

MEMOIRS
OF THE
American Museum of Natural
History.

NEW SERIES, VOL. I, PARTS I AND II

- I.—CRANIA OF TYRANNOSAURUS AND ALLOSAURUS.
II.—INTEGUMENT OF THE IGUANODONT DINOSAUR *TRACHODON*.

By HENRY FAIRFIELD OSBORN.

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NEW SERIES, VOLUME I, PART II.

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AMERICAN MUSEUM OF NATURAL HISTORY.

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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 Holzmaden, 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 <i>Trachodon mirabilis</i> , | Am. Mus. No. 5730, | Discovered by Wortman, | 1884. |
| 2. Fragment, <i>Trachodon</i> ? sp. | Am. Mus. No. 5730, | " " | ? |
| 3. " " " " | Am. Mus. No. 5863 | " " | Barnum Brown. |
| 4. Tail region, <i>Trachodon</i> ? sp. | Am. Mus. No. 5894 | " " " " | in 1906. |
| 5. Skeleton, <i>Trachodon annectens</i> , | Am. Mus. No. 5060 | " " | Sternberg in 1908. |
| 6. " <i>Trachodon</i> ? sp. | Senckenberg Mus. | " " " " | |
| 7. " <i>Trachodon</i> ? 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.

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" Fig. 1a,	" " "	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. 4a,	" " "	Key to same	p. 41
" Fig. 5,	" " "	Cervical frill region	p. 42
" Fig. 5a,	" " "	Key to same	p. 43
" Fig. 6,	" " "	Chest region	p. 44
" Fig. 6a,	" " "	Key to same	p. 44
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" Fig. 10,	" " "	Integument on forearm	p. 49
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Text Fig. 12,	Genus and species undetermined	Tail region of another Trachodont	p. 51
	(Amer. Mus. No. 5894.)		
Plate X,	<i>Trachodon mirabilis</i> , etc.	Fragments of integumentary casts	opposite p. 52
Text Fig. 13,	<i>Trachodon mirabilis</i>	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, 1a.

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. 1a) 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 $\frac{1}{13}$.

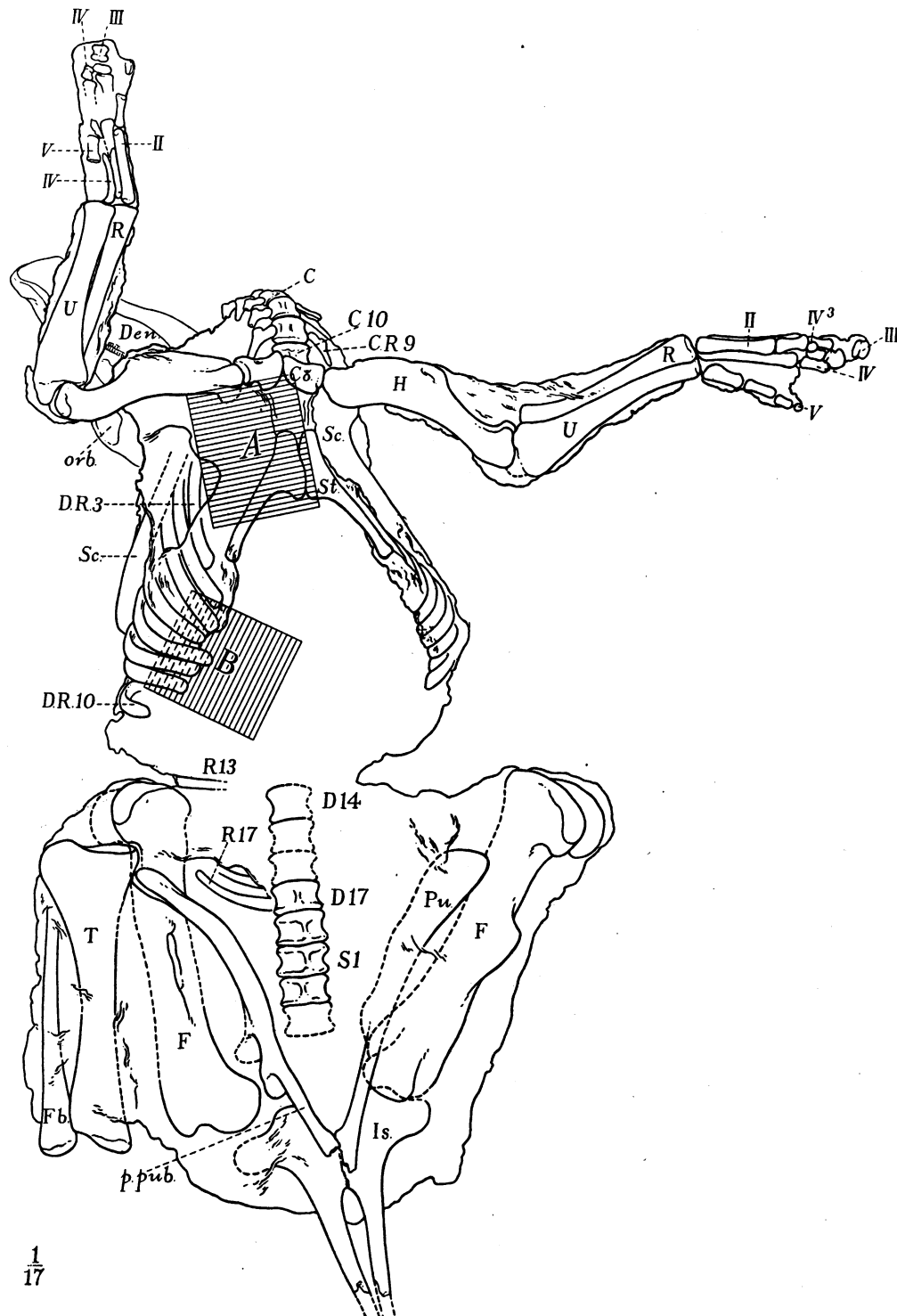


Fig. 1a. Outline of the ventral aspect of the *Trachodon annectens* 'mummy.' Designed as a key to drawings and plates. Scale $\frac{1}{17}$.
 A, location of the epidermal impression area shown in Pl. VI.
 B, location of epidermal impression area shown in Pl. VII.

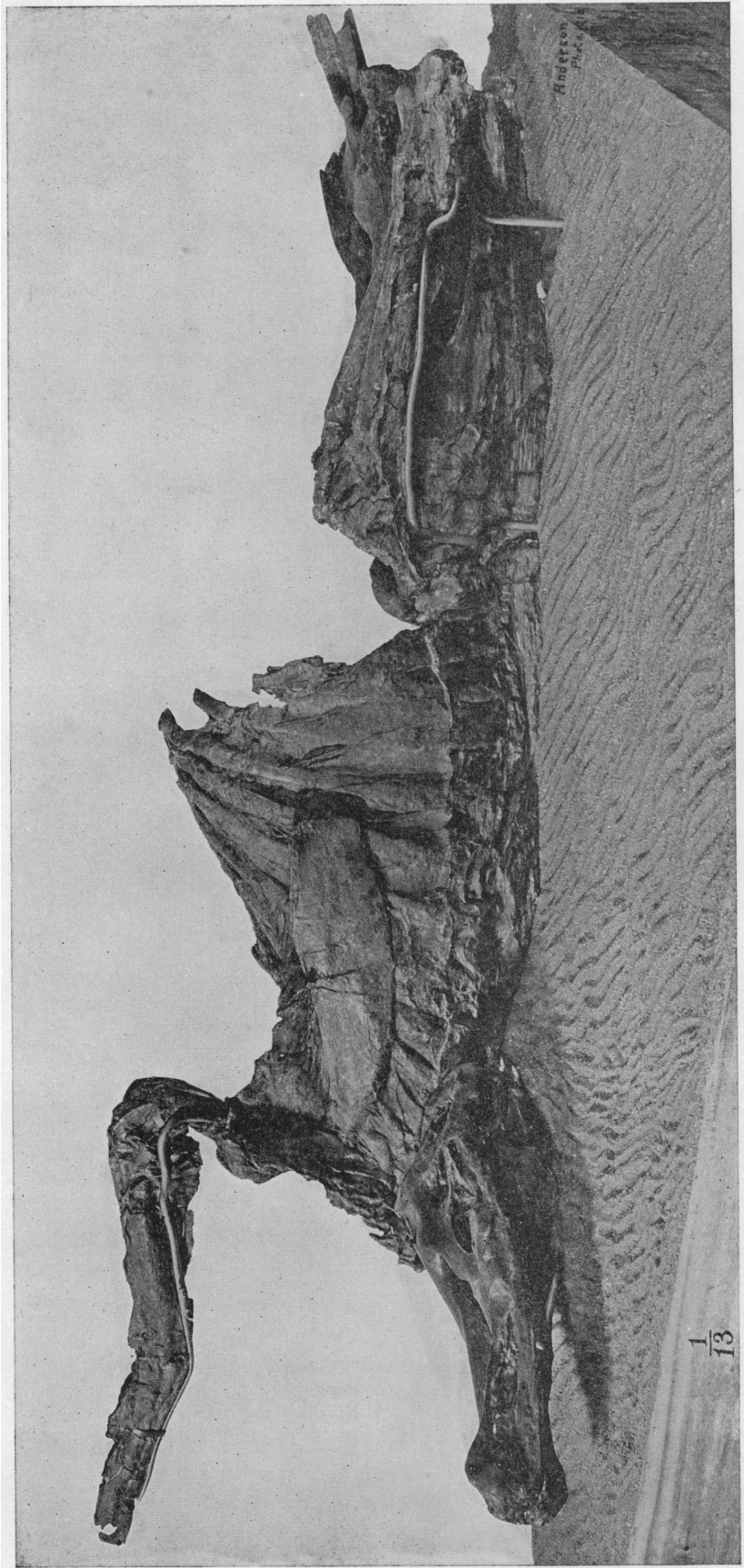


Fig. 2. View of the right side of the *Trachodon annectens* 'mummy.' Photograph by A. E. Anderson. Scale, $\frac{1}{13}$.

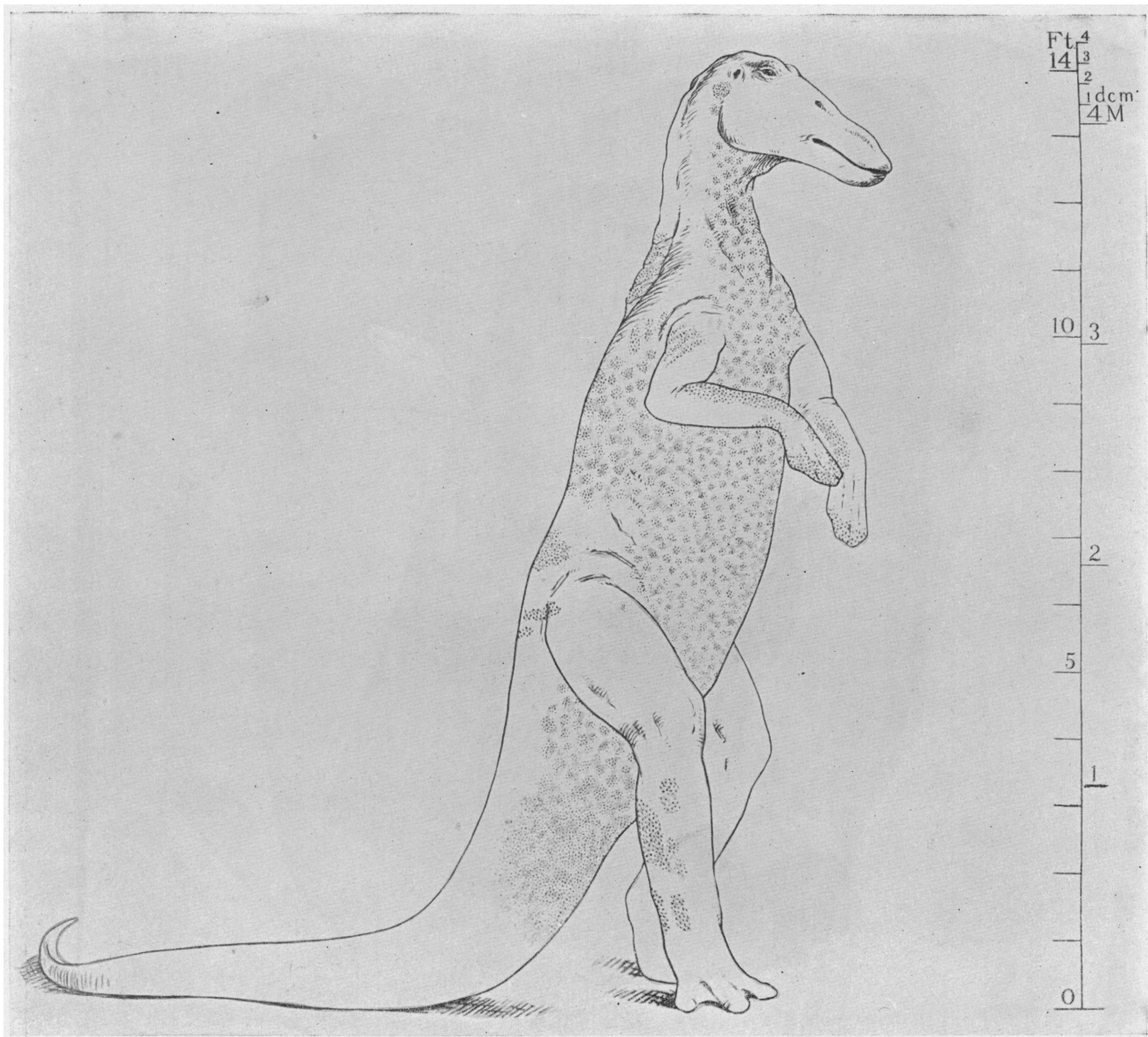


Fig. 3. Diagrammatic restoration of the body contours, integumentary outlines, and epidermal markings of *Trachodon annectens*, including the neck frill and the borders of the integument in the manus and pes. For details of the associated portions of the 'neck frill' compare Fig. 5. The 'pavement tubercle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

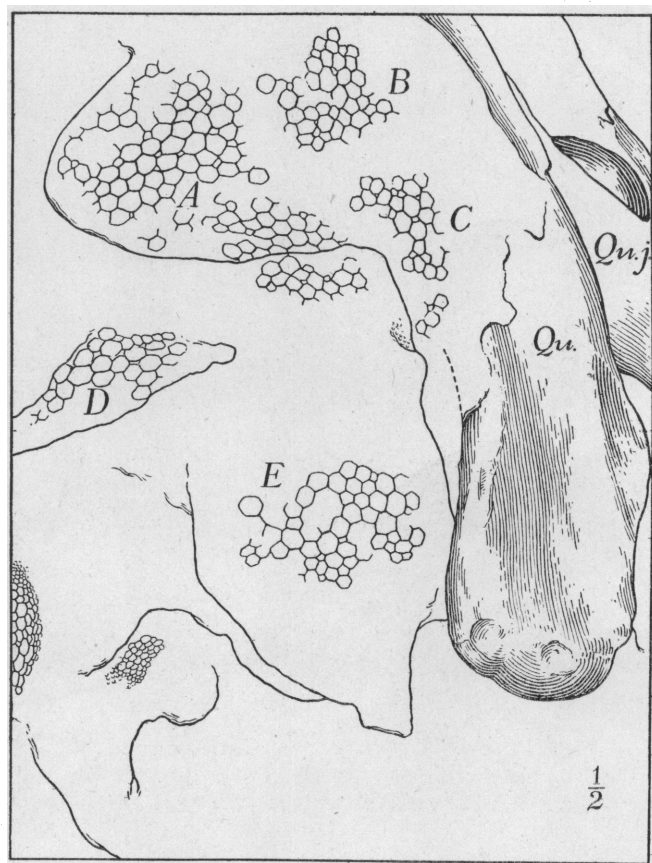


Fig. 4a. Key to Fig. 4.

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 vertebrae, 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.

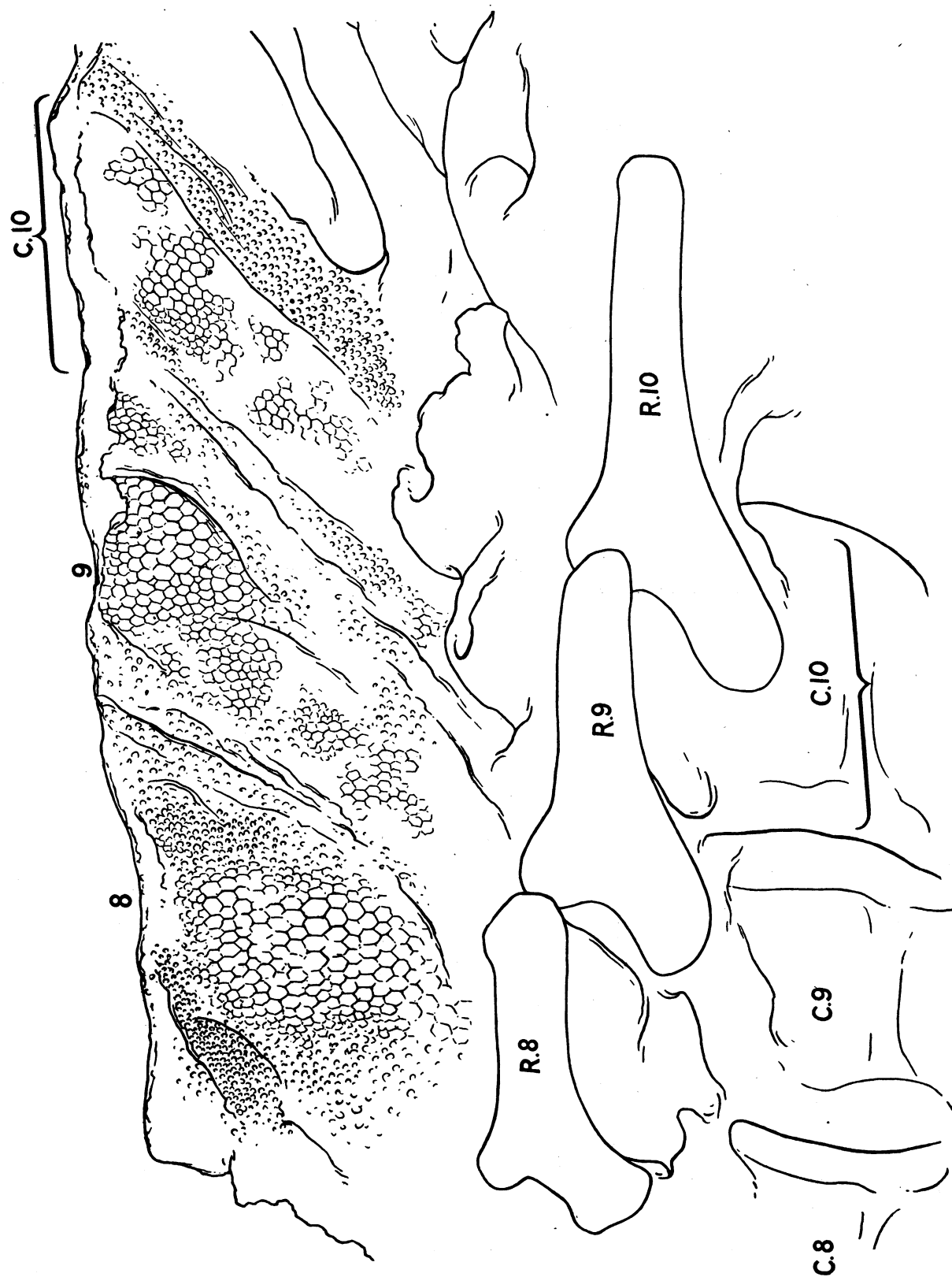


Fig. 5a. Key to Fig. 5, showing the distribution of pavement and rounded tubercles on the frill.

C. 8, C.9, C. 10, centra of cervical vertebrae 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.

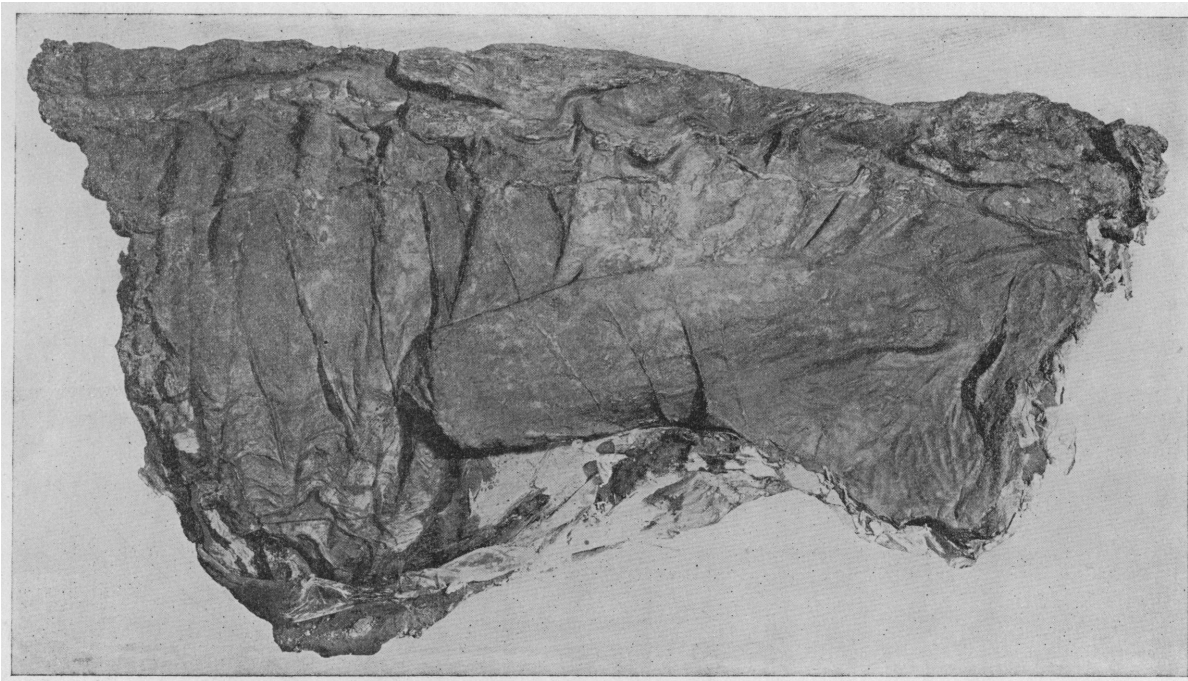


Fig. 6. Natural cast of foldings of the integument on the right side of the thorax of the *Trachodon annectens* 'mummy,' showing close appression to the ribs and scapula. Amer. Mus. No. 5060.

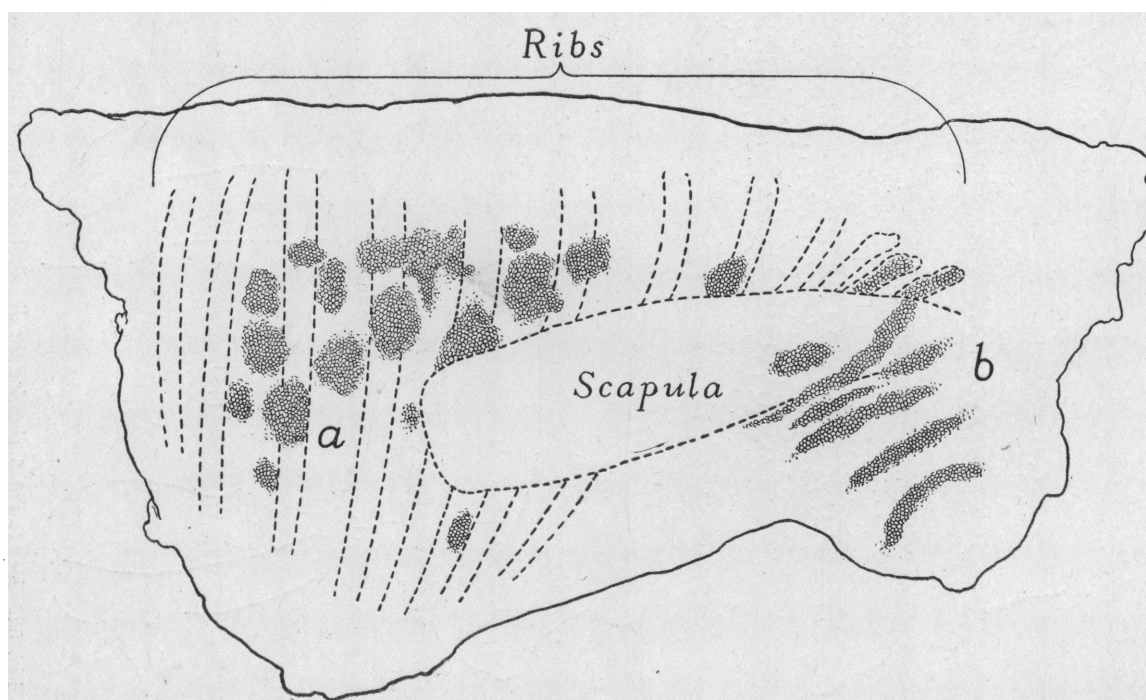


Fig. 6a. Key to Fig. 6. Showing distribution of large areas of rounded tubercles on the sides of the thorax: (a) rounded areas of pavement tubercles; (b) elongate areas of pavement tubercles above and in front of the anterior portion of the scapula.



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. 1a. 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.

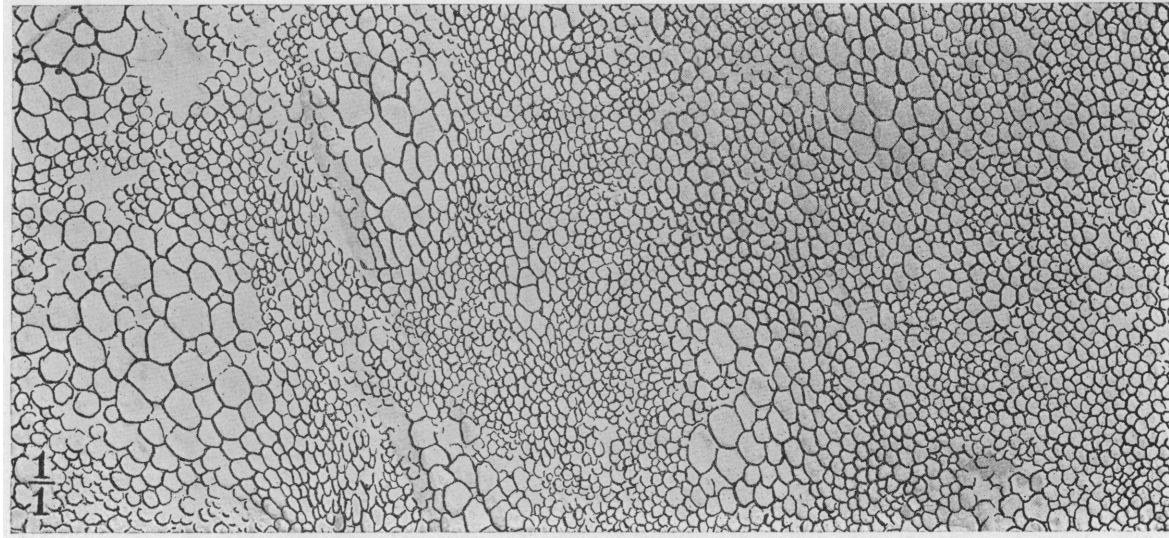


Fig. 7. Diagram showing details of the arrangement of the larger and smaller epidermal tubercles of the pectoral region; from the lower part of the area marked *A* in Fig. 1. Natural size.

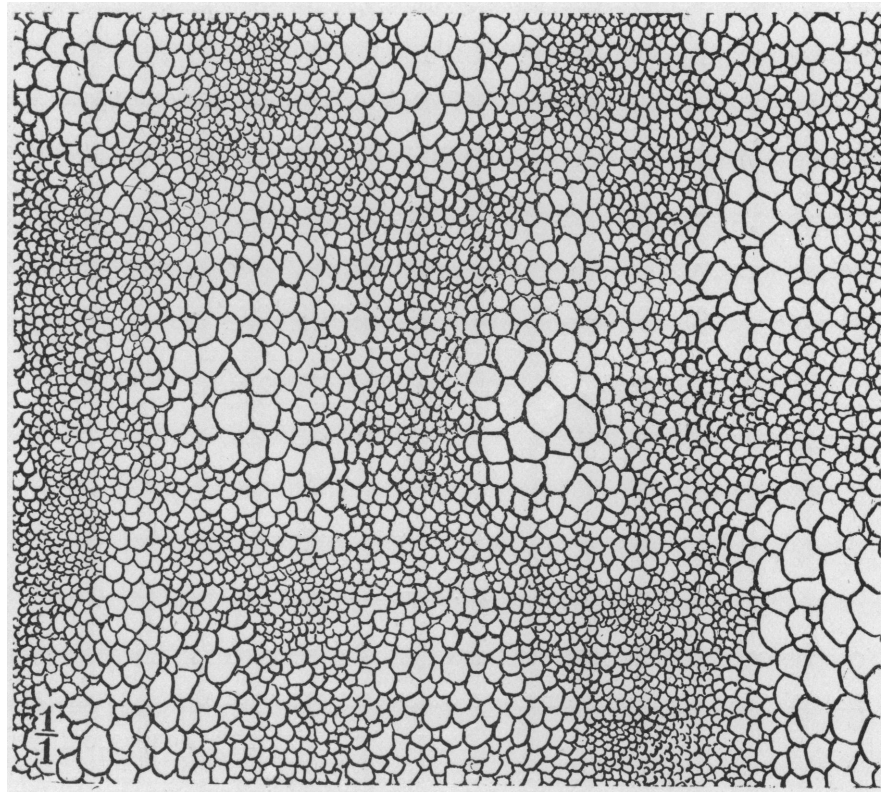


Fig. 8. Key to epidermal impressions in the abdominal region taken from the lower portion of the integument photographed in Pl. VII, showing more clearly the alternating arrangement of the clusters of large pavement tubercles upon the abdominal integument. It is possible that the pavement tubercles clusters 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-

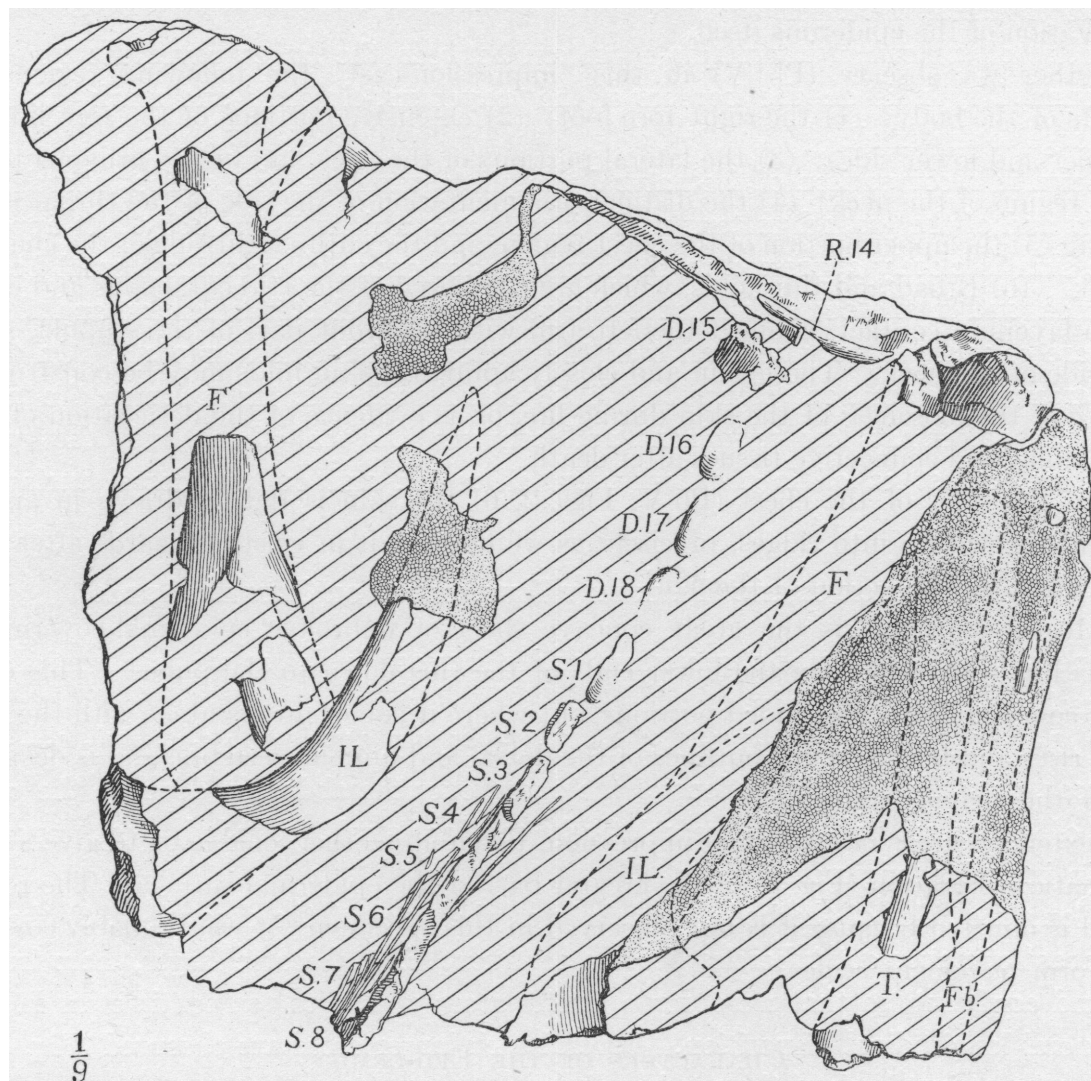


Fig. 9. Integument over the sacral and pelvic region of the *Trochodon annectens* 'mummy' showing the large and more or less confluent clusters of pavement tubercles in the dorsal region contrasted with the small and regular clusters in the abdominal integument. The darker shading indicates the areas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

IL, anterior process of the left ilium;
F, right and left femur;
T, right tibia;

Fb, right fibula;
D. 15-18, posterior dorsals;
S. 1-8, sacra.

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 tessellated 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

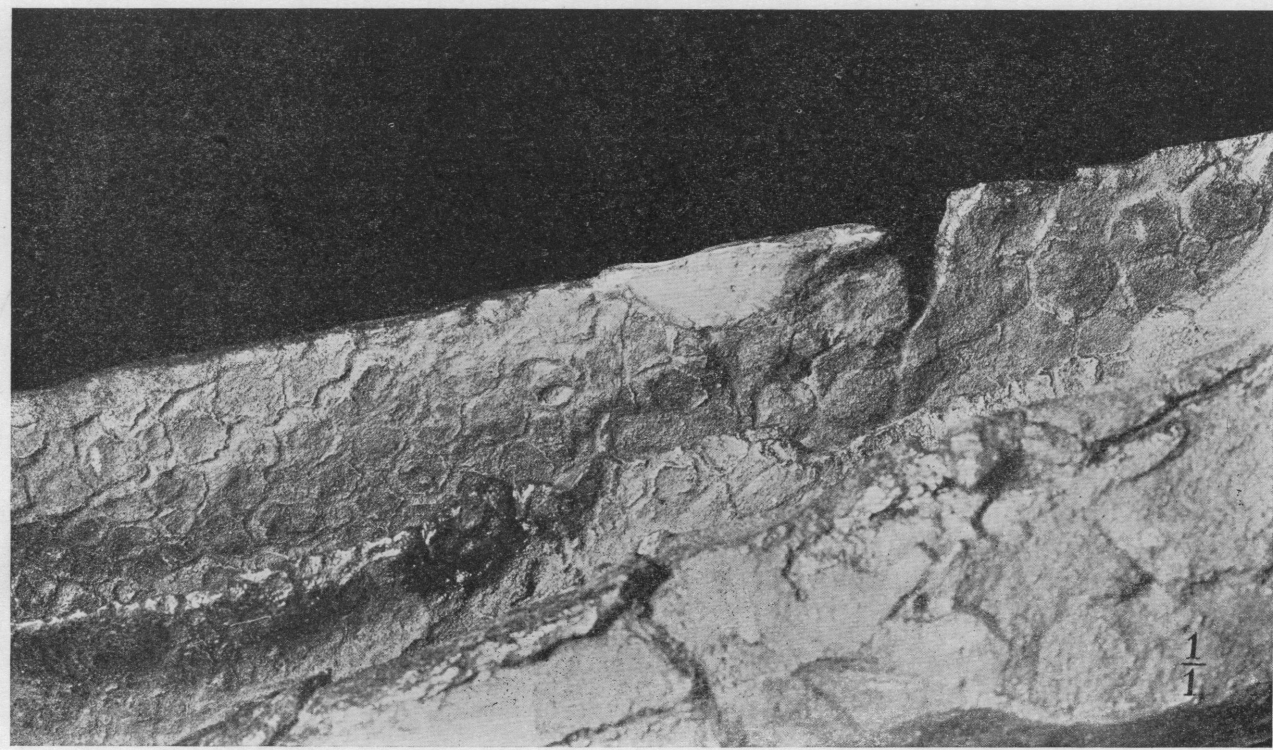


Fig. 10. Forearm integument. Natural size photograph of the large pavement scales on the outer and upper side of the left forearm of the *Trachodon annectens* 'mummy,' showing the continuous area of large irregular polygonal scales. Amer. Mus. No. 5060. Scale $\frac{1}{16}$.

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, 5a.

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 vertebrae.

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 vertebrae; 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.

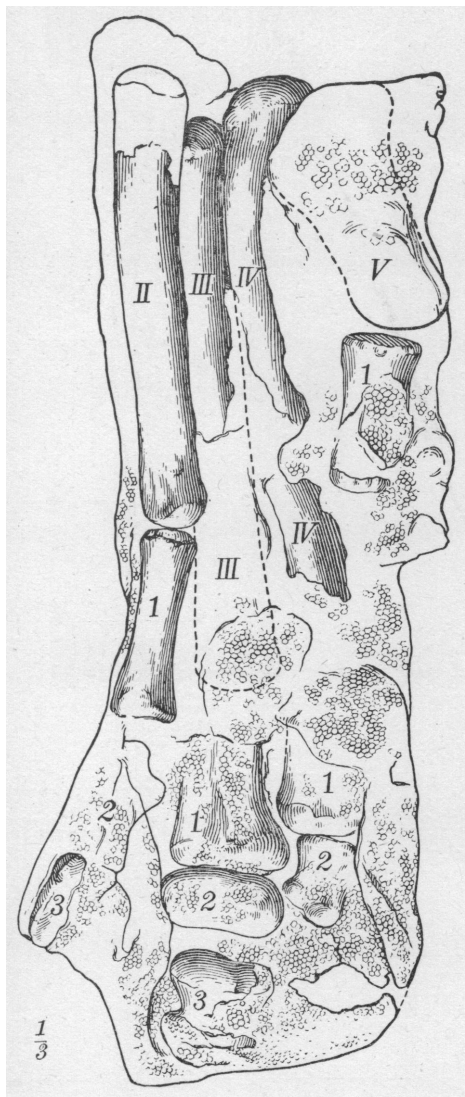


Fig. 11. Integument of the palmar surface of the right manus of the *Trachodon annectens* 'mummy,' Amer. Mus. No. 5060, showing the continuous distribution of the small pavement tubercles and apparent absence of the rounded tubercles. II-V, 2nd to 5th metapodials. Below the terminal phalanges of Mtc. 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, IIIa).

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*.

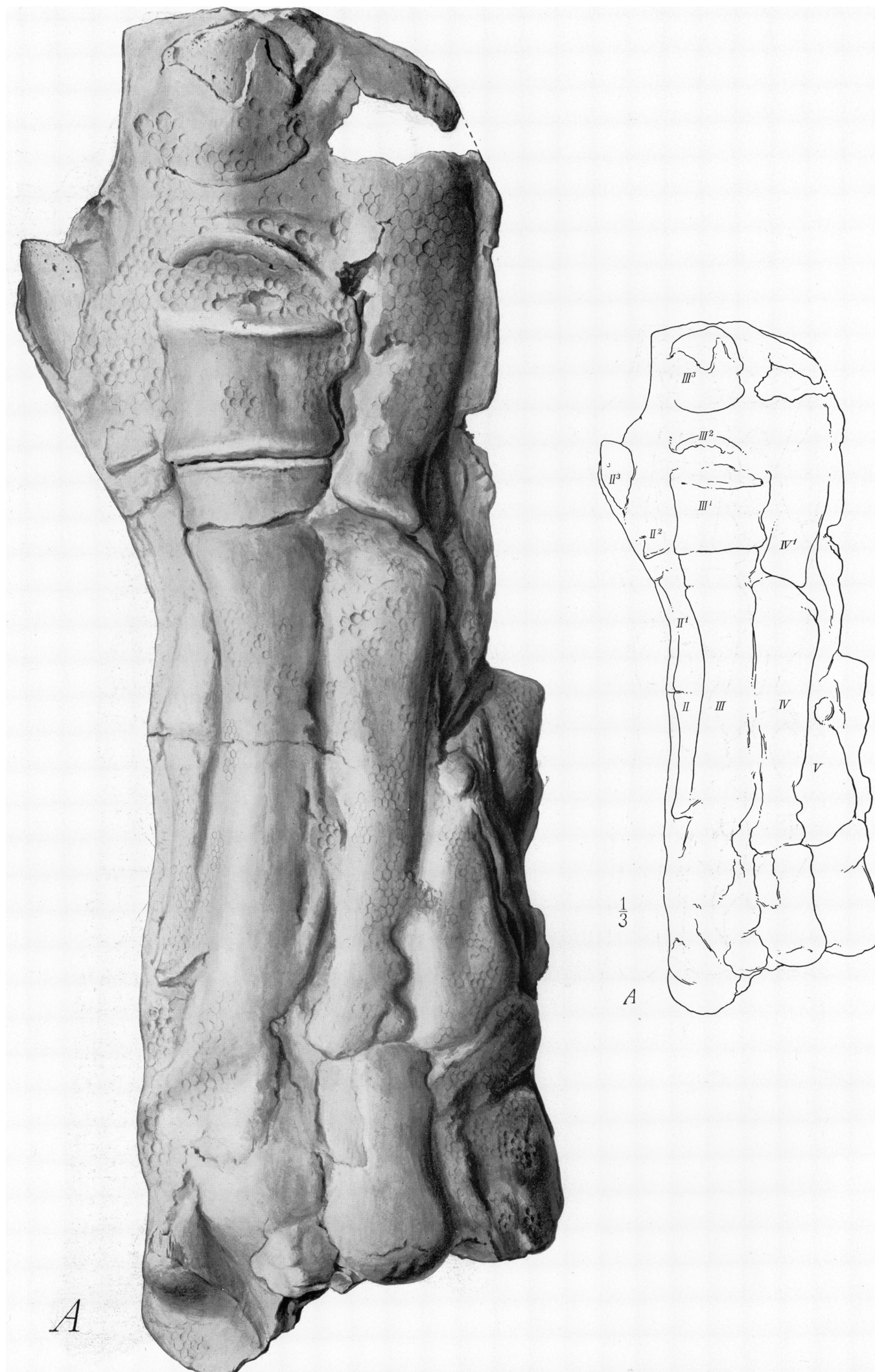


Plate VIII. Dorsal aspect of the right manus of the *Trachodon annectens* "mummy," Amer. Mus. No. 5060, showing the continuous and broken borders of the original integument together with the uniformly distributed small pavement tubercles covering the integument. This represents the dorsal aspect of the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

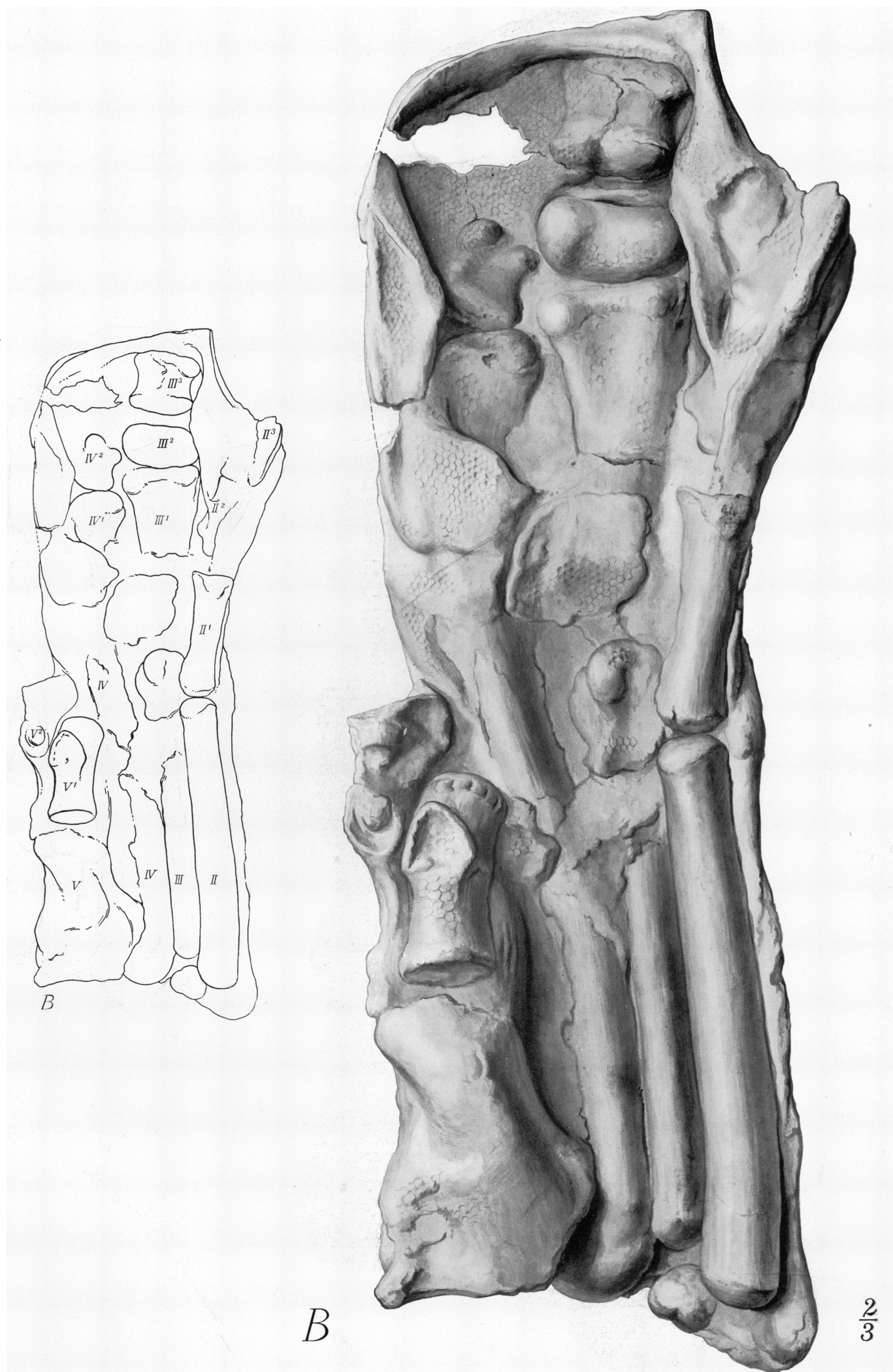


Plate IX. Palmar surface of the integument of the right manus of the *Trachodon annectens* "mummy," Amer. Mus. No. 5060, showing the continuous fold of integument extending beyond Mtc. III-IV, also the continuous and evenly distributed small polygonal pavement scales. Scale $\frac{2}{3}$.

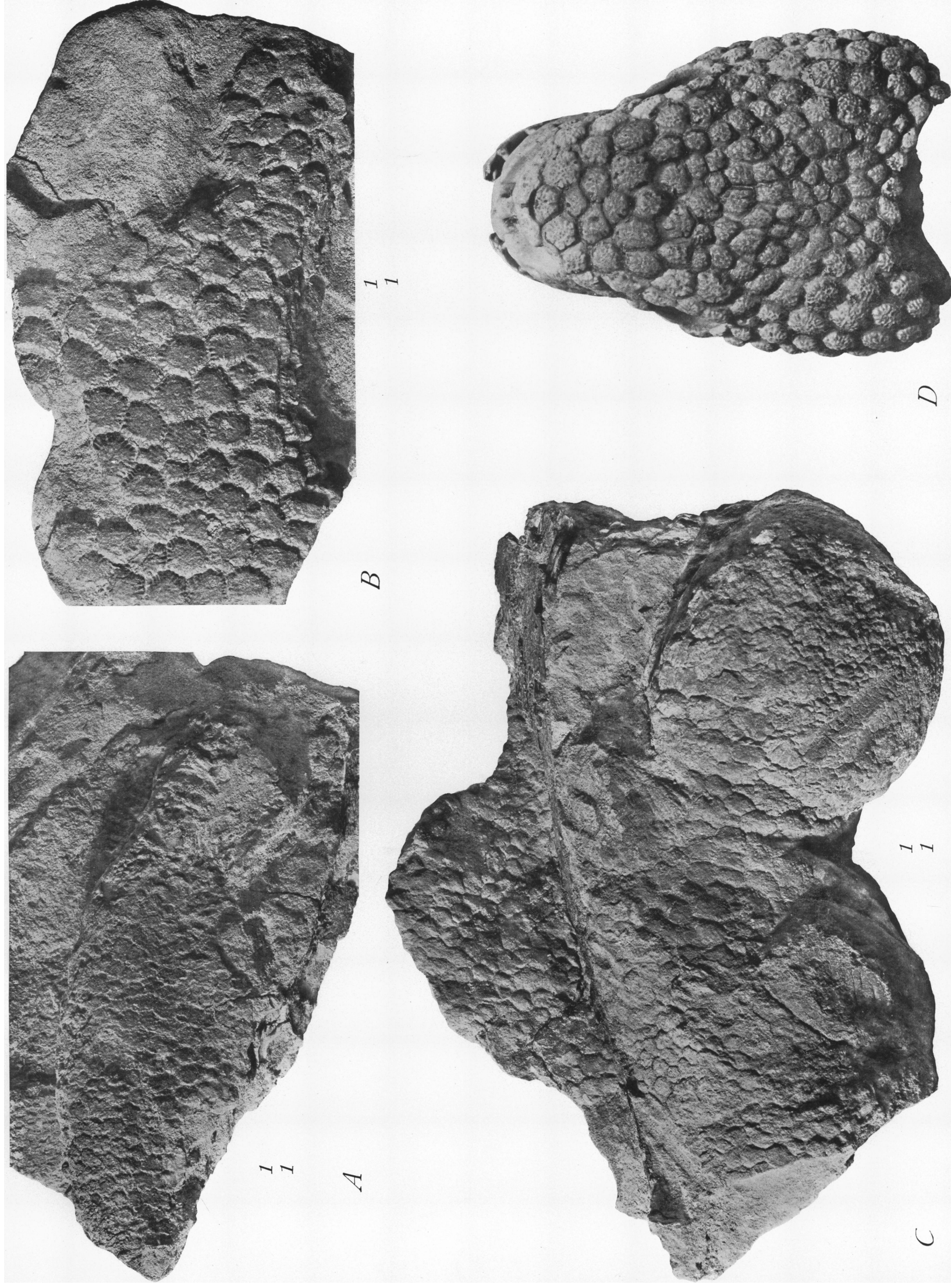


Plate X. Epidermal markings in various specimens of Trachodonts (A-C); also (D), for comparison with the tuberculated upper surface of the head of *Heloderma suspectum*, the Gila Monster.

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

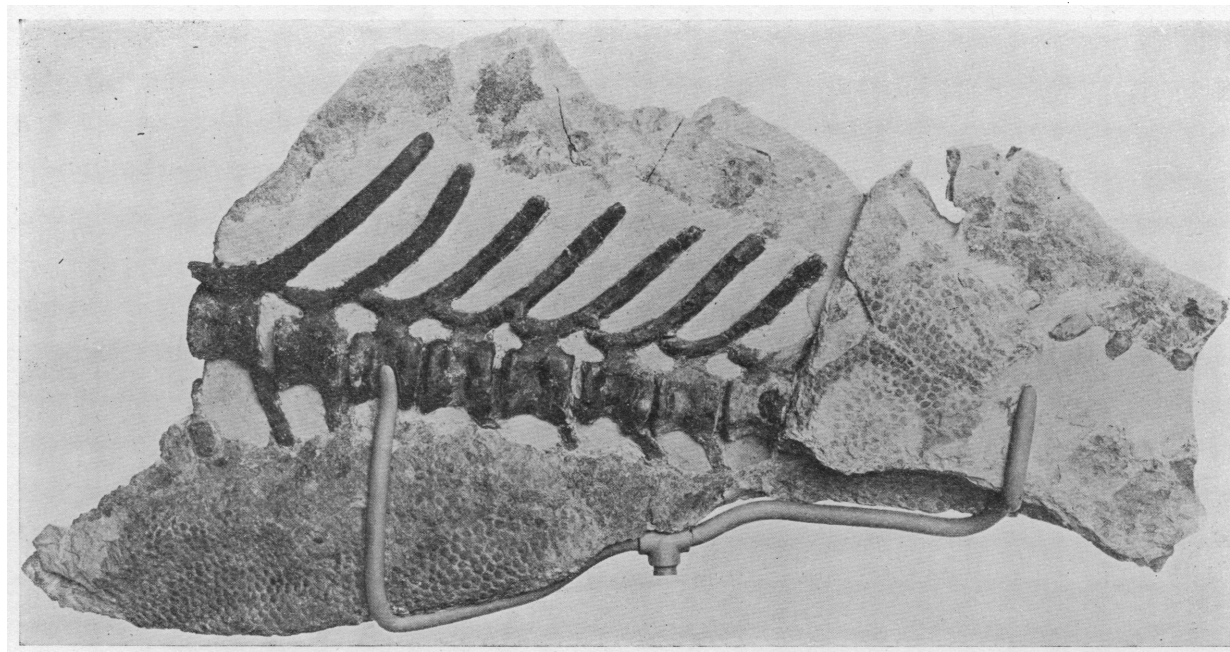


Fig. 12. Integumentary border and covering of the tail region of an undetermined genus and species of trachodont, Amer. Mus. No. 5894, showing continuous area of large pavement tubercles of inferior size. The border below the exposed caudal vertebræ appears to correspond with the ventral integumentary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

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