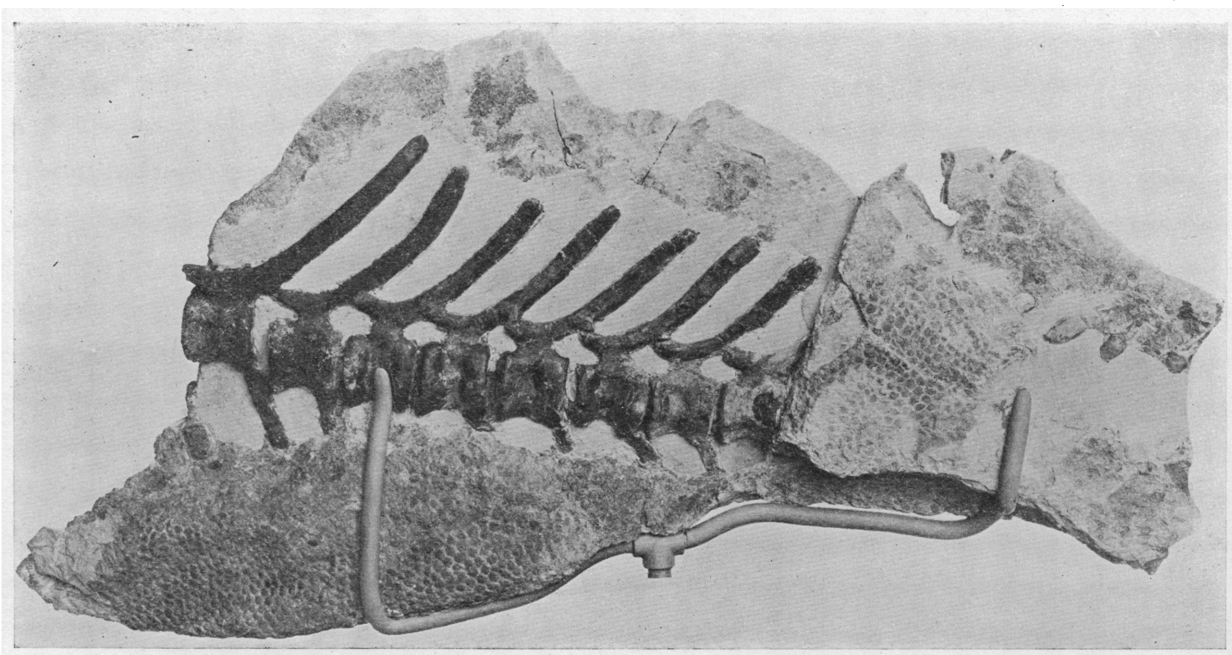

Fig. 12. Integumentary border and covering of the tail region of an undetermined genus and species of trachodont, Amer. Mus. No. 5894, showing continuous area of large pavement tubercles of inferior size. The border below the exposed caudal vertebræ appears to correspond with the ventral integumentary border of the tail.

investment of the tail, that is, the tail was entirely covered with large and regular pavement tubercles.

This inference is not drawn from the present specimen (*T. annectens*) because the whole caudal region of the 'mummy' is wanting; but the epidermal impressions are finely preserved in another specimen (Amer. Mus. No. 5894) discovered by Barnum Brown during the American Museum expedition of 1906 and provisionally referred to *T. mirabilis*. In this specimen (Fig. 12) the tail is covered with flattened pavement tubercles of larger size, or of a centimeter or more in diameter.

Theory of a Color Pattern.

The varied disposition of the tubercles into larger pavement tubercle groups on a ground tubercle area was possibly accompanied and varied in intensity by a variety of color in the pigmentation of the skin. In other words, it is a question for discussion whether the trachodonts, of this species at least, instead of being uniformly colored were not, like many of the existing reptiles, spotted or striped with patches of darker pigment arranged upon a lighter ground color.

This suggestion of a color pattern is supported chiefly by three facts: first, that the cluster areas of pavement scales concentrate and become more numerous on all the superior or dorsal surfaces of the body and limbs, just as the pigmented areas of most modern reptiles increase and intensify on the dorsal surfaces; second, along the ventral surfaces of the body, on the contrary,

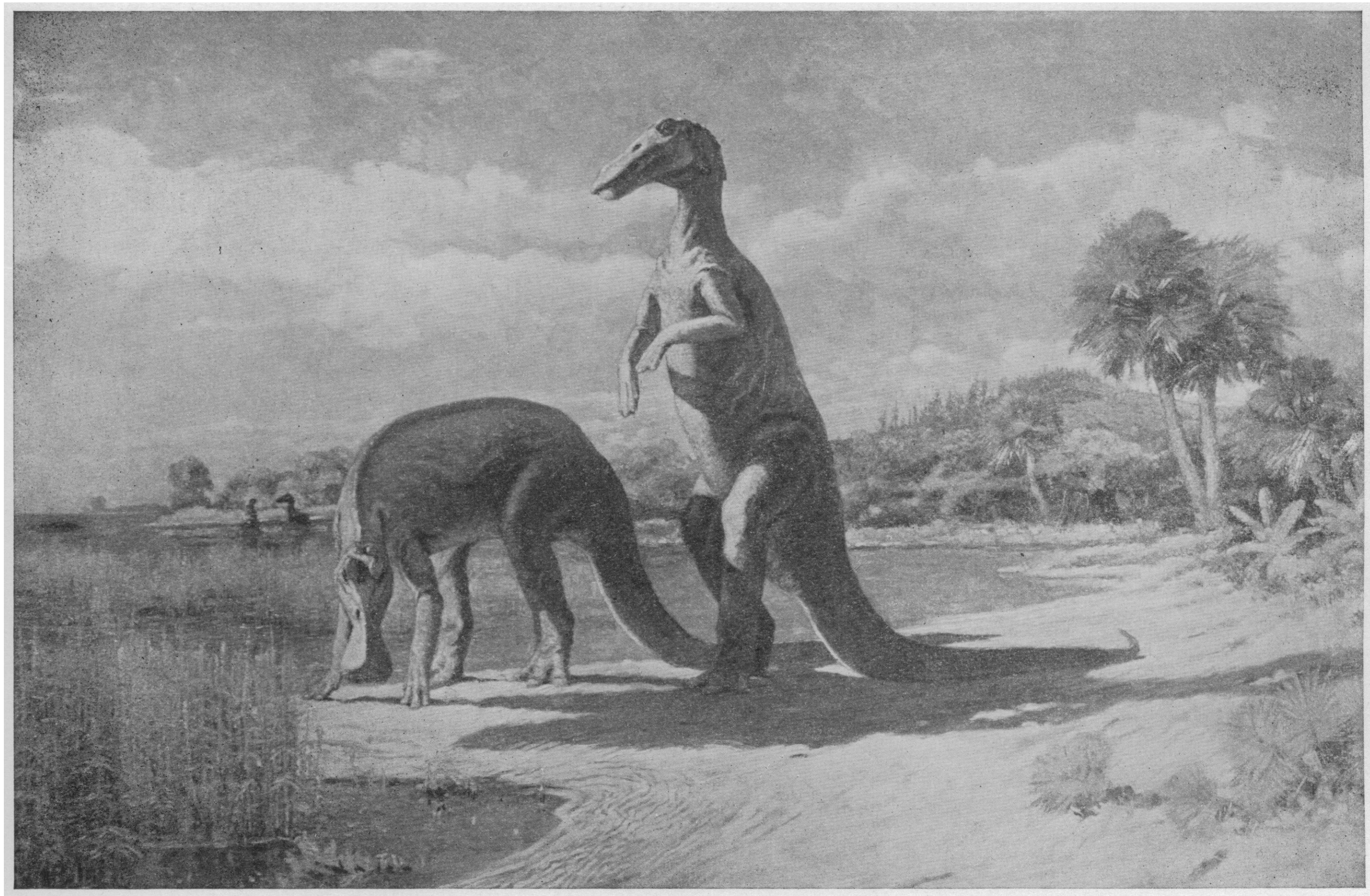

Fig. 13. Preliminary restoration of the Trachodonts of the species, *T. mirabile* Cope. Drawn by Charles R. Knight, under the Author's direction.

the pavement scales are relatively less numerous, and the cluster groups are detached and separate; third, on the inner sides of the fore limbs and on the inner sides of the thighs, especially in the upper portions, the groups of pavement scales are mostly wanting. To summarize, the parts which were least exposed to the sun correspond with the parts which in most of the existing reptiles are least supplied with pigment. A striking exception, however, is the tail, which is entirely covered with pavement tubercles, and thus according to the color hypothesis would have been entirely dark above and below.

From analogy with the existing Lacertilia and Ophidia, we may suppose that the pavement tubercle clusters represent the more deeply pigmented areas which, while widely scattered along the ventral surface of the body, were concentrated into large pigmented patches along the back, along the sides of the throat, and on the outer sides of the limbs, these being the parts principally exposed to the direct action of the sun and to the direct vision of the enemies of the trachodonts. The under surfaces of the body may have been correspondingly paler.

On this theory, the frill pattern is especially varied and brilliant, because the pavement areas are here more sharply grouped into a definite pattern than on any other part of the body.

In all parts of the body except the 'neck frill' the color pattern, if such existed, was rather irregular, the general tendency being to form a longitudinal rather than a transverse striping.

In brief, the theory that the pavement tubercles were more deeply pigmented than the ground tubercles is supported mainly by the fact of their distribution on the outer sides of the limbs and on the upper portions of the body which correspond with the more deeply pigmented areas of all existing reptiles.

Against this color-pattern theory, however, should be stated the fact that whereas the pigment of the trachodonts is theoretically correlated chiefly with the scale pattern distribution of the pavement scales, in most of the existing Lacertilia, the distribution of pigment is entirely independent of the form, pattern or distribution of the scales. In *Heloderma*, for example, in which the body is entirely covered with tubercles somewhat resembling in form the smaller tubercles of the trachodon, the distribution of pigment is entirely independent of the scale pattern.

It is to be noted further that in this species of *Trachodon*, at least, the epidermal sheathing was of an irregular character, in contrast with the very regular disposition of the scales in most of the existing Squamata. Among the Lacertilians, so far as the writer has observed, the Geckonidæ alone approach the irregular scale pattern observed in *Trachodon annectens*.

It follows that the color pattern of the trachodonts, if such existed, was also irregular and of a general cryptic, or protective character.

Habits of the Trachodonts.

Bearing upon this theory of color-pattern again is the disputed question of the terrestrial *versus* the aquatic habits of these trachodonts.

The pinnate condition of the manus described above strongly supports the view especially maintained by Barnum Brown, that the family Trachodontidæ was partly at least composed of animals which were principally aquatic in habit. If the animals belonging to the species *T. annectens* had spent any considerable part of their lives on dry land, even on the sands bordering the streams, the effects of the impact would certainly be observed in the retention of hoofs or ungues, in the coarsening of the palmar epidermis of the manus, because the fore limbs would certainly have been used occasionally, at least, in contact with the earth. There are no hoofs and the epidermal thickenings or pads are very lightly developed.

The presence of the broad marginal web of the manus and absence of enlarged tubercles either on the dorsal or ventral surface certainly tends to support the theory of a swimming rather than of a walking, or terrestrial function of the fore paddle.

As indicated in the preliminary restoration (Fig. 13) of a pair of these animals (*T. mirabile*) by Charles R. Knight, under the writer's direction, one is shown in the conventional bipedal pose, the other is in a quadrupedal pose, sustaining the fore part of the body on a muddy surface with its fore feet. In this quadrupedal pose the fore limb and manus may be considered as functioning as 'balancing' rather than as 'sustaining' organs, because in the species *T. annectens*, at least, it is evident that the manus was not used for prolonged locomotion.

(*Continued from 4th page of Cover.*)

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