

MEMOIRS  
OF THE  
American Museum of Natural  
History.

VOLUME I, PARTS IV AND V.

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Osseous and Cartilaginous.

By HENRY FAIRFIELD OSBORN.

Part V.—A Skeleton of Diplodocus.

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IV.—A COMPLETE MOSASAUR SKELETON,  
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By HENRY FAIRFIELD OSBORN.

PLATES XXI, XXII, AND XXIII.

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In the spring of 1898, Prof. S. W. Williston's fine memoir upon the Kansas Mosasaurs seemed to cover the subject completely, summing up all the facts derived from the great Kansas University collection, as well as many of the results of the labors of Cuvier, Owen, Marsh, Cope, Dollo, Baur, and others. But it appears impossible to say the last word in palaeontology. Professor Williston himself has recently described a portion of the nuchal fringe of *Platecarpus*, as well as the epidermal fin contours. The remarkable specimen which forms the subject of the present brief memoir throws new and welcome light not only upon *Tylosaurus* but upon the anatomy of the Mosasaurs in general.

Together with the practically complete bony skeleton, the chief feature is the unique preservation of the cartilages of the throat and chest, portions of the larynx, trachea, bronchi, the epicoracoids, as well as the suprascapulæ, the sternum, and sternal ribs. Originally these parts were preserved entire, and we must deeply regret that before this specimen came into possession of the Museum, much damage was done to the relatively inconspicuous cartilages, in course of removal of the bones. Nevertheless Mr. Bourne, of Scott City, Kansas, who excavated the fossil, deserves great credit for the skill and care with which the conspicuous parts were removed.<sup>1</sup>

<sup>1</sup> The specimen was examined before its purchase by Dr. W. D. Matthew, and packed for shipment by Mr. Handel T. Martin. At the time no one could judge of the existence of the cartilages or of the exceptionally complete condition of the skeleton.

The specimen reached the Museum in a series of large slabs of Kansas chalk, and was worked out under the direction of Mr. Hermann, by Mr. Thompson. With one exception, all the contours of the original slabs were preserved and fitted together by their edges, as in the original bedding; therefore the animal with all its parts, excepting a few minor pieces, lies exactly as it was imbedded in the rocks. The original matrix surrounds practically all the bones, and can be distinguished from the buff-colored outlying plaster, even in the photographs, by its somewhat darker shades. The whole is mounted upon a panel twenty-five feet long and permanently placed in a corridor which is to be devoted to marine reptiles.

*Position of the Skeleton.* — The animal lies outstretched upon its ventral surface, so that all the bones are exposed upon the dorsal or lateral surfaces, excepting the left humerus and ulna, which are overturned. The skull is crushed to

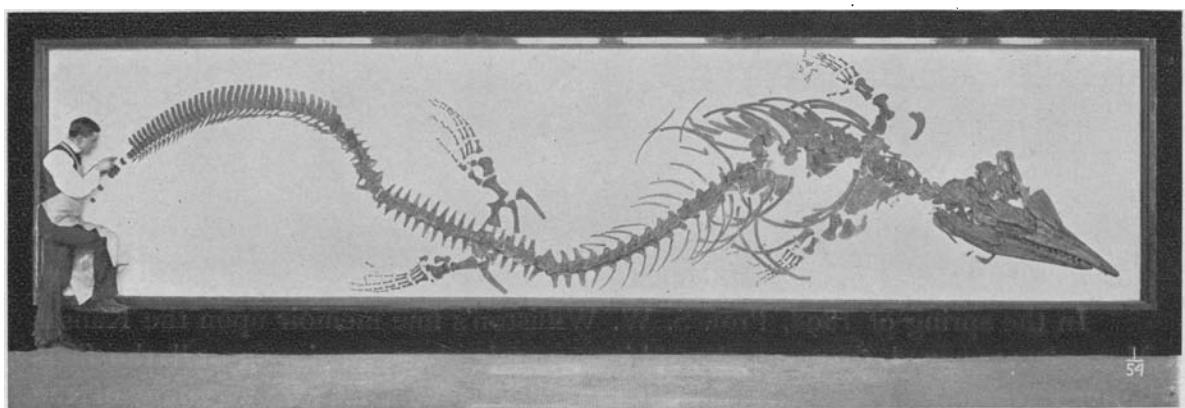


Fig. 1. Complete skeleton of *Tylosaurus dyspelor*, in frame.  $\frac{1}{4}$  nat. size.

the left, together with the vertebræ, as far back as the 6th dorsal. From the 7th to the 10th dorsals the vertebræ are confused and displaced. The 11th dorsal to 29th caudal are horizontal with the transverse processes outspread and the spines crushed to the right and left. The remaining caudals, 30th-70th, lie upon the left side apparently in a natural position. The pelvis and hind paddles have evidently shifted backwards in settling, so that the mooted question of the position of the sacral vertebræ cannot be positively settled by this specimen.

*Examination and Restoration.* — The study of the animal has been coöperative. Dr. W. D. Matthew has carefully examined several regions, and made a number of original suggestions and valuable criticisms in points of interpretation, especially as to the remarkable tail curvature, the atlas complex, and the general structure of the vertebræ. Dr. J. H. McGregor has greatly aided the writer in studying and restoring the sternal region. The photographs are the work of Mr. A. E. Anderson. The drawings are by Mr. Bruce Horsfall.

*Tylosaurus dyspelor Cope.*

*Specific Characters.* — This specimen agrees very closely in size with Cope's cotype of *T. (Liodon) dyspelor*, found in 1871 at Fort Wallace, Kansas, and described by him in the 'Cretaceous Vertebrata' (p. 167). The skull agrees exactly in size with the fine one mounted in the Munich Museum, described by Merriam (1894, Taf. II) as *T. proriger*. Size is no criterion, or at best an uncertain criterion of a species, but Williston advances (1898, p. 175) no other satisfactory means of separating *T. dyspelor* from *T. proriger*. Thirty-five feet is the length assigned by this author to the largest Tylosaurs, a length considerably exceeding that of the present specimen. It is evident that a young *T. dyspelor* might exhibit exactly the measurements of *T. proriger*.

We observe, however, in this specimen certain characters which may possibly prove to specifically distinguish this type from *T. proriger*, as follows :

1. 22 dorsals. Williston assigns 23 dorsals to *T. proriger*.
2. No rib upon the axis. A rib if present upon C.3 was certainly very small. Williston figures ribs upon both axis and C.3.
3. A dorsal curvature of the mid-region of the tail, not observed in *T. proriger*.
4. Phalanges in the manus estimated at 39. In *T. proriger*, same estimated at 47.

None of these characters, however, are absolutely determined in both types, so as to be clearly distinguishable. A summary of the chief anatomical characters is given in the conclusion.

## MEASUREMENTS AND PROPORTIONS.

## WITH SLIGHT CORRECTIONS FOR CRUSHING.

	Eng. Meas.	Metres.
Skull, from back of supratemporal arch to rostrum .....	3' 11"	1.19
Jaw, angle to rostrum, approximate.....	3' 10"	1.16
Seven cervical vertebræ, actual.....	1' 11"	.58
Twenty-two dorsal vertebræ, actual.....	7' 11"	2.41
Ten dorsals, with sternal ribs, actual.....	3' 7"	1.09
Twelve dorsals, with floating ribs, actual.....	4' 11"	1.32
Seventy caudals and pygals, actual length, as mounted (including spaces left for eight intermediate caudals towards extremity of tail).....	13' 9"	4.20
Total length of tail, estimated.....	15'	4.57
Fore paddle from head of humerus to tip, estimated .....	2' 11"	.90
Hind paddle from head of femur to tip .....	3' 3"	.98
Total length from tip of rostrum to last, or 78th, caudal, as mounted.....	27' 4 1/2"	8.34

According to Williston the tail terminates very abruptly in *Tylosaurus proriger*, in contrast with its gradual and slender termination in *Platecarpus*, as described below. If this was the case in this specimen of *T. dyspelor*, we

should not allow more than 15 inches or 38 centimetres additional, giving us a total length of about 29 feet or 8.83 metres.

The *proportions* of different regions of the body, as Williston has shown, are very characteristic of different genera of Mosasaurs. In this individual the total of 29 feet or 9 metres is roughly distributed as follows:

	Feet.	Metres.
Head and jaw.....	4	1.22
Neck.....	2	.61
Back .....	8	2.44
Tail.....	15	4.56
Total.....	<u>29</u>	<u>8.83</u>

Thus the back is four times the length of the neck, twice the length of the head, and about one half the length of the tail. In other words, the tail is longer than the other regions of the body combined. These proportions are carefully observed in Mr. Knight's restoration.

#### SKULL.

##### PLATE XXI.

The skull is crushed over to the left, and thus exposes the right side of the face, the left external nares, the naso-premaxillaries (*pmx.*), maxillaries (*mx.*) lachrymals (*la.*), prefrontals (*pr. f.*), and the complete undistorted upper surface of the frontals (*fr.*), perforated posteriorly by the pineal foramen.

From this point the supratemporal arcade (postfronto-orbital, *pf. o.*, and prosquamosal, *pr. s.*) extends upwards and backwards, making an uplifted acute angle with the squamosals (*sq.*) and squamo-parietal bar. In the space below this angle appear the parietals (*pa.*), proötics (*pro.*), exoccipitals (*eo.*, = exoparoccipitals).

The occipital bones enter to a limited degree into the condyles. The basi-cranial axis is beautifully shown:

Basioccipitals, *bo.*, with prominent basioccipital processes (which are lacking in *Varanus*).

Basisphenoid, *bs.*, with two pterygoid processes directed downwards and forwards (as in *Varanus*).

Presphenoid, *ps.*, a long splintered bar extending over the displaced left pterygoids and sclerotics, *scl.*

In the centre of the skull mass lie the left jugals, *ju.*, beneath which are the left pterygoids, *pt.*, and the right pterygoids. The right jugals lie below the jaw. The ectopterygoids are possibly represented by a small bone lying just above the proötics. The exposure of the left pterygoid is interesting because it displays a large fossa for

the epipterygoid. This element itself, ?*ep.*, is probably represented by a large rod-like bone<sup>1</sup> lying beneath the basisphenoid.

At the inferior extremity of this bone appears a slender rod which possibly represents the columella auris, or stapes.

*Supraciliare.* Below the jaw is a small element which can only be identified as a portion of the supraciliare.

The measurements of the chief of these elements are as follows:

	Mm.
Frontal plus premaxilla.....	.830
Lachrymal to tip of rostrum.....	.670
Prosquamosal and postfrontal to back of orbit.....	.305
Basioccipital to extremity of presphenoid.....	.333
Dentary, lower border.....	.665
Quadrata, greatest diameter (six inches).....	.152

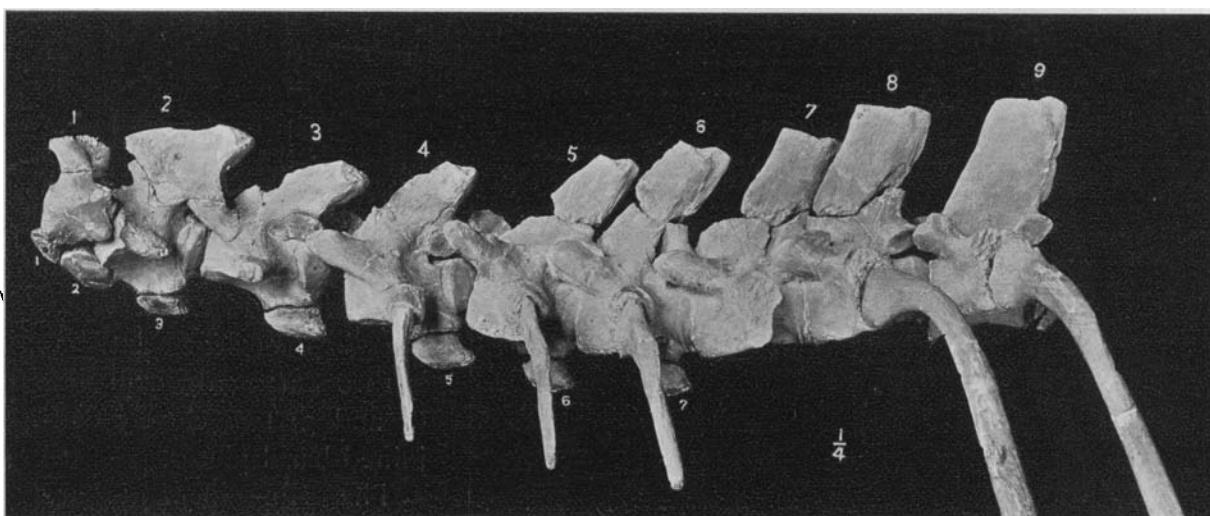


Fig. 2. Cervical series of *Platecarpus coryphaeus*, lateral view, with all bones in place.  $\frac{1}{4}$  nat. size.

The elements of the lower jaw can be readily determined, as shown in the restoration of the skull, namely the articular, surangular, coronoid, splenial, presplenial, and dentary. This is upon the acceptance of Baur's nomenclature, which is done with some hesitation. The number of teeth cannot be positively determined in either the upper or lower jaws. This specimen agrees with Merriam's figure (1894, Taf. II) in the absence of a sharp downward depression below the junction of the hinge of the jaw.

Both quadrates are displayed, that upon the right side giving a clear view of the characteristic elongation of this bone and its curvature for the ear membrane.

<sup>1</sup> This very characteristic Lacertilian element is omitted in Williston's drawings and descriptions.

## VERTEBRAE.

## PLATES XXI AND XXII.

There are positively *seven cervicals*, the number assigned to all the American Mosasaurs by Williston, and this point is of considerable importance as bearing against the supposed Dolichosaurian affinities of the Mosasaurs.

In this specimen there are certainly *twenty-two dorsals*, while Williston assigns *twenty-three dorsals* to *Tylosaurus proriger*. Merriam assigns twenty-three dorsals to *Tylosaurus* (*op. cit.*, p. 15). Williston is undoubtedly correct in placing the pelvis upon the first non rib-bearing vertebra, which thus represents the *sacral*. There are no lumbars. The number of pygals, or non chevron-bearing caudals, cannot be determined, because many chevrons are not exposed.

The vertebral formula is therefore as follows:

Cervicals .....	7
Dorsals, with sternal ribs.....	10
Dorsals, with floating ribs.....	12
Sacrals.....	1
Caudals and pygals.....	72 + (= 86 <sup>1</sup> )

## CERVICALS.



Fig. 3. Atlas and axis of *Platecarpus coryphaeus*, with left neural arch of atlas, *n.a.*, removed. Same specimen as above.  $\frac{1}{2}$  nat. size.

The ATLAS complex consists of *five* pieces, quite out of normal position. As determined by Dr. Matthew, the *odontoid* (pleurocentrum) is thrust upwards, exposing (2 and 3) two closely conjoined basal pieces.

The same elements are shown in their normal relations in a fine specimen of *Platecarpus* (Figs. 2 and 3).

What is the origin and destiny of these parts? This question deserves a brief digression.

#### INTERPRETATION OF THE ELEMENTS OF THE ATLAS AND AXIS VERTEBRAE IN MOSASAURS, LACERTILIA, AND RHYNCHOCEPHALIA.

The prevailing interpretations of the complex elements of the first two vertebrae of the neck are as follows:

<sup>1</sup> The number assigned to *T. proriger* by Williston, *op. cit.*, p. 143.

1. The pair of small dorso-lateral elements in Rhynchocephalia (see Fig. 6), certain Lacertilia, Crocodilia, Dinosauria, Pterosauria, Chelonia, are regarded by most authors as vestiges of a *proatlas*, or degenerate vertebra between the atlas and the skull. As remarked by Baur, these pieces correspond in position with 'neurapophyses.'
2. The lateral pieces of the atlas proper are unquestionably neural arches or neurapophyses.
3. The odontoid process (of the axis) is regarded as the *pleurocentrum* or *centrum* proper of the atlas, which is secondarily attached to the axis.
4. The anterior ventral piece or lower element of the atlas ring is, however, also described as a *centrum* (*i. e.*, pleurocentrum) by Baur<sup>1</sup> in his latest paper. By Gegenbaur, as possibly an 'hypapophysis' (*Vergleichende Anatomie*, 1898, p. 249). In an unpublished lecture chart Baur interprets both ventral pieces as intercentra.
5. The posterior ventral piece is described as an 'intercentrum' by Baur, as the 'atlanteal hypapophysis' by Williston, in the Mosasaurs.

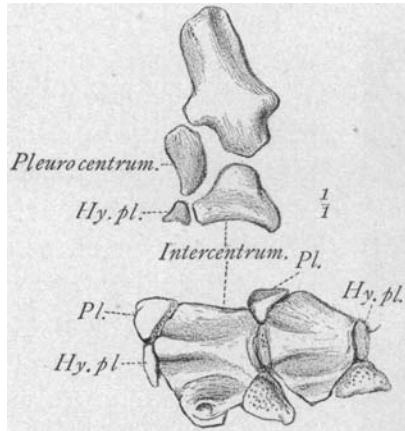


Fig. 4. Rachitomous vertebrae of *Chelydosaurus*. Fritsch. *Hy. pl.*, hypocentrum pleurale. *Pl.*, pleurocentrum. Intercen. or hypocentrum arcuale. After Fritsch.

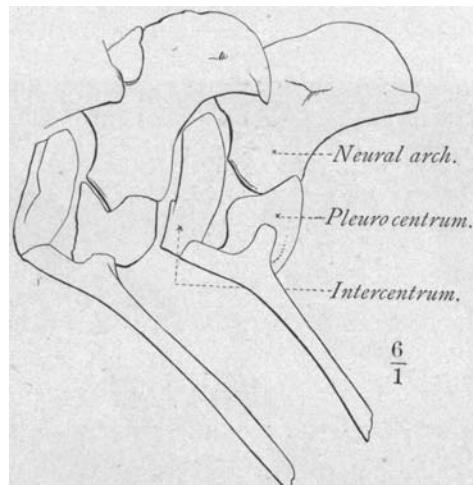


Fig. 5. Rachitomous type of *Discosaurus* Credner. Head of rib articulating with intercentrum. Tubercle of rib articulating with pleurocentrum. After Credner.

The *rachitomous prototype*.—Among the Stegocephalia we find types in which every vertebra is composed of 6 pieces as figured by Fritsch<sup>2</sup> (*Chelydosaurus Uranii*). It is possible therefore that the proatlas and atlas may represent, not two vertebrae, but one—namely, a *persistent rachitomous type*, an interpretation which would accord with the testimony of the cranio-spinal nerves. In this case the two basal pieces of the atlas of the Mosasaurs would be accounted for as

<sup>1</sup> Ueber den Proatlas einer Schildkröte. Anat. Anz., Bd. X, 1894, p. 352.

<sup>2</sup> Fauna d. Gaskohle Bohemens, Vol. II, p. 25.

homologous with the 'hypocentrum pleurale' and 'hypocentrum arcale,' of Fritsch. This is improbable.

A likelier rachitomous prototype is that given by *Discosaurus* Credner<sup>1</sup> in which it is seen (Fig. 5) that the intercentrum is in front of its corresponding pleurocentrum or centrum. Such a vertebra consists of 5 pieces. If from such an atlas prototype the pleurocentrum (*pl.*) were to be transformed into the odontoid process, the *first result would be to bring the atlas and axis intercentra together without change of form.*

This is exactly what we find in *Platecarpus*; the photographs represent a condition in which the intercentra 1 and 2 are similar in their wedge-shaped form and entirely free from the other elements of the atlas and axis (Figs. 2, 3).

#### *Conditions in the Mosasaurs, Lizards, and Sphenodon.*

This condition of *Platecarpus* is probably a primitive one. The secondary modification has been of three kinds:

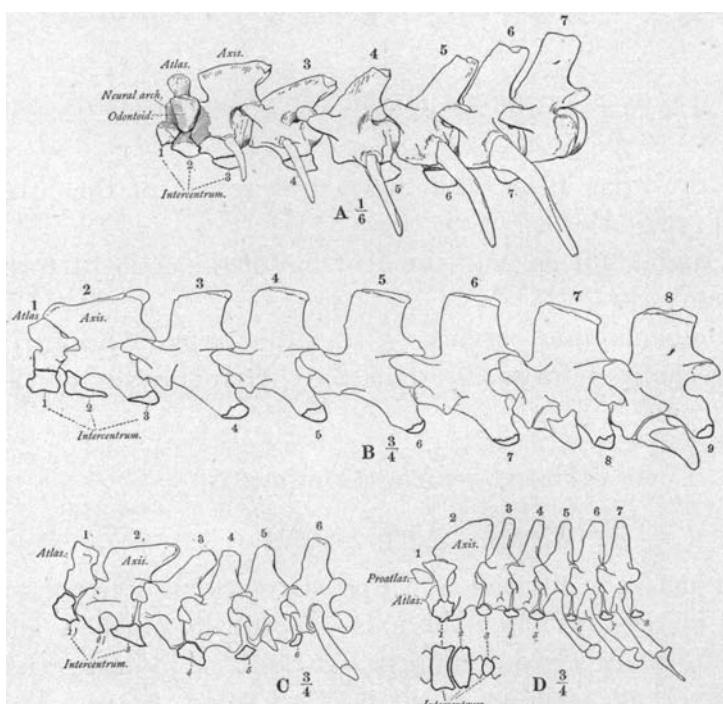


Fig. 6. Cervical Centra (Pleurocentra) and Intercentra of Lizards, *Mosasaur*, and *Sphenodon*. Intercentra 1-9 in heavy lines.

- A. *Platecarpus*, with left side of neural arch removed from Atlas, exposing odontoid.
- B. *Varanus*, with intercentra at tips of hypapophyses.
- C. *Cyclurus*, with intercentra in primitive relations except upon Axis.
- D. *Sphenodon*, with intercentra in primitive relations except upon Axis.

1. Conversion of the atlas intercentrum, into the basal piece of the atlas ring, by loss of its wedge shape and broadening of its contact with the neural-pophyses (e. g., *Varanus*, *Cyclurus*).

2. Lateral or complete union of the axis intercentrum 2 with the anterior portion of the axis centrum (e. g., *Cyclurus*, *Sphenodon*).

3. Shifting of the intercentra 3-7 forwards upon the hypapophyses of the preceding vertebrae (e. g., *Varanus*, *Platecarpus*).

The following modifications are well illustrated in the accompanying diagrams:

<sup>1</sup> Die Stegocephalen u. Saurier aus d. Rothliegenden d. Plauen'schen Grundes. IX Theil, Berlin, 1890, Taf. X, fig. 10.

- A. In *Platecarpus*, atlas and axis intercentra free and wedge-shaped. Intercentra 3-7 shifted forwards upon the *short* hypapophyses of centra 2-6.
- D. In *Sphenodon*, a proatlas; intercentrum 1 loosely connected with neural arch of atlas; intercentrum 2 completely coalesced with axis; intercentra 3-7 in their primitive position.
- B. In *Varanus*, intercentrum 1 broadly connected with atlas neural arch; intercentrum 2 forming an anterior hypapophysis upon axis, loosely connected in young, suturally united in adults; intercentra 3+ forming tips of the *long* hypapophyses of centra 2+. (This hypapophysial connection of the intercentra is an advance upon that initiated in *Platecarpus*.)
- C. In *Cyclurus*, intercentrum 1 broadly united with atlas ring; intercentrum 2 completely coalesced with axis; intercentra 3-4 in primitive position, but expanding to function as hypapophyses; intercentra 5-6 small, in primitive position.

This history of the atlas and axis complex in the Mosasaurs, Lizards, and *Sphenodon* may be summarized as follows:

1. The intercentrum of the atlas fuses with the neural arches of the atlas to form the basal portion of the ring.
2. The intercentrum of the axis fuses with the centrum of the axis to form a kind of hypapophysis.
3. The intercentra of the remaining cervicals 3-7 either remain primitive in position or are shifted forwards upon the hypapophyses of the next vertebra in front.

#### VERTEBRAE OF *TYLOSAURUS DYSPELOR* (Continued).

##### PLATE XXI.

The *axis* of *Tylosaurus* has been figured by Cope (*Cretaceous Vertebrata*, Pl. 29) with a narrow spine; in this specimen the axis is vertically crushed, and the form of the *spine* cannot be positively determined, but the base indicates that it was broad like that of *Platecarpus*; the *diapophysis* (transverse process) is a broad flattened lamella which bears no sign of a distinct rib facet; such a facet is present in *Platecarpus*, and is figured by Williston in *T. proriger* (*op. cit.*, Pl. 72). This vertebra undoubtedly bore an intercentrum.

Cervicals 2-6 are distinguished by the following characters:

1. Broad diapophysial plates (broader than those of *Platecarpus*, Fig. 2), which bear rib facets posteriorly. The rib upon C. 3, if present, was very small.
2. Neural spines, increasing in antero-posterior diameter.
3. Stout zygapophysial processes and facets.

4. The intercentra are figured upon C. 2-C. 6 (as in *Platecarpus*) by Williston, but cannot be observed in this specimen, owing to the horizontal flattening of the vertebræ.

The cervical ribs are thus less strongly developed than in *Platecarpus*, in which they are present from C. 2 to C. 7.

Cervical 7, according to Williston, in *T. proriger* has no intercentrum (hypophysial process). Cervicals 6 and 7 bear large ribs to support the muscles of the scapula which directly overlaps these ribs. (See Restoration, p. 186.)

#### DORSALS.

The ten anterior dorsals, connected directly with the sternum, are powerful vertebræ with very broad spines, well shown by photography, as they lie in side



Fig. 7. Anterior chest section of *Tylosaurus dyspelor*.  $\times \frac{1}{10}$ .

view. Dorsals 1 and 2 have broad, rib-bearing, diapophysial lamellæ like the cervicals, the rib facet being opposite the centre of the vertebra.

In dorsals 3-10 these lamellæ are absent; the diapophysis is a very stout process borne upon the anterior portion of the centrum, for the single-headed ribs.

In the twelve succeeding dorsals (D. 11-22) which lie mostly in a horizontal plane, the diapophyses are of uniform breadth, while the neural spines decrease

gradually in height and breadth. There is a very rapid decrease in the size of the zygapophyses.

#### SACRAL.

#### PLATE XXII.

In this specimen, as in the living Monitor lizards, the 30th vertebra behind the head is distinguished by the absence of a rib, and by the sudden expansion

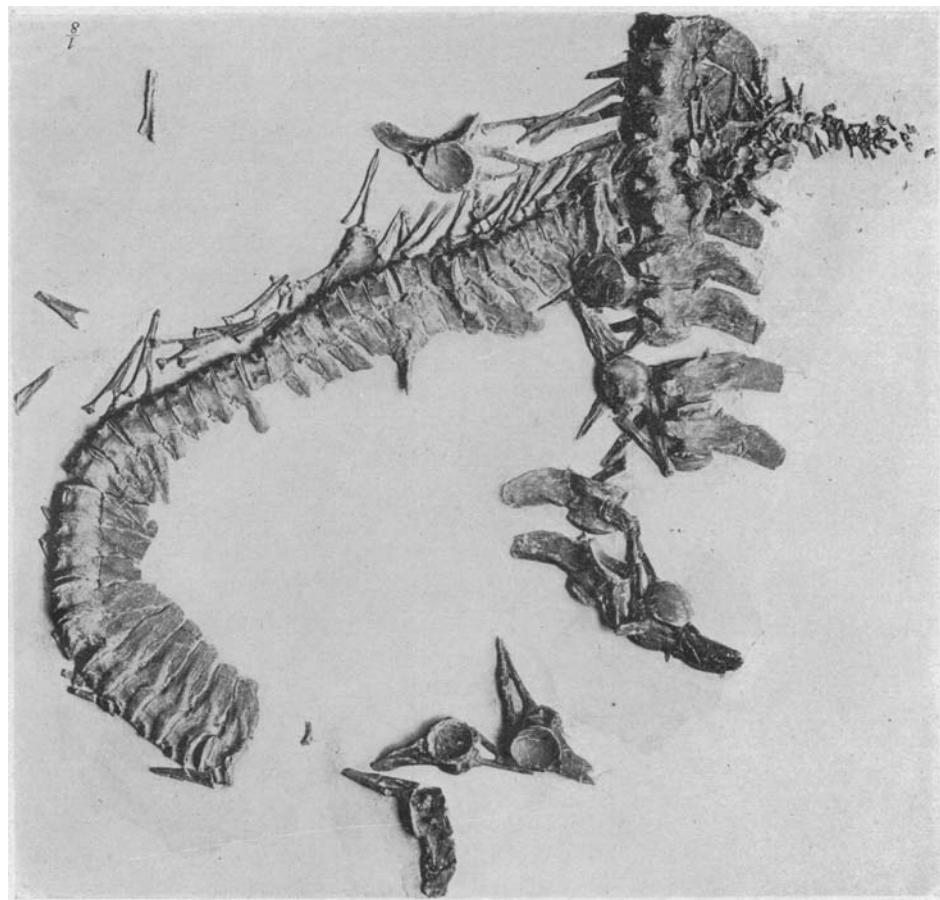


Fig. 7A. Caudals of *Platecarpus*, 83 vertebræ, all in a single series.  $\frac{1}{2}$  nat. size.

of the diapophysis. This first expanded vertebra, as determined by Williston, must be considered the sacral, analogous with the most anterior of the *two* sacrals in *Varanus*. There is a discrepancy between Williston's table (1898, p. 143) in which the sacral is said to be the 31st vertebra of the spine, and his plate 72, in which it is represented as the 32d. This vertebra is not perceptibly different in size from the pygals behind it. Unfortunately the tips of the diapophyses are not preserved, and there is no means of demonstrating positively that the ilium was attached by joint or ligament. The crest of the ilium is actually removed 28 centimetres from the tip of the diapophysis.

## PYGALS AND CAUDALS.

## PLATE XXII.

The postsacrals 1-18 continue backwards, lying in a horizontal plane and covering the line of demarcation or passage to the chevron-bearing caudals. They exhibit a gradual diminution in all their dimensions.

Beneath postsacral 11 is a small fragment of bone which represents part of a chevron.

Beneath postsacral 19 is an unmistakable chevron, and these elements are beautifully shown behind this point, especially upon caudals 29 to 63; they are deep with a wide canal for the caudal aorta.

The diapophyses steadily diminish in size as we pass from postsacral 1 to caudal 38. In caudal 30 they begin to ascend upon the sides of the centrum, and in C. 38 they rise to a point just below the neural spine. There is no sign of a diapophysis upon caudal 39.

*Caudal Fin.*—A most interesting feature is the adaptive modification of the mid-caudal centra and spines, apparently for the support of a dorsal fin.

Williston has figured the caudals of *T. proriger* as having spines of a nearly uniform height, while in *Clidastes velox* (*op. cit.*, p. 152) he describes an extension of the spines as probably designed to support a fin.

This specimen of *T. dyspelor* shows as evidence of a fin:

1. A slight upward elongation of the spines in the mid-caudal region, beginning at C. 24 (in which the spine measures 10 centimetres) to C. 39-40 (in which the spine rises to 11 centimetres) and subsiding to 10 centimetres in C. 58. At the same time the spines change from a pointed and backwardly directed to a more square, upright, and truncated form.

The vertical spine is upon C. 39; in front of this the spines of C. 1-38 lean backwards; while behind this the spines of C. 40 to C. 70 lean forwards, or are nearly upright.

2. There is some further evidence that the *upward curvature of the spine*, as shown in Plate XXII, is natural, and not due to post-mortem disturbance. This curve is beautifully indicated between C. 30 and C. 63; behind which the vertebræ dip down into the extremity of the tail. It is difficult to verify the existence of this curve in the living state by the measurement of the superior and inferior diameters of the centra. So far as measurements can be relied upon they tend to show that the vertebral centra were slightly longer above than below and thus produced the curve; the relations of the greatly reduced zygapophyses and the antero-posterior width of the spines also point to the same conclusion, for they show that if this column were straightened out the spines would come into contact. This con-

dition is so unique, however, that it must be put forward with reserve. Nothing similar is recorded by Williston. The sharp ventral flexure or angulation of the tail of *Ichthyosaurus*, below the swelling of the caudal fin is not analogous to the very gradual upward curve in *Tylosaurus*.

*Ribs and Sternum.*—We are now enabled to form a very clear idea of the general structure of the thorax, although certain details are still missing. All the true ribs are preserved on both sides, and, in spite of the havoc wrought in the



Fig. 8. Epicoracoids and Tracheal Rings of *Tylosaurus dyspelor*.  $\frac{2}{5}$  nat. size.

removal of the chest region, we find all but one of the cartilaginous ribs on the left side and extensive portions of those on the right, as well as the central area of the sternum. The careful studies and drawings of this region by Dr. J. H. McGregor show clearly the relations of the actual and restored regions, part of the preserved region being covered by the vertebræ and ribs:

#### MEASUREMENTS.

	1st.	2d.	3d.	4th.	5th.	6th.	7th.	8th.	9th.	10th.
Bony ribs.....	.51	.54	.58	.59	.60	.59	.59	.58	.57	.57
Cartilaginous ribs, estimated.....	.20	.27	.36	.40	.45	.50	.55	.63	.70	.75

*Cervical Ribs.*—The ribs of the neck are much more reduced than in *Platecarpus*. There is no evidence of a rib facet on the atlas, nor upon the axis. The third cervical bore a small rib, which is not preserved. On the 4th cervical the rib facet is larger. The 5th, 6th, and 7th cervical ribs are well preserved and measure, respectively, 17.4, 21.5, and 29 centimetres.

*Dorsal Ribs.*—The bony ribs increase in length from the 1st to the 5th, and then decrease to the 10th. The single heads are extended vertically and represent an expansion of the capitulum, or a coalescence of capitular and tubercular elements; the heads become more rounded posteriorly. The shape and curvature of the ribs, the position of the diapophyses to which they are attached, and the general form of the chest are much more similar in type to *Sphenodon* than to *Varanus*.

The cartilaginous ribs, as estimated, increase posteriorly from 20 to 75 centimetres; they taper at their junction with the bony ribs; and gradually decrease in width. They consist of broad bands which are closely concentrated and parallel as they converge towards the sides of the sternum, affording an exceedingly strong support for the thorax.

The floating ribs decrease steadily in length and curvature.

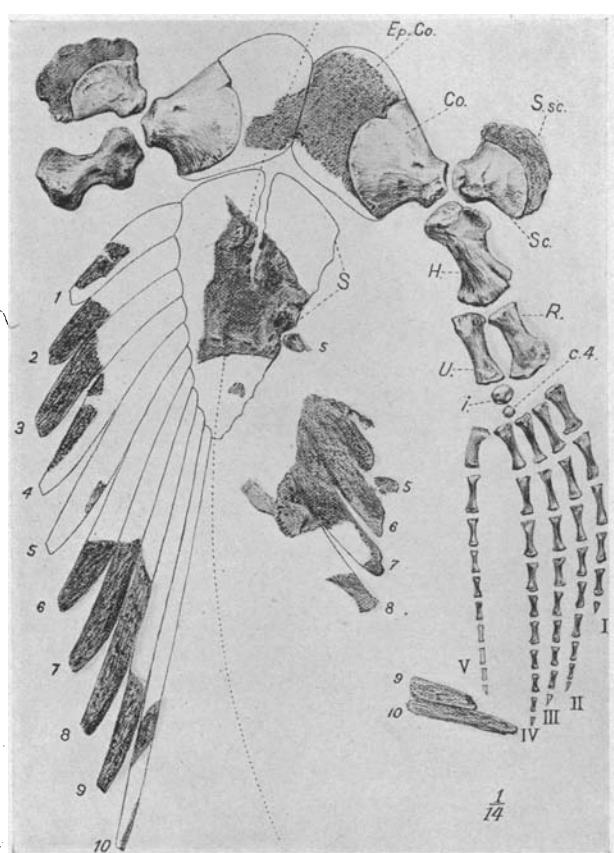


Fig. 9. Shoulder Girdle and Left Paddle of *Tylosaurus dyspelor*. Restored portions in outlines. Drawn by J. H. McGregor.  $\frac{1}{4}$  nat. size.

*Epicoracoids and Sternum.*—The coracoids do not unite in the median line as represented by Marsh, nor are they approximated as restored by Dollo in *Plioplatecarpus*. They are widely separated by epicoracoid cartilages having a united transverse diameter of about 22 centimetres. The inner ends of the bony coracoids are thus nearly nine inches apart. The borders of these epicoracoids are not clearly defined, excepting possibly the posterior border of the left epicoracoid. (See photograph.) About one half of the sternum is visible or preserved; as the cartilaginous ribs on the left side are nearly *in situ*, and those on the right approximately so, it is evident that the sternum had a triangular outline, thinning posteriorly for the junction of the 10th pair of cartilaginous ribs. The median line is slightly displaced, and, as restored by Dr. McGregor,

the entire axis is curved, corresponding with the curvature of the dorsal vertebræ. It is possible that the longitudinal crack seen in the photographs and drawing represents the anterior vacuity often observed in the median line of the degenerate sternum of lizards.

The sterno-coracoid plate thus corresponds closely with the Lacertilian type and bears a general resemblance to those of *Trachydosaurus*, *Varanus*, and *Cyclodus*, as figured by Parker. There is no evidence of the presence of an episternum (inter-clavicle). This element has recently been positively observed by Williston in *Platecarpus* ('99, p. 40), in which the limbs are more strongly developed, and it is possible even that it exists in this type although concealed by the matrix.

#### LARYNX AND TRACHEA.

Behind the basioccipital is observed a supposed lateral cartilage of the larynx? *lx.* and its mate? *lx.* appears below just between the right pterygoid and quadrate. A bit of cartilage appears behind the left quadrate, another mass in front of the right quadrate, while the trachea extends from below the axis, is unfortunately destroyed as far back as the 5th rib, and diverges into the two bronchi just behind the coracoids. The tracheal rings are well exhibited in the accompanying photograph, and the laryngeal cartilages in the photograph of the skull. These parts require a detailed comparison with the tracheal anatomy of different lizards, which is reserved for another paper.

#### ARCHES AND LIMBS.

The appendicular skeleton is remarkably well preserved.

##### *Shoulder Girdle and Fore Limb.*

###### *The Shoulder Girdle.*

—The *scapulae* are fully exposed upon both sides, with the characteristic short and broad bony blades and the extensive crescentic cartilaginous *suprascapulae*; the

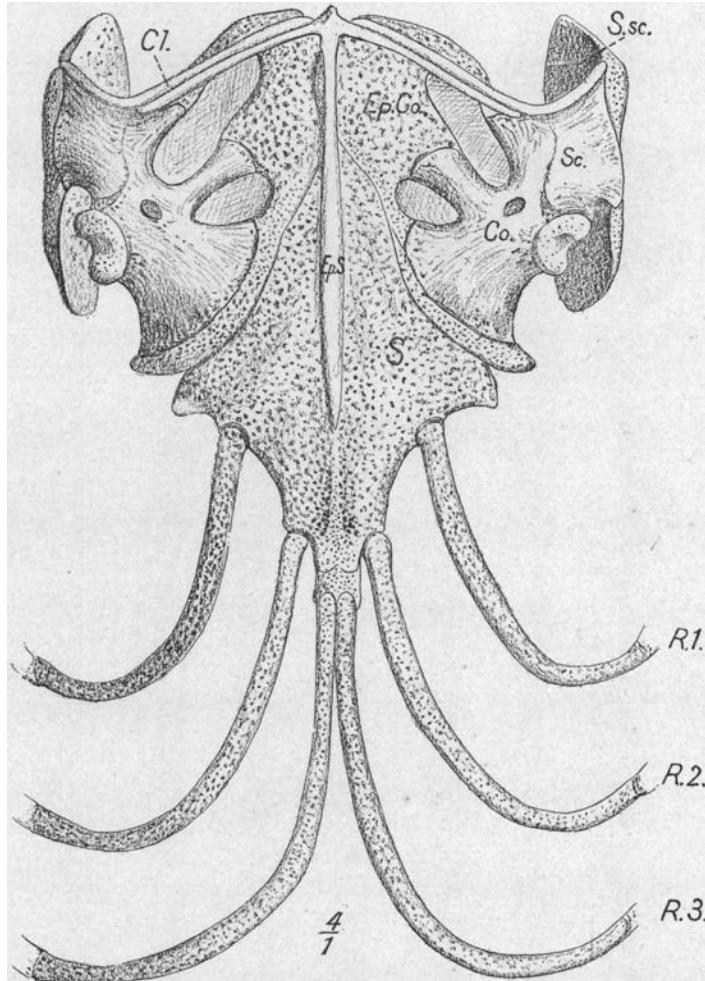


Fig. 10. Shoulder Girdle of Young Lizard, *Monitor dracæna*.  
Cl., clavicle. Co., coracoid. Ep.co., epicoracoid. Sc., scapula. S.sc., suprascapula.  
S., sternum. Ep.s., episternum. After Parker.

coracoid border of the scapula is much shorter than the glenoid border, but the coracoid facet is longer than the glenoid.



Fig. ix. Right Shoulder Girdle and Fore Limb of *Tylosaurus dyspelor*.  
nat. size.

tions, for the proximal ends are broad and the distal narrow. The dorsal sur-

The *coracoids* present sub-equal scapular and glenoid facets, a well defined oval foramen above the scapular facet; the posterior border is short and incurved, while the anterior border is long and nearly straight; the median or epicoracoid border is divided by a notch into a long arched posterior section joining with the epicoracoids and sternum, and a short flat section in front of the notch.

The two *humeri* lie in such a manner as to expose both surfaces. The right humerus presents the dorsal surface, with the more concave preaxial border anterior; the prominent deltoid crest is crushed forwards; a shallow groove lies above the radial or ectepicondyle; the longer posterior border is imperfect and partly covered. The left humerus is turned over and presents the ventral surface with the preaxial border posterior; this bone displays especially well the internal tuberosity, the deltoid crest (lying upon the scapula), the very prominent entepicondyle (not exposed on the right side), and the fractured radial head (in which a pick mark has left an artificial groove).

The *radii* present stout and relatively narrow proximal heads and thin but broad distal ends.

The *ulnae* reverse these proportions, for the proximal ends are broad and the distal narrow. The dorsal sur-

faces of all these elements are exposed, except in the left ulna, which has been overturned with the humerus so as to present the ventral surface.

*The Carpus.* — The large round element, shown on both sides, is probably the ulnare. The smaller element, shown only upon the right side, rests between metacarpalia 3 and 4 and is probably *carpale* 3, which has not been previously observed in a bony condition.

#### COMMON CHARACTERS OF FORE AND HIND PADDLES.

The metapodials and podials are somewhat displaced, but they enable us to make a reconstruction of the manus, aided by Williston's excellent photograph and outline of the paddle in *T. proriger*.

1. *Hyperphalangism* is a chief characteristic of the Tylosaur extremities. Williston's photograph shows 47 actual elements, to which 3 are added in his restoration of *T. proriger*, making 50.

Thirty-eight (38) elements are preserved in the left *fore paddle* or manus, and 44 are inserted in our restoration, or 5 metacarpals and 39 phalanges. In the *hind paddle*, or pes, 33 metatarsals and phalanges are preserved on the left side (including an isolated phalanx which lies above the 50th caudal).

The phalangeal formula is *estimated* as follows :

	MANUS.		PES.
Digit I	5	6	5
II	8	9	8
III	8	10	8
IV	9	11	8
V	9	11	6
	<i>T. dyspelor.</i>	<i>T. proriger.</i>	<i>T. dyspelor.</i>

in comparison with Williston's estimate of *T. proriger* (*op. cit.*, p. 159). Williston, however, considers that the phalanges may be subject to individual variation in number. It is apparent, so far as we can judge from this specimen, that in *T. dyspelor* the phalanges are less numerous than in *T. proriger*.

2. A second characteristic is the *marked broadening and shortening of the 5th metapodial* in both manus and pes, but especially in the pes.

The carpus, and still more the tarsus, on the postaxial (ulnar and fibular) sides is also abbreviated. The result is that the 5th digit is drawn towards the body; its elements and joints alternate with those in the I-IV digits; as a whole it is set wide apart. Williston has recently shown that the epidermal fin web conforms in its contours to this peculiarity (1899, p. 41).

3. A third characteristic is the alternation of the joints in the 1st and 5th digits with those in digits 2, 3, 4. The pes further agrees with the manus in the expansion of the proximal part of metapodial I, and in the shortening or drawing up of the first finger whereby the middle points of the phalanges of Digit I come

opposite the joints of the phalanges in Digits II, III, IV, thus greatly strengthening the paddle as a whole. A similar adaptation by alternation of the phalangeal joints is observed in some of the Plesiosaurs, in which it is carried to an extreme, for the phalanges of all the digits alternate.

#### PELVIC GIRDLE AND HIND LIMB.

FIGURE 12.

The *ilium* is well displayed upon both sides as a slender rod, tapering to its blunt superior border, which was probably united by loose ligaments with the sacral vertebra.

The *pubis* is a somewhat smaller bone, readily distinguished by a *vestigial pubic foramen* and by its square symphysial extremity.

The *ischium*,<sup>1</sup> as completely displayed upon the left side, has a very broad symphysial border, and a very prominent process upon the posterior border for the ischio-caudal muscles.

The *femur* has a prominent great trochanter, as shown upon the right side, and a greatly expanded distal extremity.

The *tibia* has a rather thin preaxial border, a broadly concave postaxial border, and distally a sharply defined *intermedium* facet.

The *fibula* is a relatively small bone, nearly symmetrical at the two ends.

As in the manus two *tarsalia* are ossified; these are the *intermedium* and *tarsale 3 or 4*. Opposite the latter upon both sides, and therefore presumably not far from its natural position, appears *metatarsale V*, a bone sharply distinguished from its fellows by its short concavo-convex borders.

#### RESTORATION OF SKELETON.

PLATE XXIII.

This specimen affords an exceptionally favorable opportunity for a restoration of the skeleton. This interesting work has been accomplished by coöperation. Dr. Matthew kindly undertook a natural-size drawing of the entire animal, succeeding especially in rearranging the vertebral column and skull. Mr. Horsfall completed the details of the skull by careful measurements and comparison with the drawings of Merriam and Williston. Dr. McGregor and the writer restored the paddles and the sternum.

The drawing is upon a one-eighth scale. There was probably a small rib upon the third and fourth cervicals which has not been indicated.

The cervical intercentra are restored from the fine specimen of *Platecarpus* represented in Figure 3.

One of the most important features of the restoration sprang from the discovery that the cartilaginous ribs of the left side are practically in their normal relations. This fact enabled us to locate definitely the lower end of the ten true

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<sup>1</sup> One of the few errors in Prof. Williston's work is the explanation of Plate 49, in which the ischium is referred to as the pubis. The text, p. 162, is correct on this point.

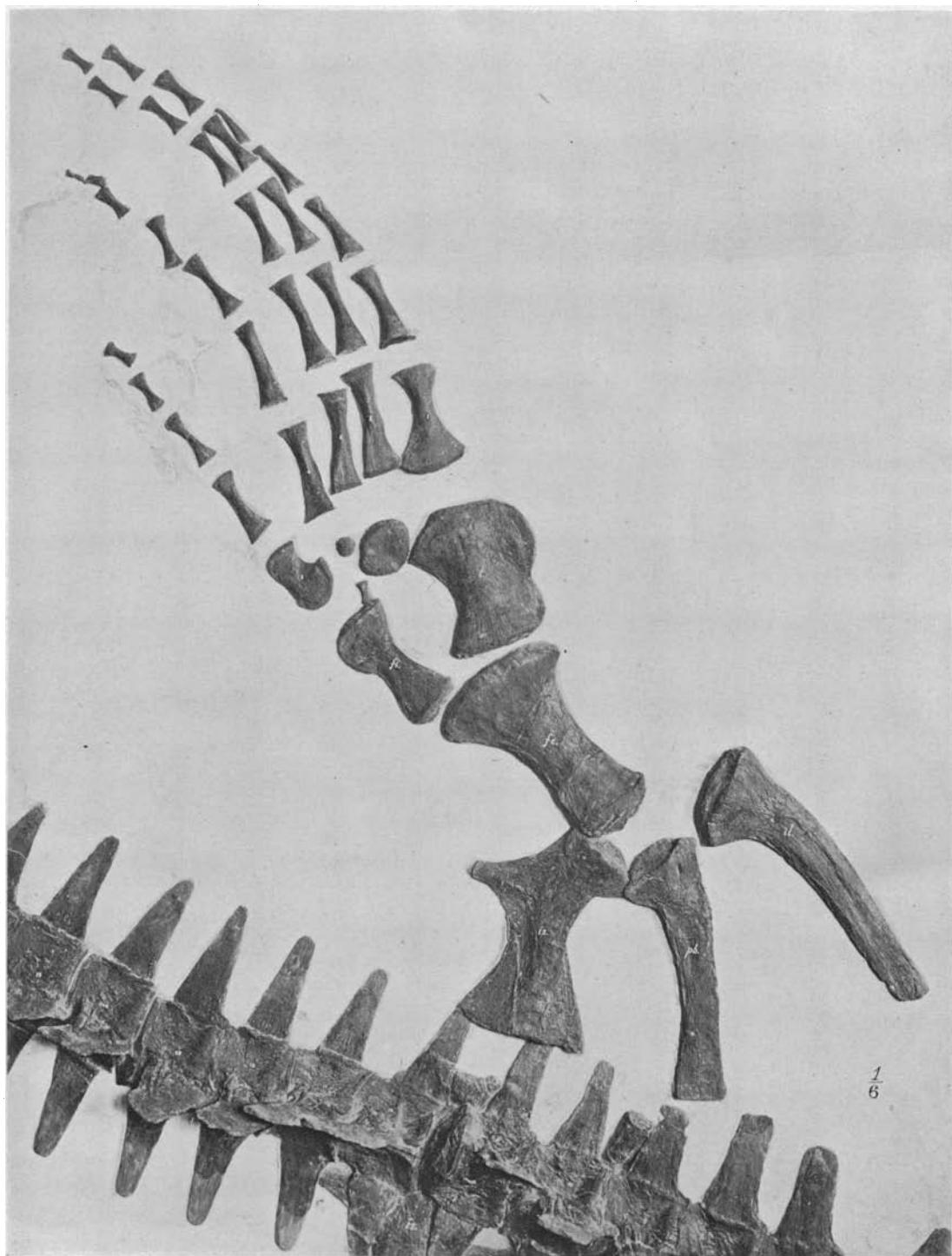


Fig. 12. Pelvic Girdle and Left Hind Limb of *Tylosaurus dyspelor*.  $\frac{1}{6}$  nat. size.

ribs, the sternum, the epicoracoids, and at the same time fix the position of the fore paddle with reference to the skull.

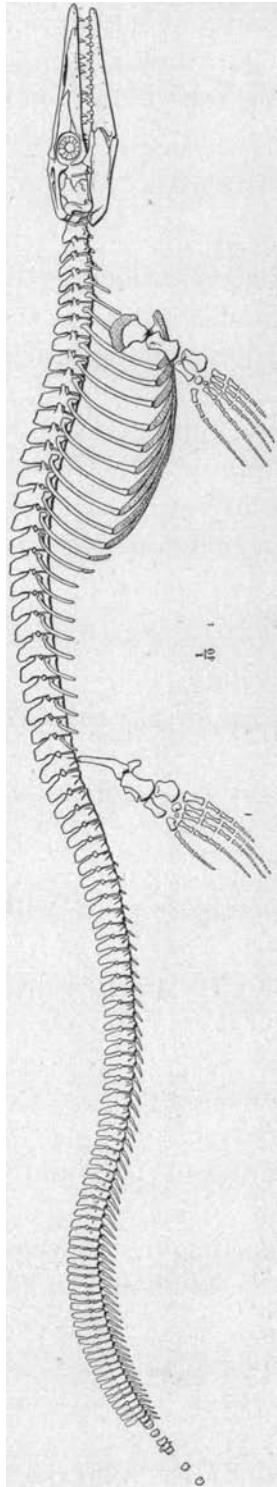


Fig. 13. *Tylosaurus dyseior*. Restoration after drawings by W. D. Matthew and Bruce Horsfall, under direction of the author.  $\frac{1}{6}$  nat. size.

As above noted, the ribs were found to resemble those of *Sphenodon* much more closely than those of *Varanus*. They are thus given in the restoration the angle, position, and foreshortening characteristic of *Sphenodon*, as the narrow anterior part of the chest expands into the broader walls of the abdomen. The ribs in the plate are perhaps a shade too heavy.

The upward curvature of the tail is designed exactly as the vertebræ lie in the specimen, for the reasons discussed upon page 178.

#### RESTORATION OF THE ANIMAL.

In the restoration of the animal, Mr. Charles Knight has taken advantage of all the information afforded by Prof. Williston's collections and descriptions, and of our detailed study of this fine specimen. The animal was first carefully modelled upon a one-ninth scale.

*Tylosaurus* was a very powerful sea swimmer, propelled chiefly by the lateral motions of the body and tail. The caudal fin was a broad expansion along the dorsal line. The proportions can be precisely determined. The

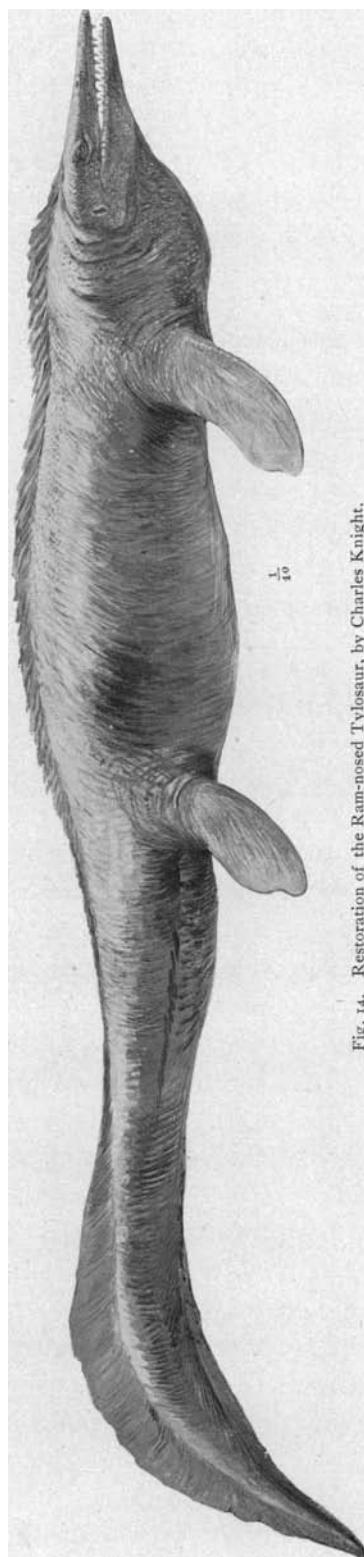


Fig. 14. Restoration of the Ram-nosed Tylosaur, by Charles Knight.

fore and hind paddles were similar in action and played a subsidiary part in guiding the animal, but were effective in the less rapid motions of the body. The indentation of the paddle border between the 4th and 5th fingers is upon Williston's authority. The nuchal fringe is also from this author's recent description of *Platecarpus*. The epidermal scaly covering is from Chancellor Snow's account of the *Tylosaurus proriger* covering. The expression of the top of the skull resembles that of *Varanus*, but in other points there is a wide departure from the Varanoid type.

#### COMPARISON WITH VARANUS.

The facts derived from this skeleton do not strengthen Baur's extreme opinion as to the intimate connection of this type with the Varanidæ. Besides the secondary degenerate adaptation to marine life shown in the girdles and appendicular skeleton, there are certain fundamental differences in the basioccipitals (p. 170) and ribs (p. 176), in fact in all parts of the skeleton. These differences fully balance or outweigh the likenesses, which have long been dwelt upon by Cuvier, Owen, and Baur, between the Mosasaurs and Varanoids, and do not even justify the assertion that the Varanidæ and Mosasaurs sprang from a common stem.

#### SUMMARY OF NEW OR DISPUTED CHARACTERS.

*Skull*.—A large epipterygoid and probably a distinct supraciliare.

*Vertebrae*.—7 cervicals, 10 dorsals connected with sternal ribs, 12 dorsals with free ribs; 1 sacral; 72 + caudals.

Axis and atlas more complex and primitive than in any recent lizard or in *Sphenodon*.

Intercentra free throughout cervical region as far as C. 6.

Dorsals 1 and 2 resembling cervicals, except in junction of ribs with sternum.

Caudals with a dorsal curvature and a central vertebra (No. 39) to which neural spines converge.

*Ribs*.—Anterior cervical ribs somewhat reduced.

Ten broad-banded cartilaginous ribs uniting with sternum.

*Arches*.—Coracoids widely separated by cartilaginous epicoracoids.

Sternum degenerate, wholly cartilaginous, triangular, and apparently without episternum.

*Respiratory Tube*.—Larynx consisting of two stout lateral cartilaginous pieces.

Trachea diverging into bronchi at anterior portion of the sternum.

*Limbs*.—A carpus with osseous ulnare and carpale 3.

Manus and pes with abbreviated 5th metapodials.

Hyperphalangy compensated for by alternation of joints in Digits I and V with those in Digits II, III, IV.

The only conclusion we are absolutely warranted in drawing is the following:

The Mosasaurs are a very ancient marine offshoot of the Lacertilia, retaining certain primitive and generalized Lacertilian characters and presenting a few resemblances in the skull to the Varanoids; they are very highly specialized throughout for marine predaceous life, and constitute a distinct subdivision of the order Lacertilia.

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VOLUME I, PART V.

A Skeleton of Diplodocus.



MEMOIRS  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY.

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V.—A SKELETON OF DIPLODOCUS.

By HENRY FAIRFIELD OSBORN.

PLATES XXIV—XXVIII.

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In the spring of 1897, one division of the American Museum exploring party was sent by the writer to the Como Bluffs of Wyoming, made famous by numerous discoveries of Dinosaurs. It was believed that this rich locality had been exhausted by the continuous excavations of the U. S. Geological Survey under the direction of Professor Marsh. The first prospecting, however, resulted in the discovery by Mr. Barnum Brown and the writer of a large femur, which guided us to the very remarkable skeleton of *Diplodocus longus* described in this Memoir. Dr. J. L. Wortman joined the party and superintended the work of excavation by Mr. Brown and others, which occupied several months.

At one time strong hopes were aroused that the entire animal would be found together. The long tail stretched off parallel with the cliff, interrupted only by a small gully which had cut through a small section of the caudals. In front of the sacrum the dorsals stretched forwards in a promising way, but the centra were wanting, and finally nothing but the neural arches remained.

The left side was found most deeply imbedded and most completely preserved in the region of the sacrum. The bones recovered are as follows: 8 posterior dorsals lacking the centra; left neural arches of 3 cervicals; sacrum, lacking centra 1 and 2, consisting of 4 vertebrae; caudals 1-21, and 23-27, complete with chevrons; portion of caudals 32, 33, 35 (estimated); ribs of three posterior dorsals; left ilium and ischium; upper three fourths of left femur; right scapula.

Not only the relative completeness of this skeleton, but the highly skilful manner in which it was taken out, render it unique. Not a fragment preserved is

missing or out of place. Upon arrival in the Museum, the reconstruction of the pelvis and sacrum proved especially difficult, but was completed successfully by Mr. Brown, under the direction of Mr. Hermann. Mr. Brown worked out the entire tail with great skill. Mr. Hermann has carefully restored the missing dorsal centra, and prepared this superb specimen for exhibition. In course of his work upon the caudals, Mr. Brown made a number of observations which have been of considerable service to the writer. The pen drawings and restoration are by Mr. Rudolph Weber; the photographs by Mr. Abram E. Anderson.

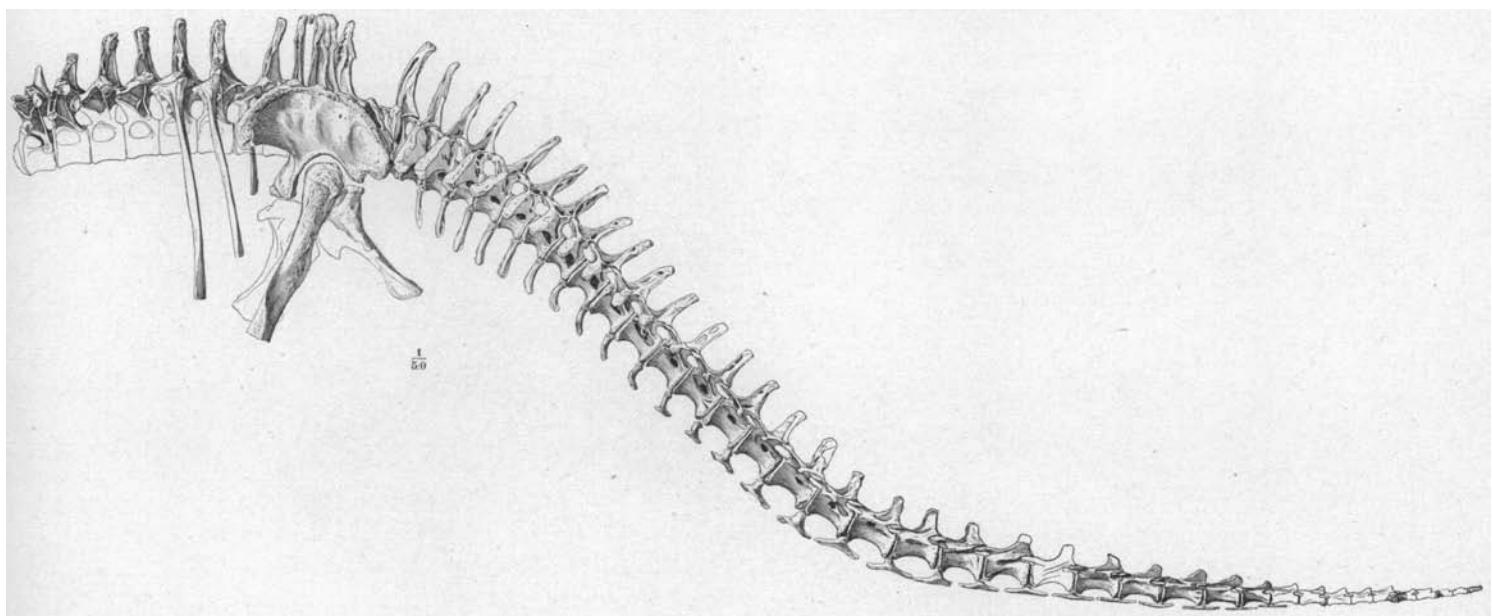


Fig. 1. Restoration Posterior half of vertebral column of the Diplodocus Skeleton with Pelvis and Femur in position.  $\frac{1}{20}$  nat. size.

#### DESCRIPTION OF SKELETON.

The points of greatest novelty are found in the vertebral column, since the only portions of this region described by Professor Marsh are a single cervical, an anterior dorsal, three sacral centra, and one caudal with chevrons.

In order to understand the general structure of the posterior half of the column, that is, from the 8th presacral backwards, the reader is at once referred to the above Restoration, Fig. 1.

A remarkable *balance between the opisthocælous presacrals and proælous postsacrals* is observed. Vertebra for vertebra they correspond very nearly in size, with a slight advantage in favor of the presacrals.

This balance, which was completed by the ponderous tail stretching out to a length of 30 feet, was probably an adaptation to the power of vertically elevating the anterior portion of the body, certainly while in the water, and quite possibly while on land.

Between these balanced dorsals and caudals are the excessively rigid sacrals, coalesced with each other and with the ilium. Thus a long balanced vertebral

lever is established with the acetabulum as a fulcrum; with opisthocœlous vertebræ in front and procœlous vertebræ behind.

The dominating principle in construction of the backbone is maximum strength with minimum weight. The ingenuity of sculpture by which this is brought about, every single vertebra differing from its fellow, baffles the Lamarckian as well as the Darwinian, and tempts us to revive the old teleological explanation.

#### CERVICAL VERTEBRAE.

Portions of three cervical vertebræ are preserved, affording an estimate as to their length. In the most anterior, a part of the centrum, the prezygapophysis, *a.z.*, and diapophysis, *t*, are preserved. In the second we see the prezygapophysis, diapophysis, and postzygapophysis, *p.z.*. In the third, only the prezygapophysis and diapophysis are preserved. The centra, *c*, and ribs, *r*, are indicated in outline.

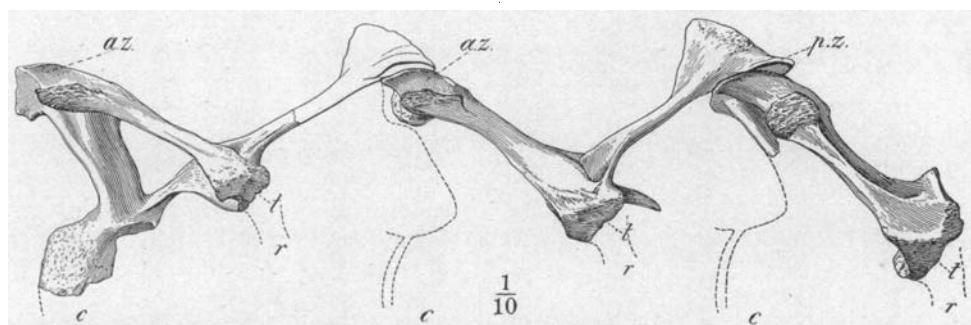


Fig. 2. Portions of three Cervicals.  $\frac{1}{10}$  nat. size.

#### DORSAL VERTEBRAE.

The number of dorsal vertebræ in the Sauropoda is still unknown. Marsh figured it at 14 in *Brontosaurus*. The writer has shown grounds for believing that the number was larger. We may provisionally adopt 15 as the number in *Diplodocus*. According to this estimate the most anterior vertebra preserved would be the eighth dorsal. It is best to enumerate the dorsals also from the sacrum forwards, namely as *presacrals* 1, 2, 3, etc. In the accompanying figures also two sets of numbers are given.

#### *General Characters of Dorsals.*

Of the 8 dorsals discovered, the 6 anterior are mounted as found, interlocked by their zygapophyses; the 2 posterior are interlocked with the sacrum.

All the dorsal vertebræ bear ribs, including two ribs which lie beneath the ilium. There are no lumbars.

The spines rise rapidly to the sacrum, which is the highest fixed point in the vertebral column.

Vertebræ without transversely expanded spines; spines paired anteriorly, single posteriorly.

The seven principal characters of the dorsals preserved are the following:

1. *Neural Spines*.—There is no nodal vertebra or sudden transition from paired spines to single spines, such as we observe in *Brontosaurus* (see Osborn, '98, 231). Neither are any of the dorsal spines transversely expanded. On the contrary, the low bifid, or laterally paired spines of the cervicals and anterior dorsals gradually converge and rise until in the 3d, 2d, and 1st presacrals (or 13th, 14th, and 15th dorsals) the spines are lofty and single, expanding into rugosities at the summits.

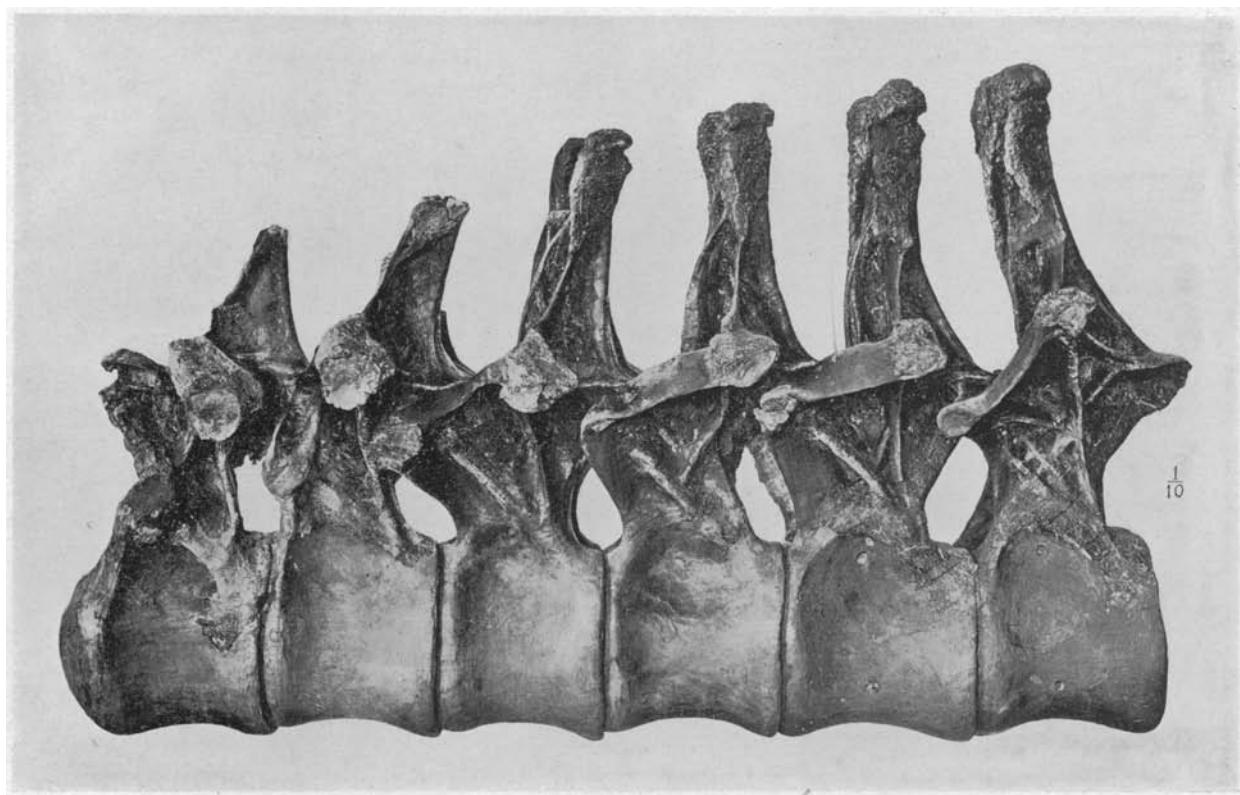


Fig. 3. Lateral view of Dorsals 8-13 (estimated) or Presacrals 8-3. Centra restored, omitting lateral cavities.  $\frac{1}{10}$  nat. size.

2. *Rib Articulations*.—The diapophyseal tubercular articulations,  $t$ , are very high throughout, while the capitular articulations,  $c$ , rise suddenly from a point just above the centrum in presacral 8 (see Fig. 7) to a high level in Ps. 5-1. The ribs are thus borne in Ps. 5-1, high above the centrum.
3. *Zygapophyses*.—Ps. 8-1 have very extended zygapophyses extending into the hyposphen-hypantrum articulations below.

4. *Laminar Buttresses*.—The neural arches and spines are sculptured into thin laminar buttresses which reduce the weight to the last degree. As best shown in Figs. 4 and 7, these are *constructed in such a manner as to connect all the principal points of strain and stress*, as follows:
- Vertical Median Laminæ of Neural Spine, bracing against antero-posterior strains.
  - Prespinal lamina*, *a.s.*, rising upon the inner sides of the prezygapophyses and extending upwards to top of the bifid or single neural spines.

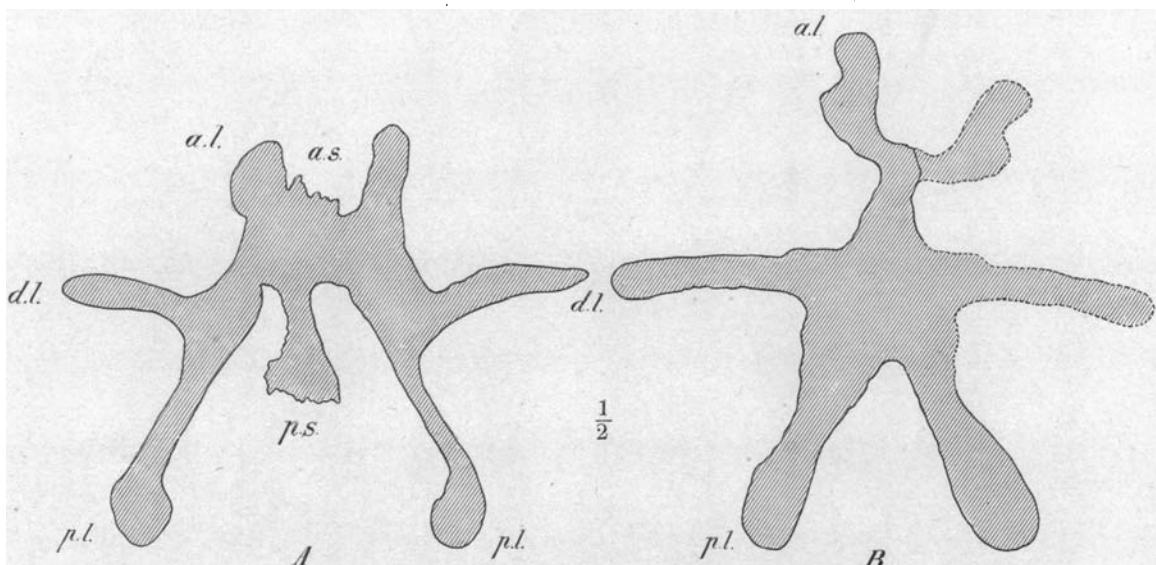


Fig. 4 A. Neural spine of 6th Presacral, transverse section, showing eight laminæ.

*a.s.*, prespinal lamina; *p.s.*, postspinal lamina; *a.l.*, prezygapophysial lamina; *p.l.*, postzygapophysial lamina; *d.l.*, diapophysial lamina.

Fig. 4 B. Neural spine of 4th Presacral, transverse section, showing six laminæ.

- Postspinal lamina*, *p.s.*, rising from postzygapophysial lamina and extending upwards to top of spines.
- Horizontal Laminæ, *h.l.*, between Neural Spine and Neural Arch.
- Horizontal lamina*, connecting prezygapophysis with rib capitular, rib tubercular facets, and postzygapophyses.
- Lateral Vertical Laminæ.
- Prezygapophysial lamina*, *a.l.*, descending vertically from anterior borders of spine above prezygapophyses, through rib capitulum facet to centrum, forming anterior border of neural arch.
- Diapophysial lamina*, *d.l.*, or *transverse process*, descending from side of spine, through prominent rugosity for tubercle of rib, downwards into neural arch.
- Postzygapophysial lamina*, *p.l.*, descending from posterior borders of spine, through postzygapophyses, to form posterior border of neural arch.

## d. Oblique Laminæ.

7. *Oblique and intersecting laminæ.* Extending upon sides of neural arch from prezygapophyses downwards and backwards, and from postzygapophyses downwards and forwards. Also minor laminæ intersecting each other at sides of neural arch, *o.l.* (See Ps. 3.)

The vertebræ are thus reduced in weight and increased in strength in the most effective manner.

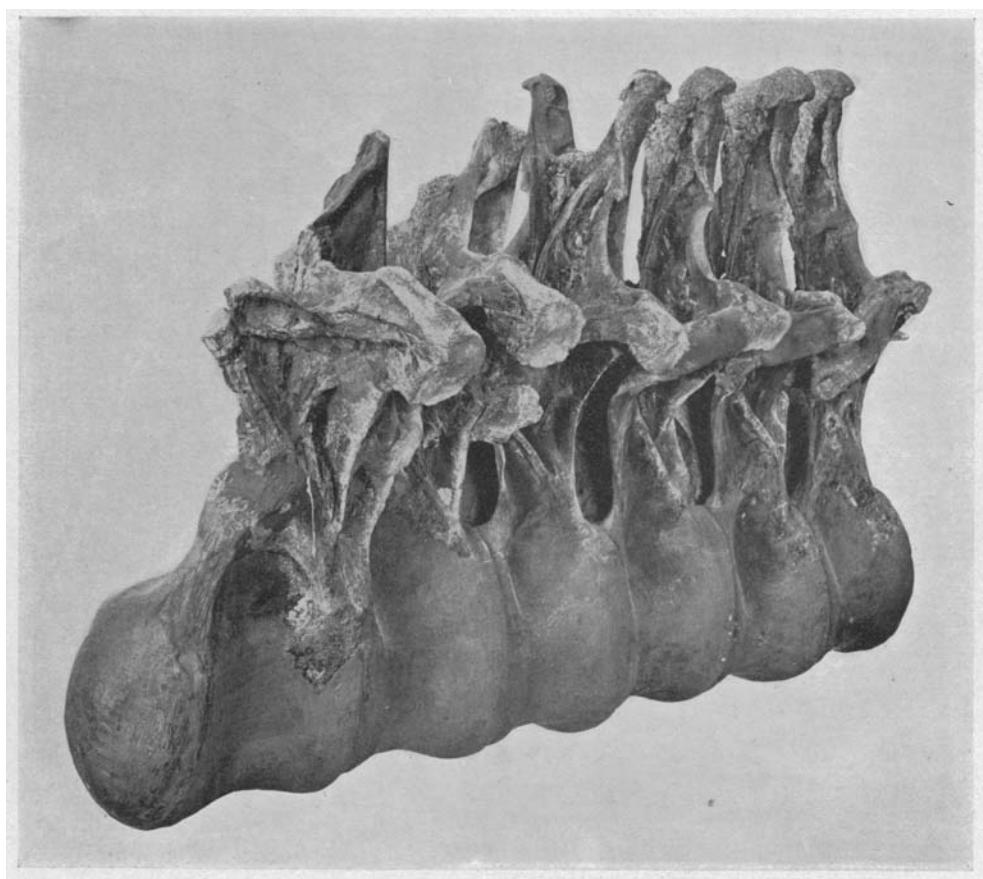


Fig. 5. Oblique anterior view of Presacrals 8-3, showing convergence of Spines, Diapophyses, and Diapophyseal Laminæ.

These laminar buttresses are proportioned in the successive vertebræ to meet the peculiar mechanical strains of each, no two vertebræ being alike.

Similar laminæ, differently proportioned and less elaborate, are seen in *Brontosaurus* and other Sauropoda.

5. *Lateral Cavities of Centra.* — The centra are practically destroyed. In Ps. 8 alone is observed the upper border of a lateral excavation which was undoubtedly developed in all the others as in the anterior caudals.

6. *Opisthocælism.* — All the dorsals are opisthocœlous.
7. *Asymmetry.* — Not only are successive vertebræ unlike but the same vertebræ vary in structure upon opposite sides. In some instances they are decidedly asymmetrical. There is probably much individual

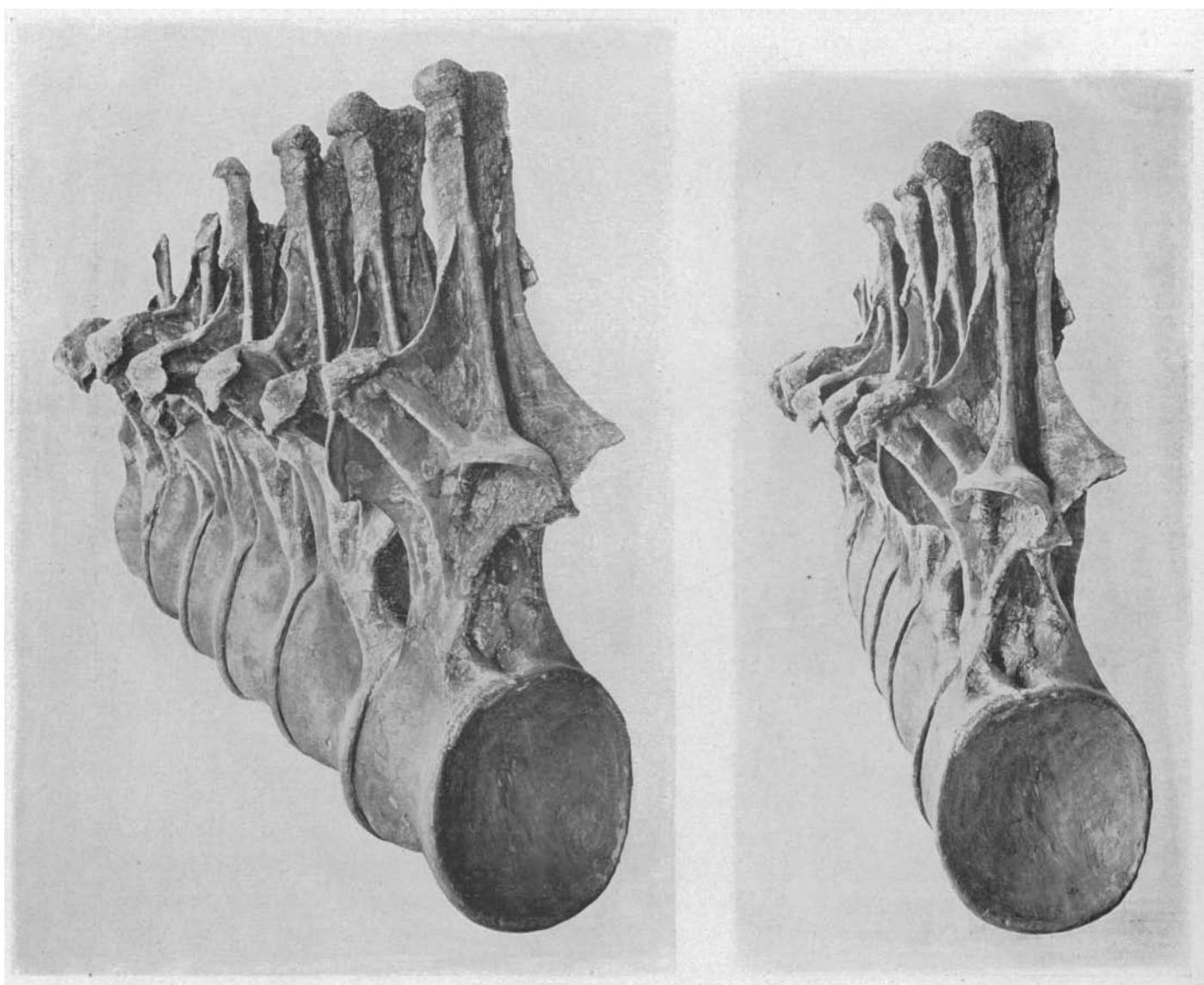


Fig. 6. Posterior oblique views of Presacrals 8-3, showing Postspinal, Postzygapophysial, Horizontal, and Diapophysial Laminæ. Also Hypophen.

variation in these grotesque forms. As already observed by the writer ('98, p. 227), a marked characteristic of the Sauropoda or Cetiosauria is the sudden form change in the successive dorsal vertebræ. Each bone requires a detailed description.

*Special Characters of Dorsals.*

8th presacral or 8th dorsal. Condition: the summits of the paired spines broken away; the neural arch crushed posteriorly; prezygapophyses and lower part of arch wanting. Characters: shallow lateral cavity; capitular facet of rib large, on anterior portion of neural arch slightly above level of centrum; rib tubercle facet much more elevated, with its supporting vertical and oblique laminae placed very far back.

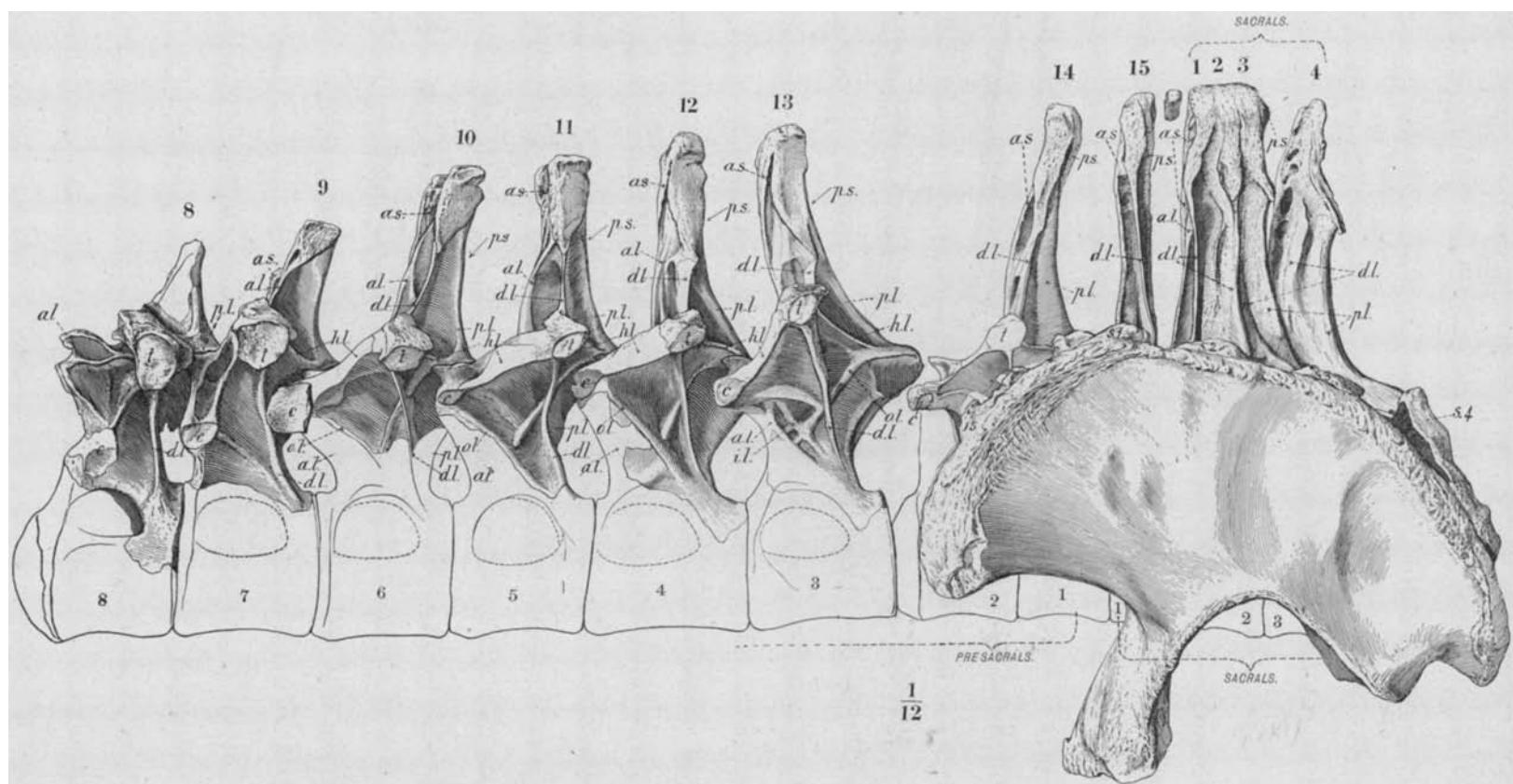


Fig. 7. Dorsals, Sacrals, and Ilium, showing the development of the Laminae.  
*a.s.*, prespinal lamina; *p.s.*, postspinal lamina; *a.l.*, prezygapophysial lamina; *d.l.*, diapophysial lamina; *p.l.*, postzygapophysial lamina; *h.l.*, horizontal lamina; *o.l.*, oblique lamina; *i.l.*, intersecting lamina; *c.*, capitular facet; *t.*, tubercular facet; *s.1-s.4*, diapophysial rugosities.

7th presacral or 9th dorsal. Condition: nearly complete above centrum. Characters: capitular rib facet placed midway between centrum and prezygapophyses; horizontal lamina more strongly developed; diapophysial lamina descending far back upon centrum; paired neural spines forked or bifid at top, with broad connecting lamina between them.

6th presacral or 10th dorsal. Condition: completely preserved above centrum. Characters: paired neural spines united to a point  $\frac{1}{3}$  from summit; prominent prezygapophysial laminae on either side of prespinal lamina diverging at summit into paired spines, with the stout prespinal rugosity between them; postspinal lamina becoming prominent; side of spine with a prominent muscular rugosity

which tapers inferiorly into diapophysial lamina, this lamina more slender below and not descending to centrum, postzygapophysial lamina projecting behind it; capitulum of rib attached still higher.

5th presacral or 11th dorsal. Condition: lacking inferior portion of neural arch. As in D. 10, a pair of prezygapophysial laminæ on either side of prespinal lamina. Characters more progressive than preceding, as follows: neural spines early confluent at summit; prespinal laminæ more prominent; postspinal lami-

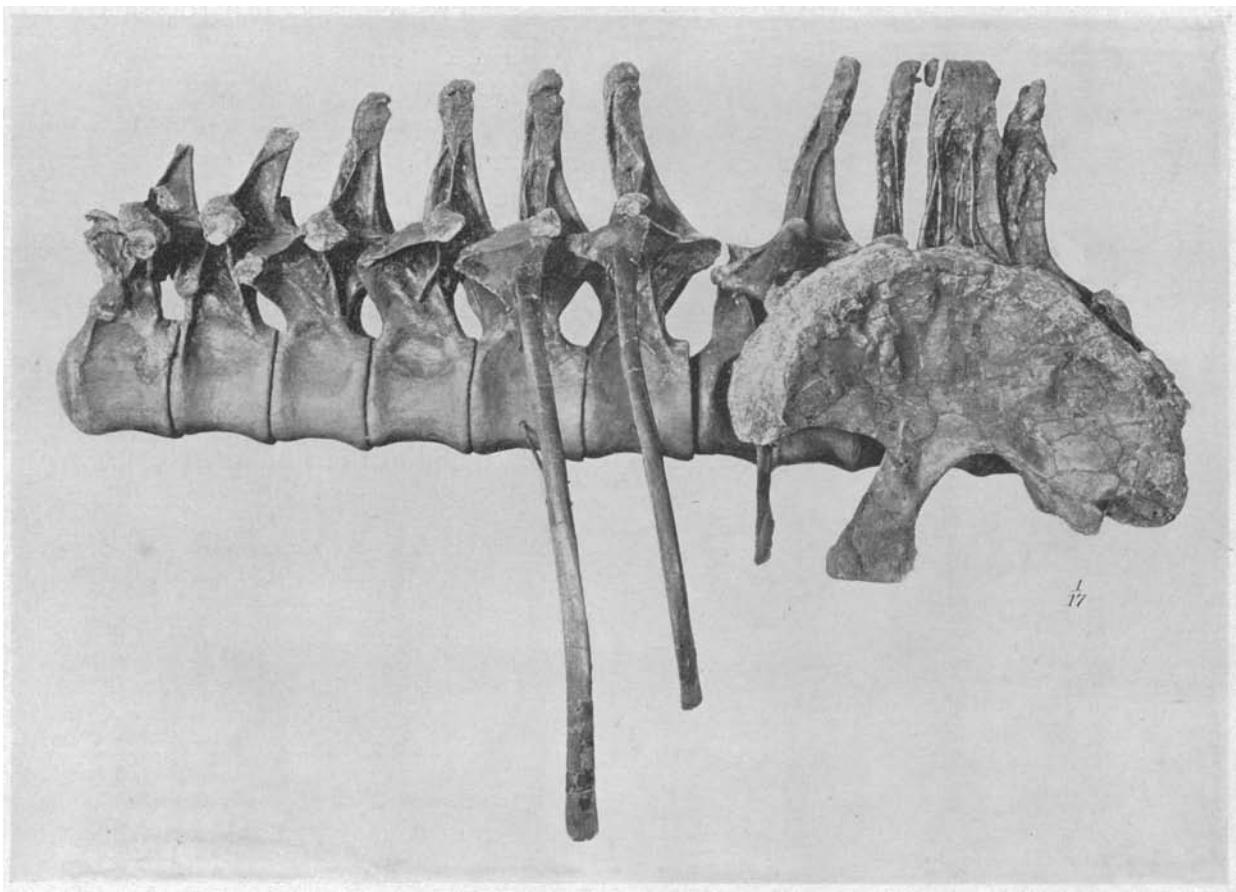


Fig. 8. Dorsals, Sacrals, and Ilium.  $\frac{1}{7}$  nat. size.

næ more prominent; capitulum of rib within  $4\frac{1}{2}$  cm. of prezygapophysis; diapophysial lamina more prominent above, directed downward and forward below tubercle. Oblique laminæ on neural arch more conspicuous.

4th presacral or 12th dorsal. Condition: complete above centrum with rib attached. Characters: prezygapophysial lamina not rising so high upon spine; all the laminæ (except the intersecting) well developed; capitular facet elevated; neural spine broadened at top, single, with slight median depression. The rib is well preserved, length approximate 130 cm., the capitulum and tuberculum being

nearly upon one level and connected by a broad plate which is sculptured upon the inner surface; it passes from the plate into a triangular mid and inferior section.

3d presacral or 13th dorsal. Condition: complete except prezygapophysis and lower portion of centrum. All typical laminæ strongly developed, including the oblique and intersecting laminæ. Neural spine single, with broad rugosity at summit. This is the most elaborately constructed and typical vertebra of the dorsal series. The rib is shorter than the preceding, length approximately 118 cm.

Presacrals 2 and 1 (dorsals 14 and 15) are of great interest because, as in the Struthious birds, the ribs they bear lie behind the ilium, the 14th being still free, the 15th having coalesced with the ilium. The analogy with *Apteryx* (Fig. 9) is very striking.

2d presacral or 14th dorsal. Condition: portions of neural arch and spine preserved. Characters: The neural spine is expanded and flattened at the summit, with prominent prespinal and postspinal laminæ which are extremely rugose, and indicate the presence of powerful interspinous ligaments. Portions of the anterior oblique and intersecting laminæ are preserved. The rib is complete, measuring 68 cm. (not including curvature); it projects well down below the level of the iliac crest, and is entirely free from the ilium.

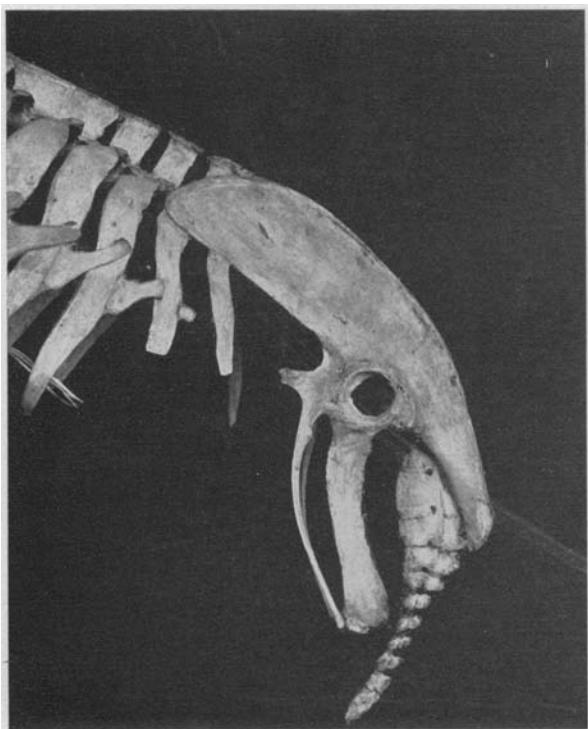


Fig. 9. Posterior Dorsals and Pelvis of *Apteryx*, showing Ilium overlapping two Posterior Ribs.

1st presacral or 15th dorsal. Condition: upper portion of the neural arch and spine preserved. This vertebra lies distinctly in front of the neck of the ilium, with which the first true sacral unites; it also lacks the sacral arcade springing from the centrum. It must therefore be considered the last dorsal.

Nevertheless, it coalesces with the superior border of the ilium by a bar (Fig. 7, R. 15) which may be considered either a metamorphosed rib or an expansion of the metapophysial lamina. If this element is a rib then *Diplodocus* presents a condition clearly analogous to that in *Struthio* (Fig. 10), in which the last rib all but unites with the ilium.

## SACRAL VERTEBRÆ.

PLATES XXV AND XXVI.

A sharp and very ancient or primitive line of demarcation separates the sacral vertebræ from the dorsals, namely:

1. *Sacral ribs*.—The possession of sacral ribs springing directly from the sides of the centra. These are profoundly different from the elevated posterior dorsal ribs which spring from the junction of the neural spine and neural arch. The sacrum therefore does not expand by the addition of posterior dorsals.
2. *Vertical laminar diapophyses*.—The possession of broad, plate-like, transverse processes which consist of the *diapophysial laminae* above described. These laminae, as in the dorsals, are connected above with thin plates ascending to the summit rugosity of the neural spines, and descend below to unite with the sacral ribs.
  - a. Each of these laminae unites upon its outer side throughout its whole length with the ilium, and each appears above the iliac crest as a *diapophysial rugosity* homologous or in a continuous series with the rugosities above the rib tubercle facets in the dorsals. (See Fig. 7,  $s^1, s^2, s^3, s^4$ .)
  - b. These laminae form the boundaries of three pairs of cavities between the sacrals and the ilia. These cavities open above and below. They are partly shut in above by expansions of the horizontal laminae.
  - c. This arrangement is wholly dissimilar to that in *Struthio*, as is seen by a comparison of Figures 8 and 10; in *Struthio* there are no laminar plates, the union is by the ribs, diapophyses, and summits of the spines. It is similar to that in *Morosaurus*, as recently described and figured by Williston ('98, p. 175). These sacra (*Morosaurus*, Kansas

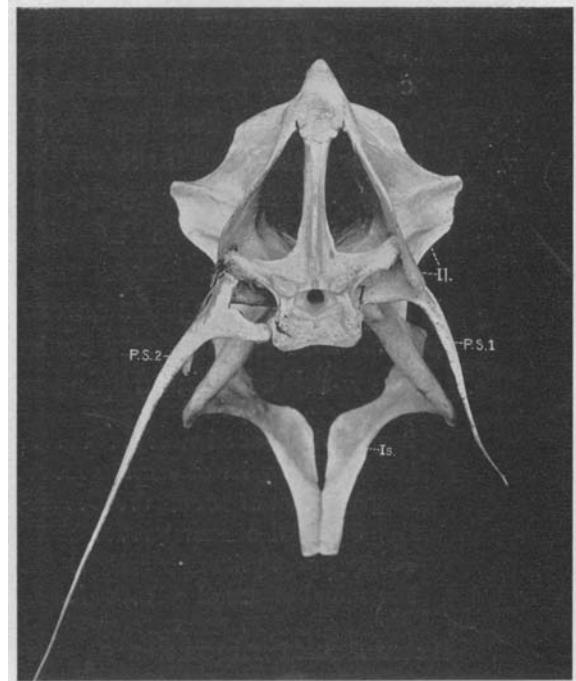


Fig. 10. Anterior view of Sacral Region in *Struthio*, showing two Dorsal Ribs, P.S. 1, P.S. 2, beneath Ilium. Also union of Ilium with Neural Spines, Diapophyses, and Ribs.

Museum, and *Diplodocus*, American Museum) clear up the hitherto incompletely understood relations of the sacrals to the ilia.<sup>1</sup>

- d.* The sacrum of a supposed young *Morosaurus* figured by Marsh ('96, Plate 33) represents the *sacro-iliac union as exclusively composed of sacral ribs*, i. e., free elements at junction of centra and neural arches, which are mistakenly termed 'transverse processes' by Marsh. This cannot be the case in *Diplodocus*, because we see the very extensive diapophysial laminæ, arising as outgrowths of the neural arch, and evidently coalescing with the sacral ribs below. These laminæ are serially homologous with the transverse processes of the dorsals, and morphologically are quite distinct from ribs.

It is possible that the simple rib connection of the young *Morosaurus* is a juvenile character, and that the compound, or pleuro-diapophysial connection, is an adult or growth character.

- 3. Four sacrals.*—There are four rib-bearing true sacral vertebræ in *Diplodocus* instead of three as hitherto described by Marsh.

- a.* The *three anterior sacrals*, constituting the primitive Dinosaur sacrum, are firmly united by their neural spines. These three spines coalesce into a single very robust spine, showing the diapophysial laminæ separate; the antero-posterior diameter of this spine is far less than that of the three coalesced spines of *Brontosaurus* or *Morosaurus*; this compound spine exhibits the following laminæ (See Fig. 7):

Prespinal of sacral 1.....	<i>a. s.</i>
Prezygapophysial of sacral 1.....	<i>a. l.</i>
Diapophysial of sacral 1.....	<i>d. l.</i>
Diapophysial of sacral 2.....	<i>d. l.</i>
Postzygapophysial of sacral 3.....	<i>p. l.</i>
Postspinal of sacral 3.....	<i>p. s.</i>

- b.* The muscular rugosities at the sides of the neural spines descend upon the diapophysial laminæ in the dorsals and in sacrals 1 and 2; in sacrals 3 and 4, and in the caudals, the rugosities descend upon the postzygapophysial laminæ. This difference constitutes evidence that:

- 4. Posterior sacral-caudals.*—The sacrum of Cetiosaurus is reinforced by the addition not of dorsals, but of anterior caudals. The third sacral was probably the first of the anterior caudals to be added in an ancestral stage of evolution.

- a.* The fourth sacral<sup>2</sup> is still more conspicuously a modified caudal. It unites firmly with the third by its centrum, but its neural spine is entirely

<sup>1</sup> In his latest article upon the Sauropoda ('98, p. 487), Marsh states in his definition of the order: "Each sacral vertebra supports its own sacral rib or transverse process; no diapophyses on sacral vertebræ." A sacral rib, however, is not a transverse process, and it is evident that in these animals, as in the birds, both elements constitute the sacral arcæde.

<sup>2</sup> This vertebra was broken off in Marsh's specimen (see '96, Plate 28), leading him to describe and figure this animal as possessing only three sacrals.

separate above the level of the prezygapophyses. Its diapophysial lamina unites with the posterior border of the ilium only. This lamina passes downwards and forwards into a very powerful sacral rib which unites with the neck of the ilium.

5. *Double sacro-iliac union.*—The sacral ribs unite with the neck of the ilium; the diapophysial laminæ unite with the plates and crests of the ilium.

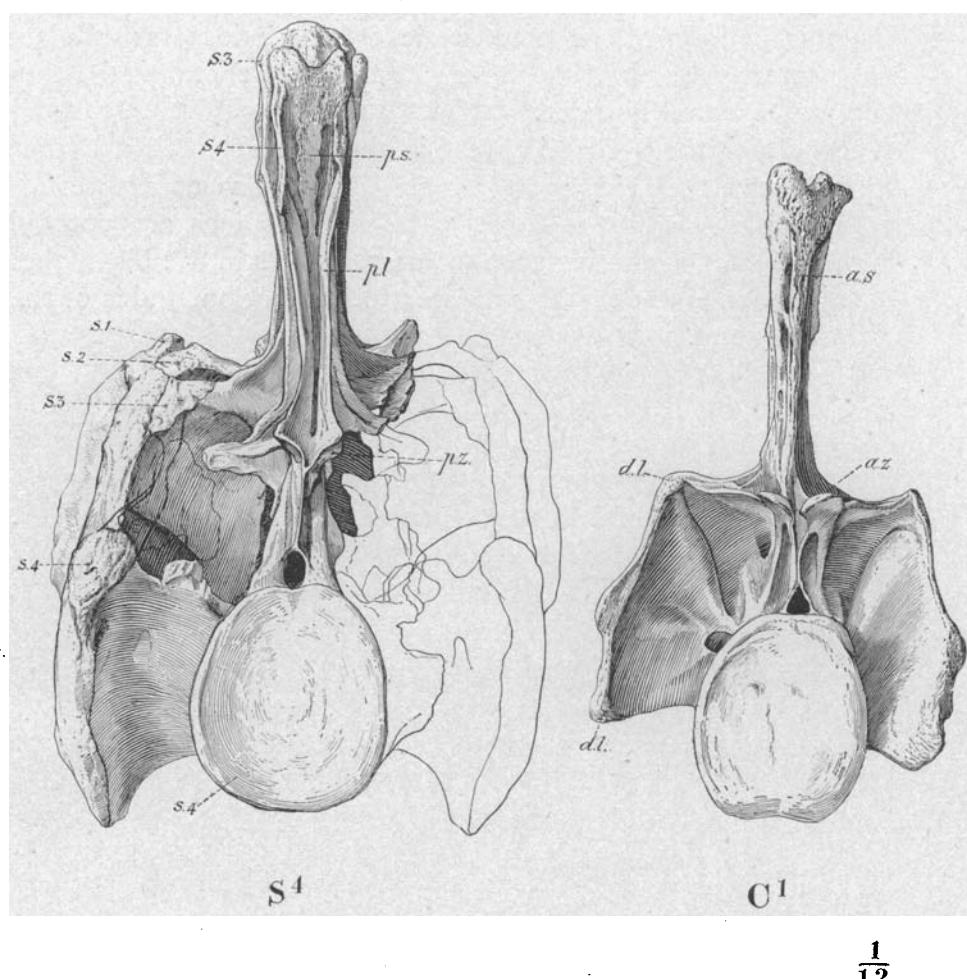


Fig. 11. Posterior view of Sacrum and Ilium; also anterior view of 1st Caudal, showing fundamental similarity between 4th Sacral and 1st Caudal.

#### *Relations of Sacrum and Ilium.*

1. This is the first instance among the Sauropoda in which a nearly complete sacrum has been found attached to the ilium.
  - a. This fortunate circumstance determines *the correct position of the ilium with relation to the sacrum*, and shows that the entire pelvic girdle has been incorrectly placed in all the figures and restorations of Marsh;

his error consisted in his placing the anterior and posterior acetabular borders, or pubic and ischiac peduncles, of the ilium upon the same horizontal plane, thus directing the superior iliac crest backwards, and altering the natural angle of the entire pelvis.

- b. The anterior acetabular or pubic peduncle in *Diplodocus* is demonstrated to be far below the level of the posterior acetabular or ischiac peduncle; thus the iliac crest is directed mainly upwards. This position of the ilium is undoubtedly characteristic of all Cetiosaurs; it places the pubes more vertically, and the ischia more horizontally than they have been represented hitherto.
- 2. The second point of great interest is the great elevation of the sacral spines above the ilium and the uniquely extensive and powerful union between the sacrum and ilia. The sacral spines are not only the highest spines in the vertebral column, but, as in the birds, the sacroiliac junction is the centre of power and of motion, and is of the most rigid character.

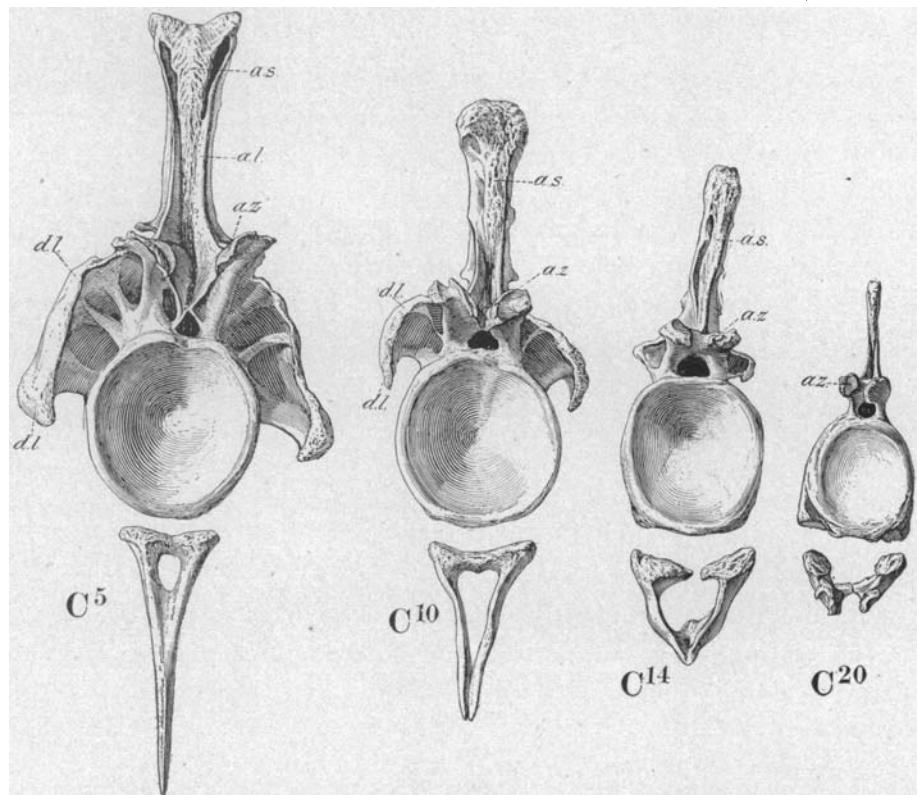


Fig. 12. Anterior view of characteristic Caudals, showing rapid change in the character of spines, Diapophyses, Centra, and Chevrons,  $\frac{1}{2}$  nat. size.

#### CAUDAL VERTEBRAE.

The completeness of the tail with its chevrons is of great moment; but few are missing as indicated in the restoration upon page 192.

37 caudals is the number estimated. 29 is the number fully or partly preserved. 26 chevrons are preserved. The length of the tail is estimated at 9 metres, or about 29 feet — this estimate is obtained by the addition of the actual lengths of the centra as follows :

*Antero-Posterior Diameter of Centra.*

1st Caudal.....	.152	20th Caudal.....	.300
2d     ".....	.163	21st     ".....	.297
3d     ".....	.182	22d     ".....	.296
4th     ".....	.193	23d     ".....	.285
5th     ".....	.205	24th     ".....	.272
6th     ".....	.210	25th     ".....	.255
7th     ".....	.216	26th     ".....	.242
8th     " (estimated).....	.215	27th     ".....	.225
9th     ".....	.214	28th     " (estimated).....	.212
10th     ".....	.241	29th     ".....	.201
11th     ".....	.267	30th     ".....	.190
12th     ".....	.277	31st     ".....	.172
13th     ".....	.270	32d     ".....	.161
14th     ".....	.305	33d     ".....	.151
15th     ".....	.290	34th     ".....	.147
16th     ".....	.318	35th     ".....	.135
17th     ".....	.300	36th     ".....	.117
18th     ".....	.320	37th     ".....	.107
19th     ".....	.310		

The caudals thus steadily increase in length from the first to the 18th and then steadily diminish towards the extremity. Sudden contrasts in measurement in the table above are due to distortion.

*General Characters of Caudals.*

PLATES XXVII AND XXVIII.

Totally dissimilar from the caudals of other reptiles, and even from those of other Dinosaurs, the caudals of Sauropoda or Cetiosauria are distinguished by profound changes in different regions. *Diplodocus*<sup>1</sup> seems to be even more remarkable in this respect than *Brontosaurus*.

1. All the caudals are procoelous.
2. As to chevrons there are four types (compare Figures 12 and 13) which unless found together would not have been considered as belonging to the same animal.
3. *Lateral cavities* of the centra extend from the first to the 18th caudal, gradually diminishing in extent.  
An *inferior concavity* characterizes all the centra and sharply distinguishes them from those of *Brontosaurus*.
4. As to proportion the anterior caudals are *short*, relatively *broad*, and spreading with heavy rugosities, as the seat of the powerful muscula-

<sup>1</sup> The latest definition of the Diplodocidae by Marsh ('98, p. 488) was published after he had examined the tail of the specimen here described. It includes a partial correction of his earlier definition of the caudal characters.

ture of the tail, sacrum, and femur. The median caudals (of the type first described by Marsh) are *long, narrow*, and contracted, as the seat of the propelling fin; the posterior caudals are long, slender cylinders.

5. The neural spines pass from the elevated rugose type (resembling that of the dorsals and sacrals), anteriorly, to a thin, laterally compressed type in the mid or fin region. This is evidence that the anterior caudals were of service in the vertical motions of the sacrum and back (as explained below) as well as in the lateral motions of the tail.
6. *Inferior horizontal lamina.* — The mechanical construction of the anterior caudals is most superb. In addition to the laminæ characteristic of the dorsals we find an *inferior horizontal lamina*. This is designed to brace the diapophysial lamina below against the heavy lateral strains of the femoro-caudal and ischio-caudal muscles; this lamina forms the dorsal wall of the lateral cavity.
7. The prezygapophyses, in caudals 1-12, are braced by two supplementary X laminæ which cross each other above the neural arch in front (see Fig. 12 X, C. 1-C. 5). The postzygapophyses are braced by a median vertical I lamina.

There are thus upon both sides and in the median line *eleven* laminæ in the caudals, in contrast with *eight* laminæ in the dorsals.

8. There is no hyposphen-hypantrum extension of the zygapophyses as in the dorsals.
9. The neural spines in certain vertebræ are hollow — that is, traversed by vertical tubular cavities.
10. In addition to the laminæ and cavities which are consecutively developed, almost every inch of surface is pocketed and sculptured with secondary hollows, intersecting and oblique bars. The mechanical elaboration is thus even more extreme than in the dorsals. Each of the anterior caudals requires a separate description, which should be followed by the reader in connection with Figs. 11, 12, 13, and Plates XXVII and XXVIII.

#### *Special Characters of Caudals.*

*1st Caudal.* — Summit of neural spine cleft as in posterior sacral and third presacral. Prespinal and postzygapophysial laminæ very strong; postspinal, prezygapophysial and upper portion of diapophysial laminæ very weakly developed.

Winglike diapophysial laminæ opposite neural arch, with a concave anterior surface pocketed at its junction with the centrum, supported or braced above by a horizontal lamina.

#### *Note 1. — Progressive Changes in Caudals 1-12.*

- a. Disappearance of median cleft in summit of spine, in C. 8.

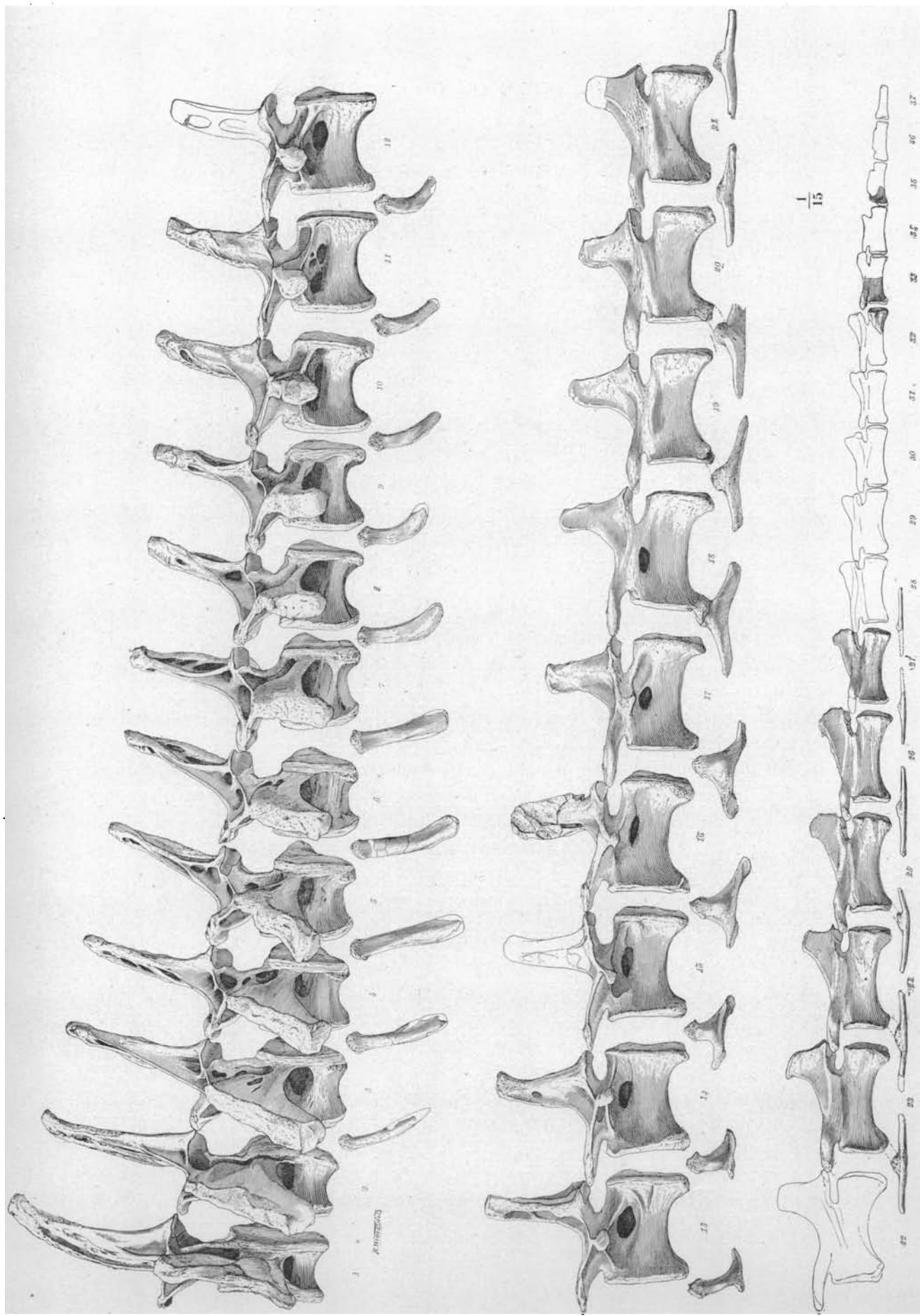


Fig. 13. Lateral view of entire caudal series.  $\frac{1}{15}$  nat. size. Caudals connected with chevrons by dotted lines are those in which a very close union existed.

- b. Disappearance of upper or neural spine portion of diapophysial lamina, in C. 3.
- c. Gradual decrease of superior horizontal lamina and increase of inferior horizontal lamina.

It thus appears that in addition to the general changes of form, centra, cavities, etc., noted on page 205, each vertebra has a distinctive development of its laminæ in adjustment to its particular stresses and strains.

*2d Caudal.* — Resembling C. 1 with more concave diapophysial lamina, presenting a broadly rugose outer border, and feebler prespinal lamina.

*3d Caudal.* — Differing from preceding in absence of upper portion of diapophysial lamina. Prespinal lamina still less prominent, prezygapophysial laminæ more prominent.

*Note 2. — Compensatory Development of Laminæ.*

It is apparent that the prespinal and prezygapophysial, postspinal and postzygapophysial laminæ are *mutually compensatory*, that is: strong prespinal, weak prezygapophysial; weak postspinal, strong postzygapophysial, or *vice versa*. This compensation is especially evident between caudals 4 and 7, 8 and 12, as explained below.

*4th to 7th Caudals.* — Distinguished by rapid increase of prezygapophysial laminæ with compensatory decrease of prespinal lamina, increase of postspinal lamina, and decrease of postzygapophysial laminæ.

The anterior view (Fig. 12) of caudal 5 gives an exceptionally clear view of the X zygapophysial laminæ, also of the secondary laminæ bracing the diapophysial lamina.

*Caudals 8—12* exactly reverse the progression shown in C. 4—7. They show a decrease of the prezygapophysial laminæ and an increase of the prespinal laminæ; an increase of the postzygapophysial laminæ and a decrease of the postspinal laminæ.

*Caudal 8* is the first with an uncleft spine.

All the centra have a long, deep concavity below.

The elongation of the centra and zygapophyses and diminution of the diapophyses becomes very rapid.

*Caudals 13—16* include the complete transition from the robust anterior type, to which powerful muscles were attached, to the laterally compressed posterior type which supported the caudal fin, and were moved principally by tendinous extensions of the anterior muscles. Between C. 9 and 17 also a complete change in the chevrons occurs. The change is as follows:

The diapophyses and lateral cavities persist into C. 16 on the right side.

The cavities persist as far back as C. 18 on the left side.

The pre- and postzygapophysial laminæ become laterally compressed and subside into the spine, which is elongated antero-posteriorly.

*Caudals 17-27* exhibit the laterally compressed moderately procœlous character of C. 16 with a gradual diminution in size; all the characteristic features disappear except the form of the centrum with its long inferior concavity. The chevrons undergo a series of changes.

#### CAUDAL CHEVRONS.

The most anterior chevron appears behind the second caudal. The chevrons are chiefly attached, in some cases connected, with the vertebræ behind them. For the sake of clearness the chevrons may be enumerated with the vertebræ, the most anterior chevron being termed chevron 3. Chevon 18 is firmly coalesced with caudal 18, enabling us to positively determine the position of all those in front of it.

There are no less than five types of chevrons:

*Chevrons 3-9* are of the typically reptilian form, with a small hæmal canal completely surrounded by bone, extending downwards into a long, laterally compressed spine. (Figs. 12, 13.)

*Chevrons 10-12* are shorter, with a large hæmal canal, closed above and open below by a fissure which divides the spine into two halves. These halves are in contact but not actually conjoined. (Figs. 12, 13.)

*Chevrons 13-14* are closed below and suddenly expand antero-posteriorly at the base of the hæmal arch. C. 14 is open above the hæmal canal. All chevrons behind C. 13 are open above the hæmal canal.

*Chevrons 15-19.* The upper portion of the chevron which unites with the centrum is much reduced. The lower portion expands antero-posteriorly and a long median opening appears between the two halves, which are still connected at the ends.

*Chevrons 20-28.* The connection of the elongated lower halves disappears and the chevrons consist of a pair of slender parallel rods, wholly separated, and attached upon the outer lower angles of the centra.

#### ARCHES.

Of the pelvic girdle the left ilium and ischium were found.

The *ilium* is finely preserved; the superior crest is perfect, but the anterior border is flattened or crushed inwards instead of turning sharply out to allow space for the two posterior ribs which lie in behind it.

The superior crest, as above noted upon page 203, is directed mainly upwards, not backwards as heretofore indicated by Marsh; the rugose border of the crest is surmounted or emphasized by five diapophysial rugosities, that is, those springing from the first presacral vertebra, and from the four sacrals. The anterior border exhibits a thin horizontal portion below the crest and a very heavy pre-acetabular bar or pubic peduncle; this bar connects with the broad supra-acetabular neck of the ilium along which the sacral ribs are attached.

The function of this pre-acetabular bar appears to have been to support the weight of the body when the anterior portion of the trunk was raised and the tail depressed. Then the femur was shifted backwards and the head forwards in its socket, so as to transfer the body weight to the anterior border of the acetabulum. This bar or peduncle then came into service.

The posterior iliac border is extremely short.

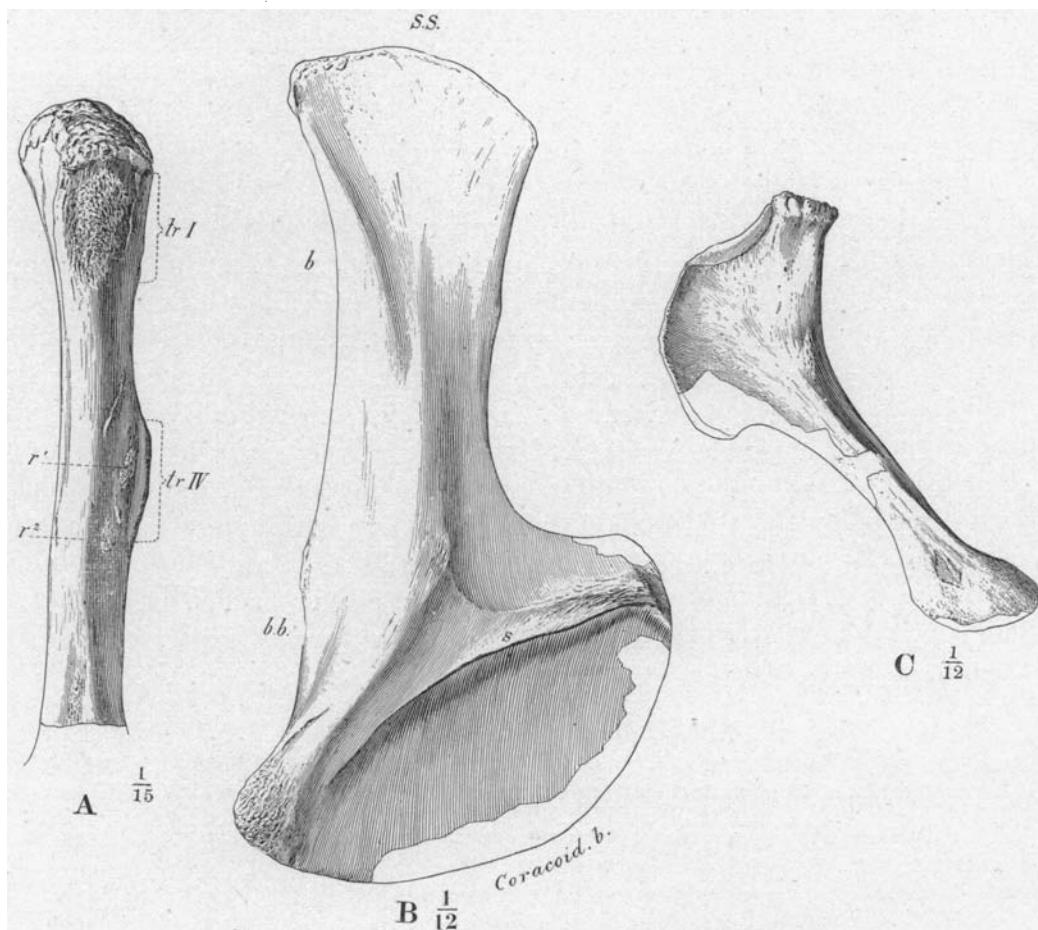


Fig. 14. A, External view of Left Femur,  $\frac{1}{15}$ . B, External view of Right Scapula,  $\frac{1}{12}$ . C, External view of Left Ischium,  $\frac{1}{12}$ . The anterior border of the Ischium should be produced into a hook below.

The *ischia* of *Diplodocus* are distinguished by their long symphysial union in the median line and coalescence near the extremities. In this specimen the anterior portion of the lower border is restored. Another specimen more recently found in Bone Cabin Quarry, shows that just behind the junction with the pubes the inferior border thins out and terminates in a sharp hook, as represented by Marsh. A similar hook has been observed by us in *Brontosaurus*.

The *pubes* are wanting in this specimen but have been found associated with ischia in Bone Cabin Quarry and will be described subsequently in a paper upon the limbs of *Diplodocus*.

Of the shoulder girdle only the *scapula* is preserved. Singularly enough this is the right scapula, for most of the skeleton represents the left side. It lacks the anterior-inferior border. It is distinguished by the gradual expansion of the blade towards the supra-scapular border, *ss.*, by the subequal dimensions of the blade, *b*, and coracoidal portion or body, *bb*, and by the exceptional prominence of the spine, *s*, which descends obliquely across the body.

#### LIMBS.

The *femur* is a highly characteristic bone. It is distinguished by a prominent trochanter placed on the posterior border, near the middle of the shaft, which apparently corresponds with the *fourth trochanter, tr<sup>4</sup>*, of Dollo.<sup>1</sup> This is for the insertion of the great *femoro-caudal* muscles of birds and Dinosaurs.

This is the most powerful rugosity among a group in this portion of the shaft. Just superior to it upon the inner side is a smaller rugosity; presumably for the *femoro-ischial* muscles. Upon the outer side of the shaft opposite this trochanter are two lesser muscle-insertion areas. The great trochanter *tr<sup>1</sup>*, occupies an extensively rugose area.

This femur is much more slender than that of *Brontosaurus* and has rather the proportions of the *Amphicælias altus* femur described by Cope. The part preserved measures 1.21 m.; the circumference of the shaft just above the 4th trochanter is .52; just below the 4th trochanter it is .53. The circumference of the femur of a full-grown Brontosaur in our collection is .72, or 2 feet 5 inches. The lower portion of the shaft begins to expand to form the condyles; it hardly appears that this femur could have attained the length assigned by Cope to the *Amphicælias altus* femur, namely, 1.930.

#### MEASUREMENTS OF SKELETON.

	Feet.	Metres.
Estimated height of 10th dorsal (from centre of centrum).....	2.7	.80
" 11th " " " " " .....	2.9	.844
" 12th " " " " " .....	2.10	.880
" 13th " " " " " .....	3.	.912
" 14th " (from edge of centrum).....	3.3	.986
" " Sacrals 1-4.....	3.3	.986
Length of 12th rib (from tubercle to extremity).....	4.4	1.320
" 13th " .....	3.7	1.100
" 14th " .....	2.7	.794
Ilium, antero-posterior diameter of crest.....	3.3	1.
" vertical diameter above pubic peduncle.....	2.5	.738
Scapula, vertical diameter.....	4.5	1.360
" transverse " .....	1.10	.338
Ischium, from iliac border to extremity.....	2.10	.851

#### SUMMARY OF NEW CHARACTERS.

The greatly extended and revised knowledge afforded by this specimen may now be summarized. Most of the observations made by the late Professor O. C.

<sup>1</sup> Note s. l. présence chez les oiseaux du 'troisième trochanter' des dinosauriens et sur la fonction de celui-ci. Bull. d. Mus. Roy. d. Hist. Nat. d. Belgique, Mars, 1883.

Marsh upon this genus are here confirmed; the principal exceptions from his statements relate to (1) the position of the ilium, (2) the number of sacral vertebræ, (3) the structure of the caudal chevrons, (4) the size of the animal.

*Dorsals.* The neural spines arise from the convergence of paired cervical spines.

There are no nodal or broad-spined dorsals as in *Brontosaurus*.

The rib articulations are greatly elevated in the posterior dorsals.

The two posterior dorsals are placed behind the ilium and bear one free and one coalesced or vestigial rib.

*Sacrals.* There are four sacrals, three of which exhibit a complete coalescence of the spines, the fourth being more free and like a caudal. The sacro-iliac union is by means of sacral ribs and diapophysial plates.

Additions to the sacrum are made from the caudal series.

*Caudals.* All the anterior caudals have broad diapophysial laminæ. These plates were first observed by the writer in *Brontosaurus* or *Camarasaurus*. There are five distinct types of chevrons. One of these, belonging to the 18th or 19th caudal, is the type to which Marsh assigned the name *Diplodocus*.

*Ilium.* The superior crest of the ilium is directed upwards, and the coalesced sacrals form the centre of motion and the highest portion of the vertebral column.

There is a balance of weight between the dorsals and anterior caudals. The laminar construction of the dorsals, sacrals, and caudals is shown to exhibit a unity of type, with local differences adjusted to special stresses and strains.

#### RESTORATION AND HABITS OF DIPLODOCUS.

FIGURE I.

We must await the discovery of the complete limbs and neck before *Diplodocus* can be completely restored. Yet a number of important points regarding the general structure of the animal can be established now.

The length of the entire skeleton was considerably greater than estimated by Marsh. The known and estimated linear measurements are as follows:

	Feet.	Metres.
Caudals.....	30	9.11+
Sacrals .....	2	.60+
Dorsals (estimated).....	12	3.65
Cervicals (estimated).....	12	3.65
Skull.....	2	.61
Total .....	58	17.62+

The animal was about 60 feet in length and relatively more elevated and more slender than *Brontosaurus*. The proportions of the shafts of the femora,

namely, *Diplodocus* 5, *Brontosaurus* 7, probably give us an approximate idea of the weight ratio—that is, *Diplodocus* had about five sevenths the bulk of *Brontosaurus*.

We must consider as three of the most important advances in our general knowledge of the structure of these animals: first, the establishment of the sacral spines as the highest point in the backbone; second, of the sacrum and ilium as a centre of power and motion; third, of the balance between the dorsals and caudals.

We observe in Marsh's restoration of *Brontosaurus*, a pioneer work of very great difficulty, that the mid-dorsal region is made the highest point in the backbone; that the sacral region is subordinate; that the tail (in which 8 or 10 anterior caudals are now known to be omitted) is an *appendage* of the body instead of an important locomotor organ of the body. In all these points Marsh's restoration is probably incorrect.

*Diplodocus* gives us a new and different conception of the Cetiosaurs or Sauropoda, one which increases their ability as aquatic reptiles, and specializes the functions of the tail. The tail constituted one half the length of the animal, and was of immense service as a propeller in enabling it to swim rapidly through the water, the broad anterior portion being provided with very powerful lateral muscles, and the compressed posterior portion being controlled by tendons and made effective by a vertical fin.

The tail, secondly, functioned as a lever to balance the weight of the dorsals, anterior limbs, neck, and head, and to raise the entire forward portion of the body upwards. This power was certainly exerted while the animal was in the water, and possibly also while upon land. Thus the quadrupedal Dinosaurs occasionally assumed the position characteristic of the bipedal Dinosaurs—namely, a tripododal position, the body supported upon the hind feet and the tail.

Thirdly, the *supporting function* of the posterior half of the tail is indicated by the sudden change in the shape of the chevrons at the 13th caudal; the chevrons of caudals 13 to 19 indicate the region to which part of the main weight of the body was transmitted; these chevrons are powerful and broadly spread out at the bottom. The 18th chevron is firmly ankylosed with the centrum; the 19th, 20th, 21st, 23d, 24th, 25th, are firmly connected with the centra by sutural surfaces, though not ankylosed.

What may be termed the 'supporting and balancing' tail of the Hadrosaurs, Iguanodonts, and Megalosaurs is of a much simpler type than this 'balancing, supporting, and propelling' tail of the Cetiosaurs.

There is a traditional view that these animals were ponderous and sluggish. This view may apply in a measure to *Brontosaurus*. In the case of *Diplodocus* it is certainly unsupported by facts.

As compared with the Crocodilian or Cetacean type, the axial skeleton of *Diplodocus* is a marvel of construction. It is a mechanical triumph of great size, lightness, and strength. Judging by the excessive rugosity of the vertebræ and

limbs, the powerful interspinous ligaments attached to the pre- and post-spinal laminæ, the backwardly directed rugosities at the summits of the diapophysial laminæ in the dorsals, and of the postzygapophysial laminæ in the caudals, the animal was capable not only of powerful but of very rapid movements. In contrast with *Brontosaurus* it was essentially long and light-limbed and agile. Its tail was a means of defence upon land and a means of rapid escape by water from its numerous carnivorous foes. Its food probably consisted of some very large and nutritious species of water-plant. The anterior claws may have been used in uprooting such plants, while the delicate anterior teeth were employed for prehensile purposes only. The plants may have been drawn down the throat in large quantities without mastication, since there were no grinding teeth whatever. It is only by some such means as these that these enormous animals could have obtained sufficient food to support their great bulk.

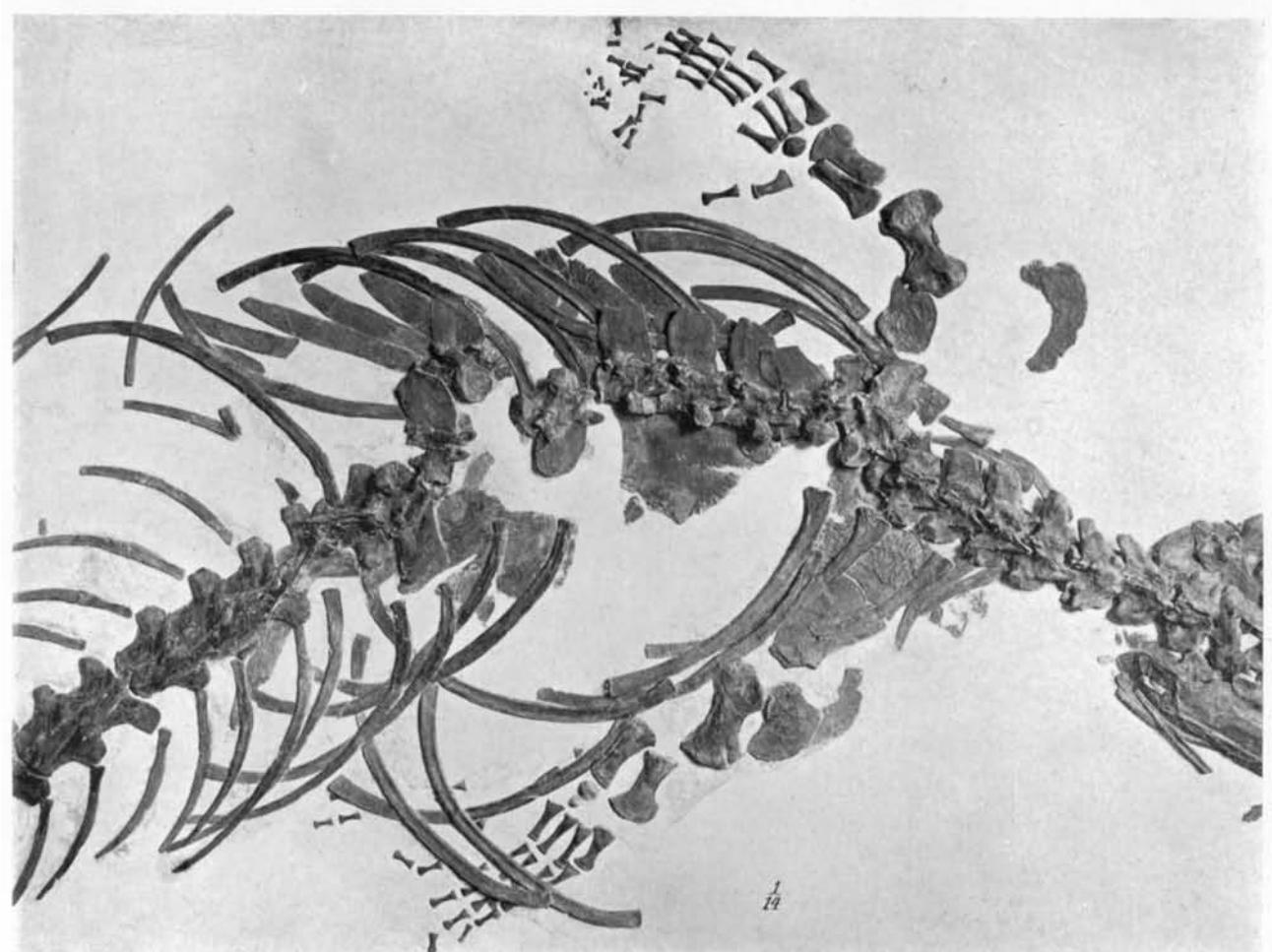
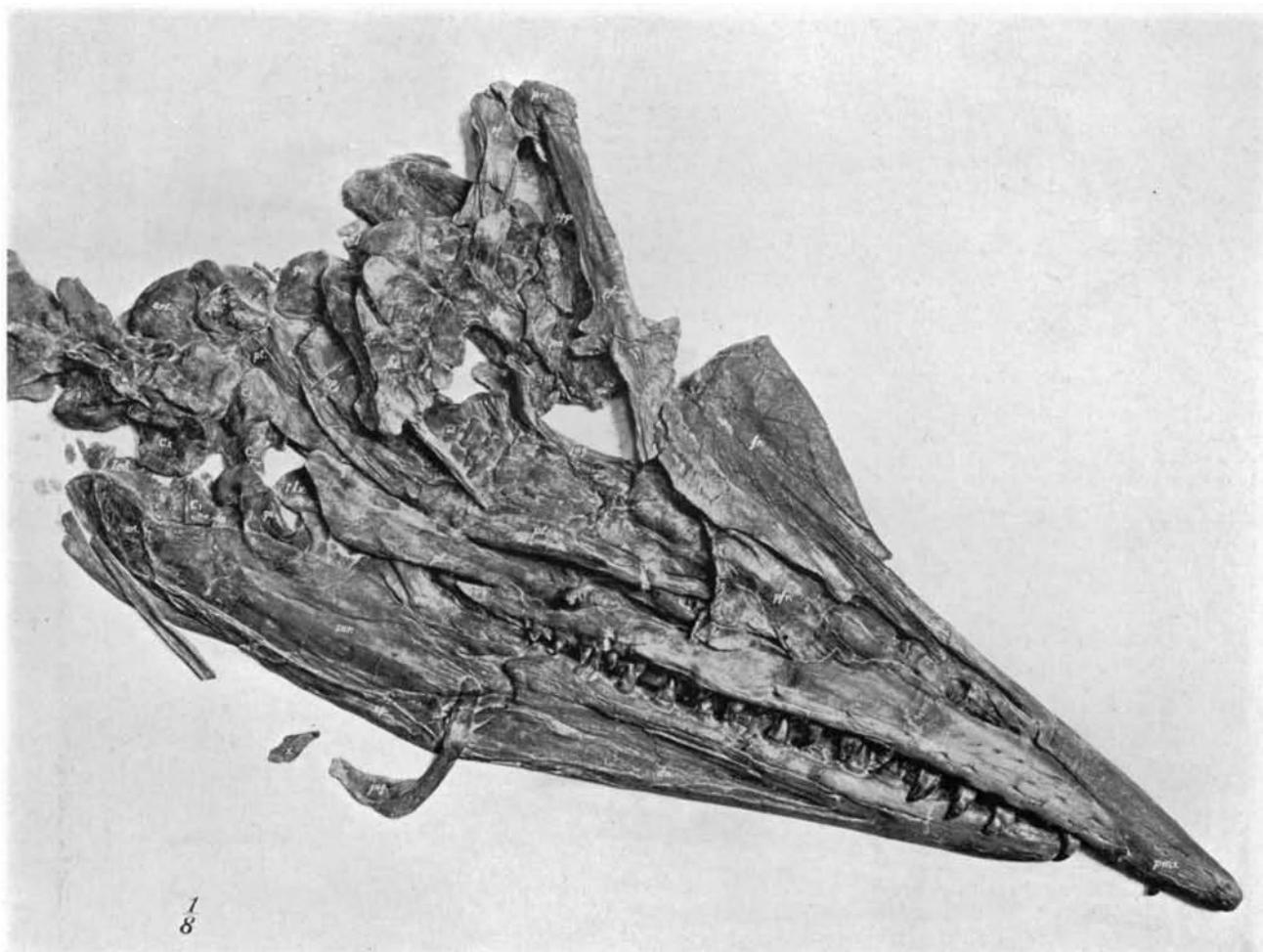
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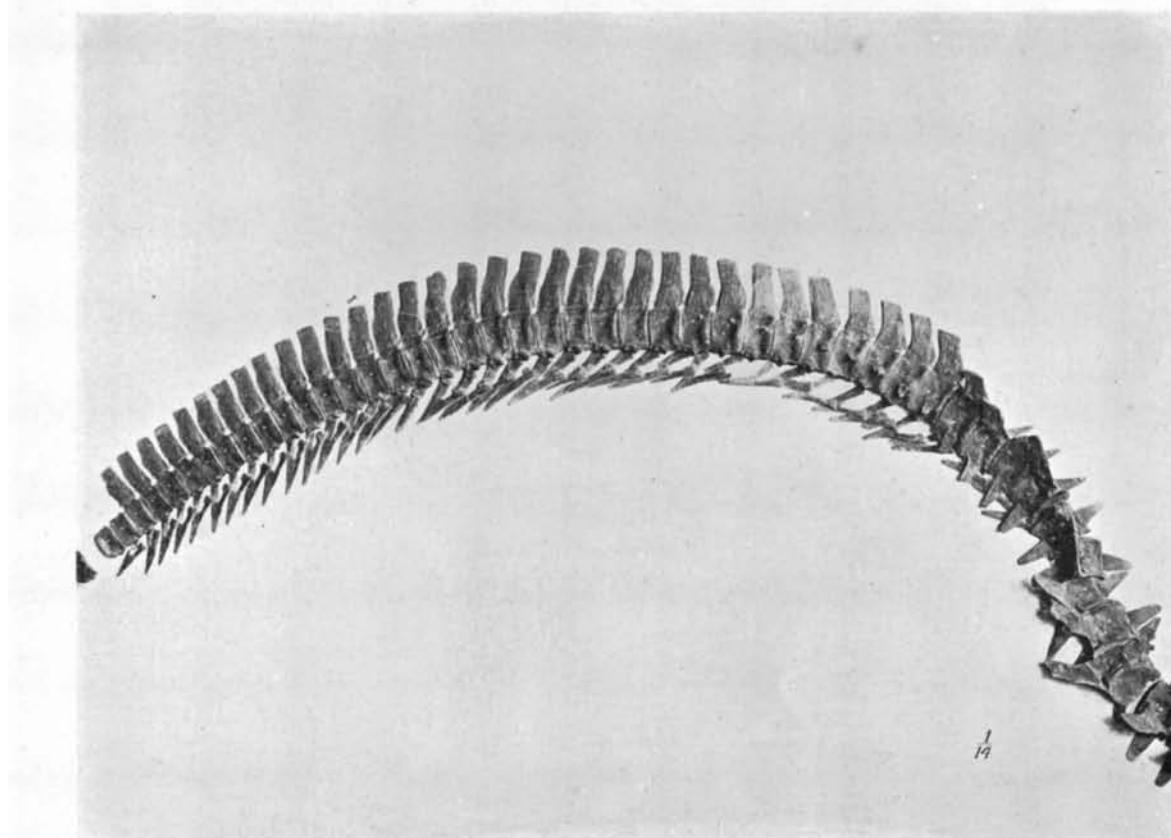
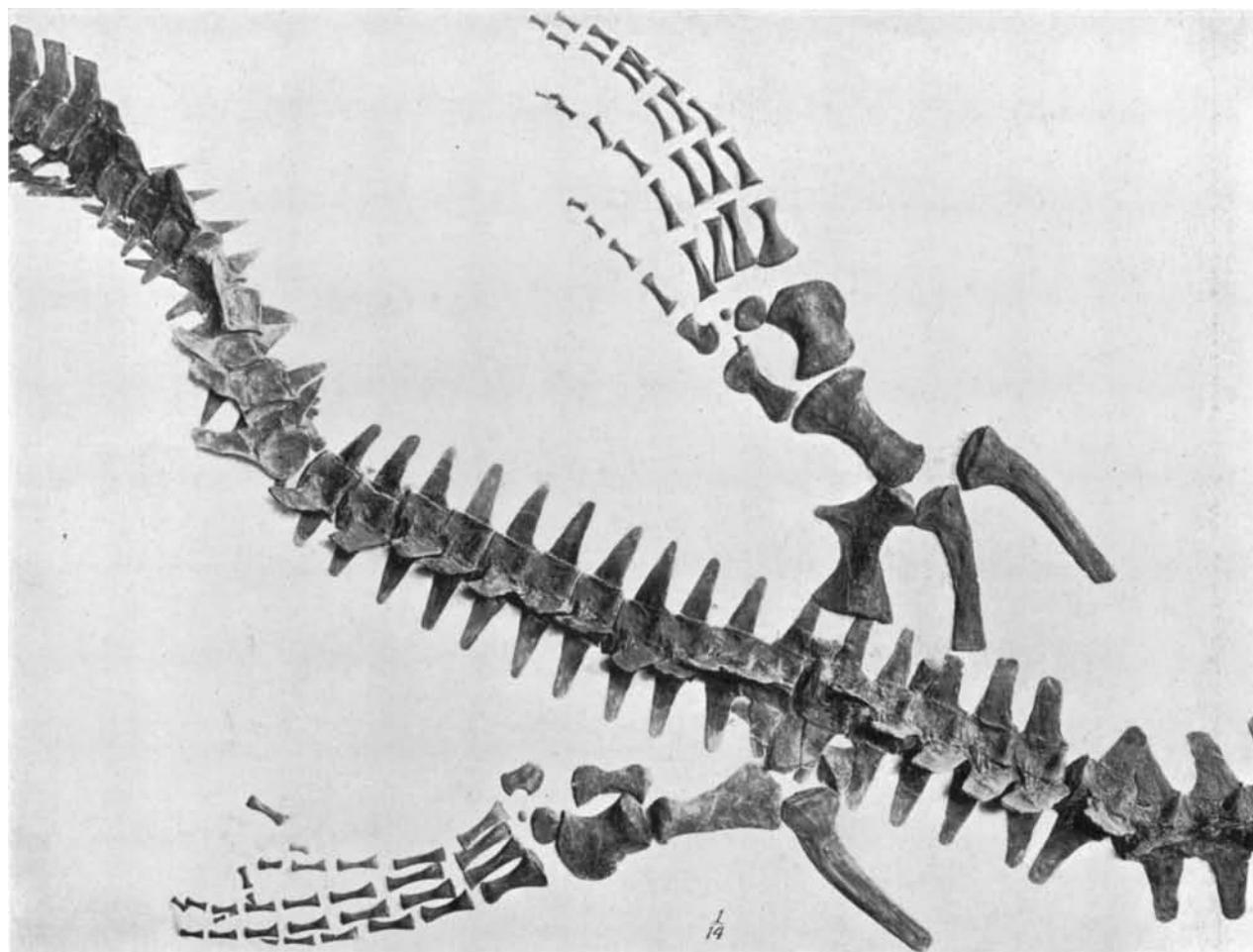




TYLOSAURUS DYSPELOR.

UPPER FIGURE.—Skull,  $\frac{1}{8}$  natural size.

LOWER FIGURE—Chest and neck section, and shoulder girdle,  $\frac{1}{4}$  natural size.

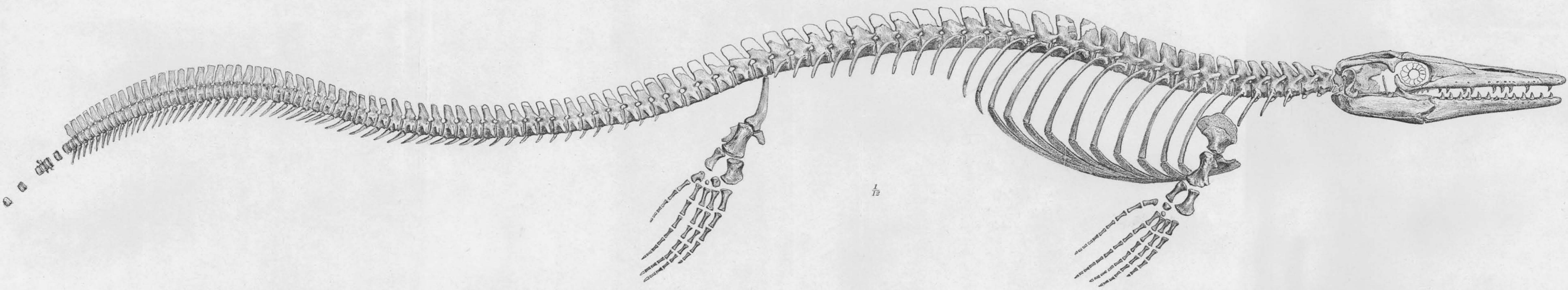


TYLOSAURUS DYSPELOR.

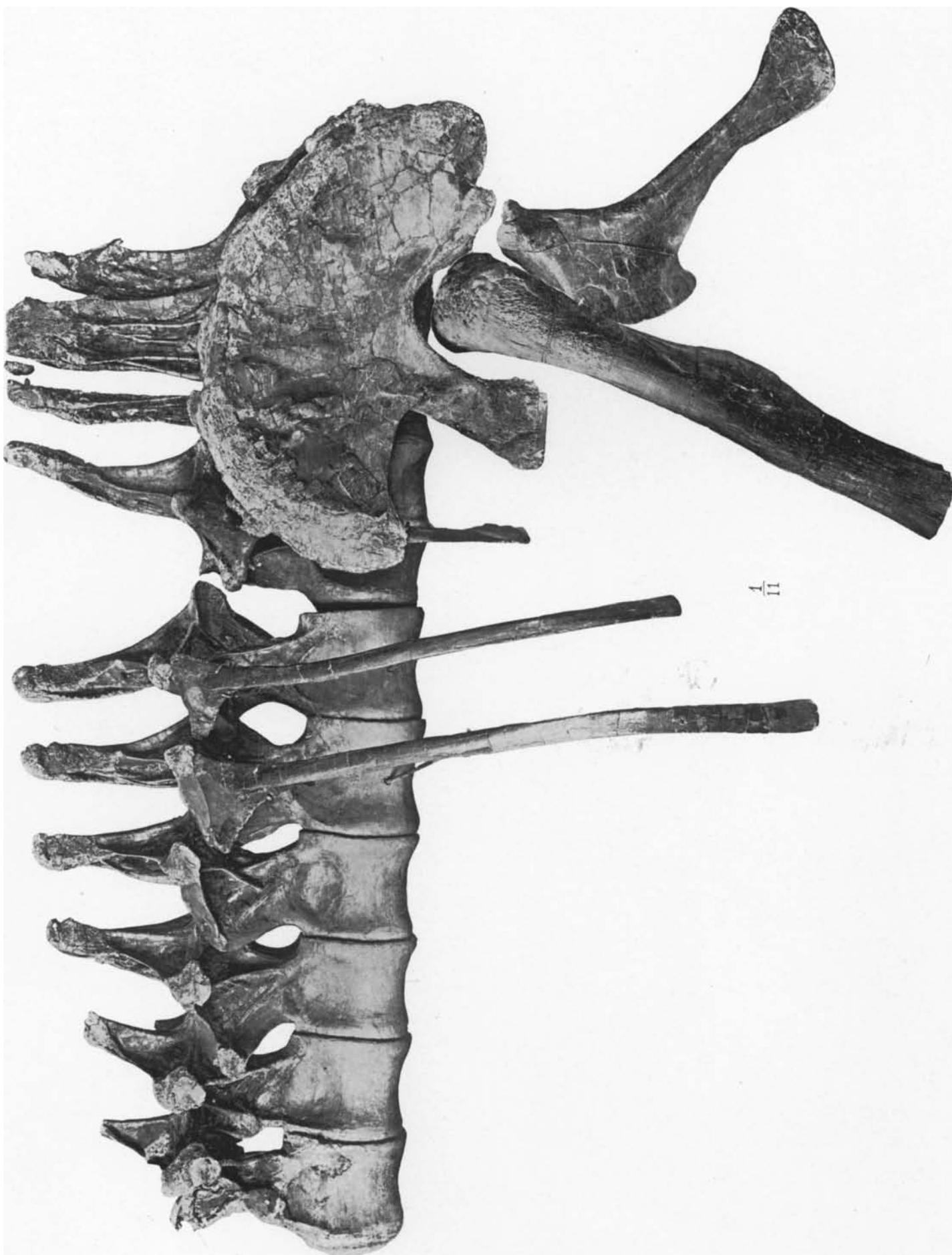
UPPER FIGURE.—Sacral and pygal section of pelvic girdle,  $\frac{1}{4}$  natural size.

LOWER FIGURE.—Caudal vertebræ, showing natural curvature,  $\frac{1}{4}$  natural size.





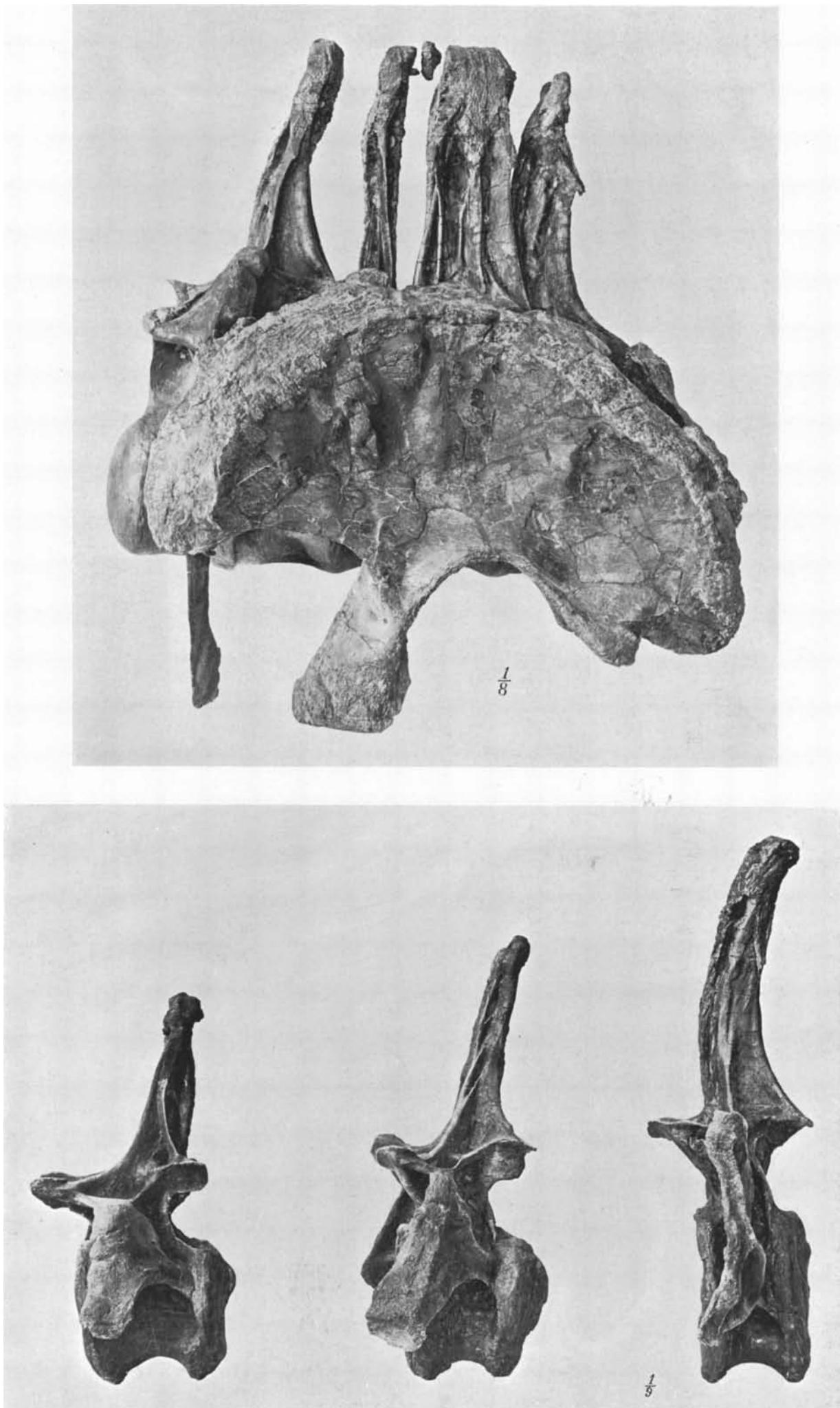




DIPLOPODUS LONGUS.

Dorsals, Sacra, Ilium, Ischium, and Femur,  $\frac{1}{11}$  natural size.



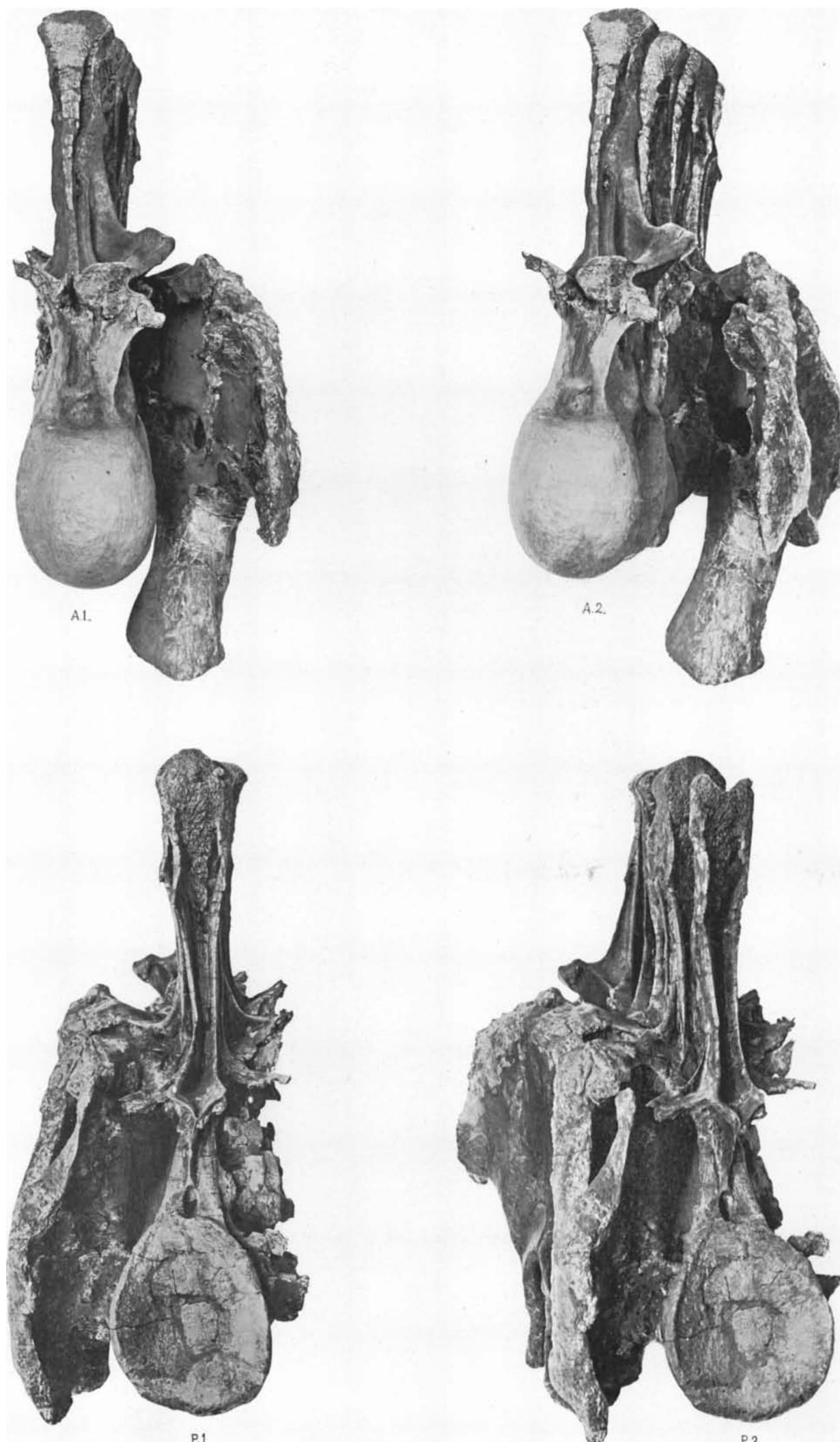


DIPLODOCUS LONGUS.

UPPER FIGURE.—Lateral view of posterior Dorsals, Sacrum, and Ilium,  $\frac{1}{8}$  natural size.

LOWER FIGURE.—Lateral view of 1st, 4th, and 7th Caudals,  $\frac{1}{9}$  natural size.



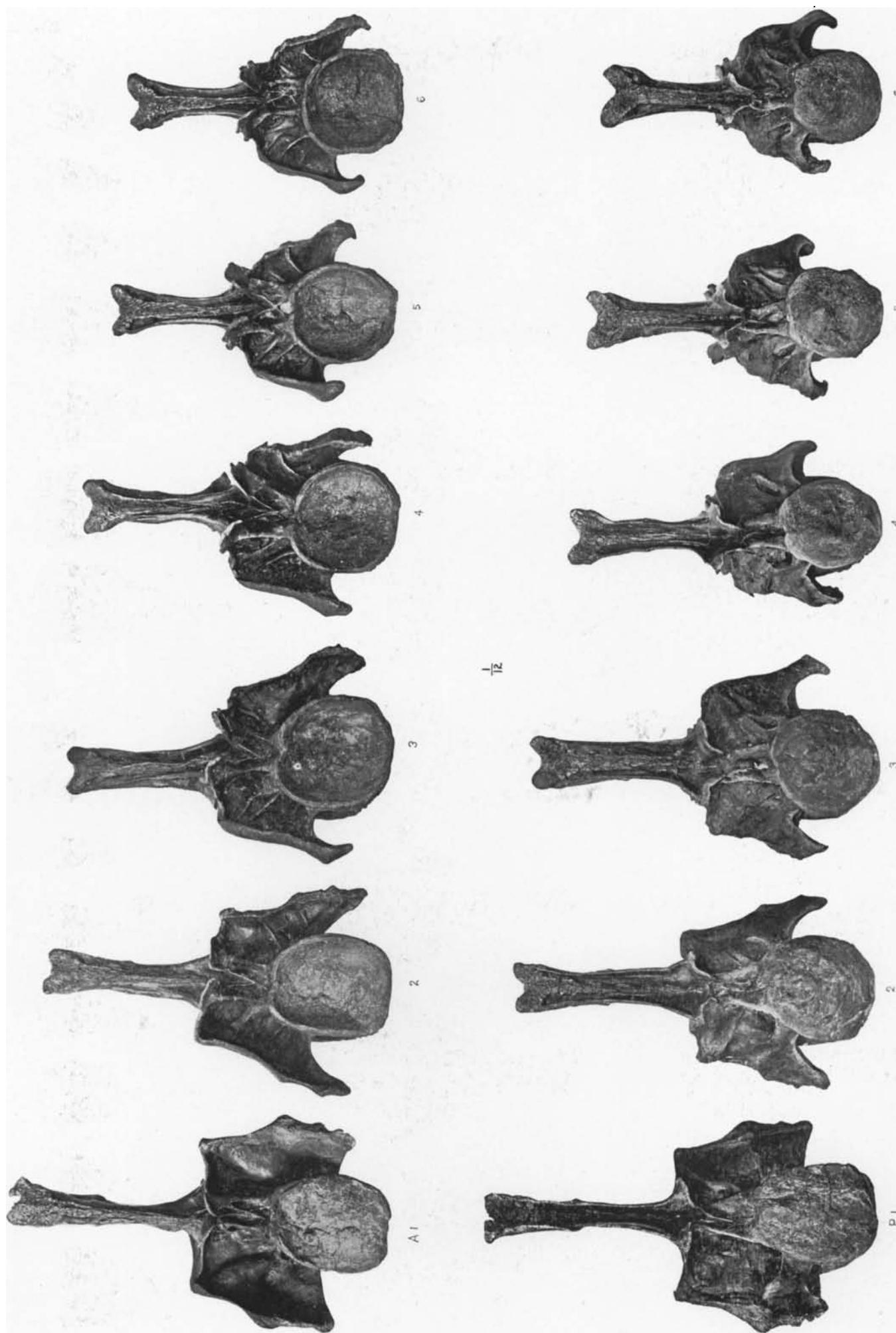


DIPLODOCUS LONGUS.

Anterior, oblique, and posterior views of Sacrum and Ilium.

A.1, anterior direct view, A.2, oblique; P.1, posterior direct, P.2, oblique.



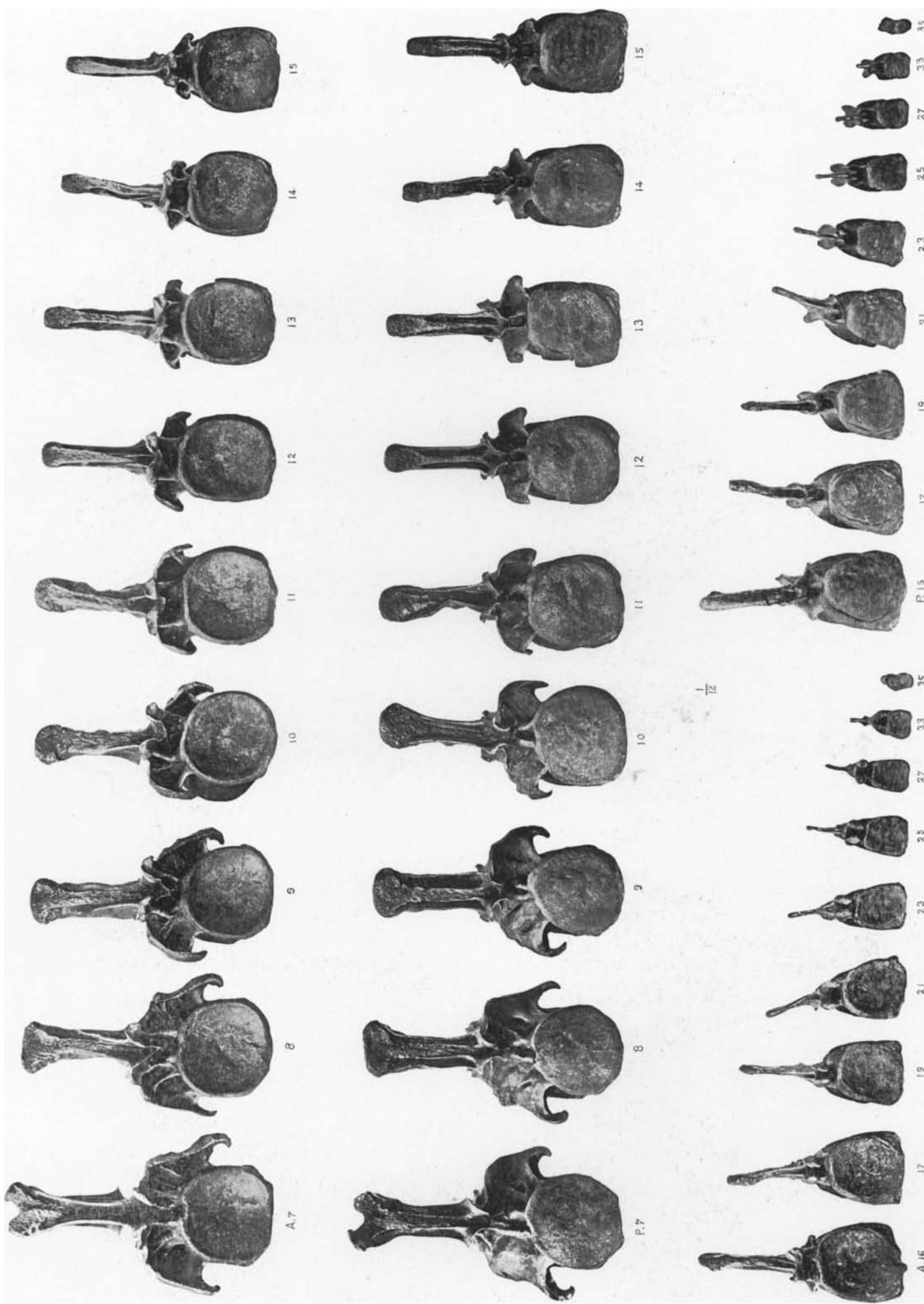


DIPLOCERASPIS LONGUS.

Anterior and posterior views of Caudals 1-6,  $\frac{1}{2}$  natural size.

A, anterior view; P, posterior view.





*Diplodocus longus.*

Anterior and posterior views of Caudals 7-35,  $\frac{1}{12}$  natural size.

*A*, anterior; *P*, posterior.



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