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STRUCTURE AND RELATIONSHIPS OF OPISTHOCŒLIAN DINOSAURS.

PART I.

APATOSAURUS MARSH

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STRUCTURE AND RELATIONSHIPS OF OPISTHOCŒLIAN DINOSAURS.

PART I.

APATOSAURUS* MARSH.

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The genus *Brontosaurus* Marsh was described† in 1879 from a well preserved skeleton found near Lake Como, Wyoming. The completeness of this specimen and the widely published restorations based upon it have caused this genus to be long regarded as the best known of all the American Opisthocœlia.‡ However, many questions of morphology were left in doubt by this famous specimen. No skull which could be identified with the genus has ever been described; that figured in Marsh's restoration is based upon a comparison with the skull of *Morosaurus*. The structure of the hind feet was not made clear until figured by Osborn in 1899,§ while the structure of the fore foot remained a matter of conjecture until figured by Hatcher in 1902.‖ The vertebral formula of the dorsal and caudal series, as well as many sacral and pelvic characters, has remained to be determined by an unusually well preserved skeleton just placed upon exhibition in the Field Columbian Museum.

The specimen under consideration (Mus. No. 7163) was collected by the Museum Paleontological Expedition of 1901, in charge of the writer, ably assisted by Mr. H. W. Menke. It was found in the Grand River Valley near Fruita, Colorado, in a geological horizon ¶ probably equivalent to the Como Beds of Wyoming. The specimen was discovered in the fall of 1900, but owing to the lateness of the season, its removal was deferred until the following spring.

When found the last cervical vertebra was projecting from a steep hillside. The thoracic series led diagonally into the face of the hill, leaving the distal ends of a number of ribs exposed and partially broken

* *Brontosaurus*, Marsh, is shown to be a synonym of *Apatosaurus*.

† Am. Jour. Sc. Vol. xviii, p. 503.

‡ Sauropoda and Cetiosauria are shown to be synonyms of Opisthocœlia.

§ Bull. Am. Mus. of Nat. Hist., Vol. xii, pp. 161–172.

‖ Annals of the Carnegie Museum, Vol. i, pp. 156–76.

¶ See "The Dinosaur Beds of the Grand River Valley of Colorado," this publication, Geol. Series, No. 9.

away. Ten feet farther along the bank the distal end of the femur appeared. So hard was the concretionary matrix, in which the skeleton was encased, that drills and dynamite were at once called into service in order to make the excavation necessary for its removal. When the pelvis was reached the face of the stripping was eighteen feet in height. From this point the series of caudal vertebræ curved backward, and dipping rapidly with the strata, led almost directly into the hillside. These conditions made it necessary to resort to tunneling. Accordingly a chamber twenty feet in length by eight feet in breadth was excavated before the search for displaced caudal vertebræ was abandoned.

The specimen as a whole was lying upon its right side, and apparently the entire skeleton had been present when embedded. The cervical vertebræ and the fore legs had been carried away by a process of erosion so slow that comparatively few fragments were found upon the surface. The vertebræ from the last cervical to the thirteenth caudal were but slightly displaced from their normal position. (See frontispiece.) The remaining ten caudal vertebræ recovered were found more and more dissociated, until tunneling for them became unprofitable. Some of the chevrons were associated with the vertebræ, but most of them were displaced. The ribs were found in close apposition with their respective vertebræ. The right ilium was in position and coössified with the sacrum; the femur was scarcely removed from the acetabulum. The pubes and ischia were slightly displaced; the left ilium was fragmentary.

This specimen has been prepared for exhibition with great care and patience, employing the energies of three skilled men for more than eighteen months. The spines and transverse processes of the vertebræ were more or less distorted by the compressure to which they had been subjected in the matrix. So far as was practicable, these distortions have been readjusted. The inevitable missing fragments have been replaced by plaster and carefully colored to match the adjacent parts. All portions thus restored are marked out by a line not so conspicuous as to mar the general appearance of the specimen, but distinct enough to be readily recognized when examined closely.

For information concerning the type specimen of *Brontosaurus*, and for advice in the preparation of this paper, the writer is indebted to Dr. S. W. Williston of the Museum staff.

SYNONYMY.

The number of terms applied to the group of reptiles variously designated as Sauropoda, Cetiosauria, and Opisthocœlia has led to

confusion, at once annoying to the investigator and puzzling to the student. The oldest member of the group and the best known of the European genera is *Cardiodon*.* This was described by Owen in 1841, and for a long time included under the Crocodilia.

The first recognition of the ordinal rank of the Cardiodont reptiles was offered by Owen in 1859, when he proposed for them the name Opisthocœlia, as one of three suborders of crocodiles. The group was characterized as follows:† "The small group of Crocodilia, so called, is an artificial one, based upon more or less of the anterior trunk vertebræ being united by ball-and-socket joints, but having the ball in front instead of, as in modern crocodiles, behind. Cuvier first pointed out this peculiarity in a crocodilian from the Oxfordian beds at Honfleur and the Kimmeridgian at Havre. The Reporter has described similar opisthocœlian vertebræ from the Great Oölite at Chipping Norton, from the Upper Lias of Whitby, and of much larger size, from the Wealden formations of Sussex and the Isle of Wight. These specimens probably belonged, as suggested by him in 1841 and 1842, to the fore part of the same vertebral column as the vertebræ, flat in the fore part and slightly hollow behind, on which he founded the genus *Cetiosaurus*."

In this classification Owen was followed by Haeckel, but Huxley, in the following year, included *Cardiodon* in the Iguanodontidæ. In 1874 Seeley, describing the genus *Craterosaurus*, proposed for the same forms the order Cetiosauria, which he included under the subclass Dinosauria:‡ "My fossil presents some remarkable differences from other figured Dinosaurian specimens, and I have thought it worthy of the attention of the Society, as indicating that distinct ordinal groups are probably confounded under the name Dinosauria. For if the skull be Dinosaurian which was figured by Mr. Hulke as probably that of *Iguanodon* (and of its Dinosaurian character I entertain no doubt), and the specimen now described be Dinosaurian, in the ordinary sense of the term, as I believe, then no one will doubt the propriety of placing the latter animal, with its indisputable lacertian characteristics, in a distinct ordinal group from the Wealden animal, which has the skull closed anteriorly in a way to which no Lacertilian makes an approximation.

"This difference is, indeed, in harmony with lacertian differences in portions of the skull in *Cetiosaurus*; so that had there been any

* In a recent publication by Lucy P. Bush *Cardiodon* is shown to have priority over *Cetiosaurus*. Am. Jour. Sc., Vol. xvi, p. 96.

† Report British Association for the Advancement of Science, 1859, p. 164.

‡ Q. J. G. S. of London, Vol. xxx, p. 690.

reason for suspecting that the Potton fossil belonged to the Cetiosauria, I should have felt no difficulty in regarding it as the base of a Cetiosaurian cranium. . . . . On the whole, I regard the bone as indicating that in at least one Order of the Sub-class Dinosauria the bones of the base of the cranium were Rhyncocephalian rather than Avian."

In 1878 Marsh proposed to raise his previously established group Atlantosauridæ to the rank of suborder, and to include in it the genera *Atlantosaurus*, *Apatosaurus*, *Morosaurus*, and *Diplodocus*.* The suborder was clearly defined with regard to American groups, but the European forms and their previous classification were ignored, although a number of them clearly fall within the same family groups.

In this way these three synonymous terms have been adopted and used by various writers. "Opisthocœlia" has the undisputed claim to priority. As applied, it included as its characteristic representative *Cardiodon*, the best known of the European forms. In its primary significance it is descriptive of all the well known forms, both European and American, which have since been included in the group. It was followed by Haeckel and in part by Cope and Baur. The one objection which has been urged against the term is, that it was proposed to be applied to a subdivision of the Crocodilia. This objection is not valid, since there are no opisthocœlous crocodiles with which the group can be confused. The homogeneity of the group according to the first definition was recognized when it was bodily transferred by Seeley into the Dinosauria, when it was defined as Sauropoda by Marsh, and when it was made an independent order by Baur. Its inclusion under the Crocodilia was designated at the outset as artificial; its present inclusion under the Dinosauria was regarded by Baur as equally artificial. If this be true, the same objection will hold against the terms later applied.

The term "*Cetiosauria*" has gained favor owing chiefly to the fact that it was offered as a subdivision of the Dinosauria and hence has coincided more nearly with later classification. It was based upon a distinction between the Cetiosaurian and Iguanodon skull, but that distinction had been taken for granted by earlier writers, and was only made necessary by Huxley's erroneous reference of *Cardiodon* to the Iguanodontidæ.

As regards the term "Sauropoda," it must be recognized that it was based upon a much more complete knowledge of the group, and as a result was much more clearly defined. But if we were to demand complete knowledge of structure and affinities, in support of a group name, very few genera and families now accepted would stand.

* Am. Jour. Sc., Vol. xvi, p. 412.

The three terms, then, are essentially co-ordinate and co-extensive. "Opisthocœlia" has priority, and is entitled to preference. The term will therefore be used in this paper to designate the order; "Cetiosauria" and "Sauropoda" being regarded as synonyms.

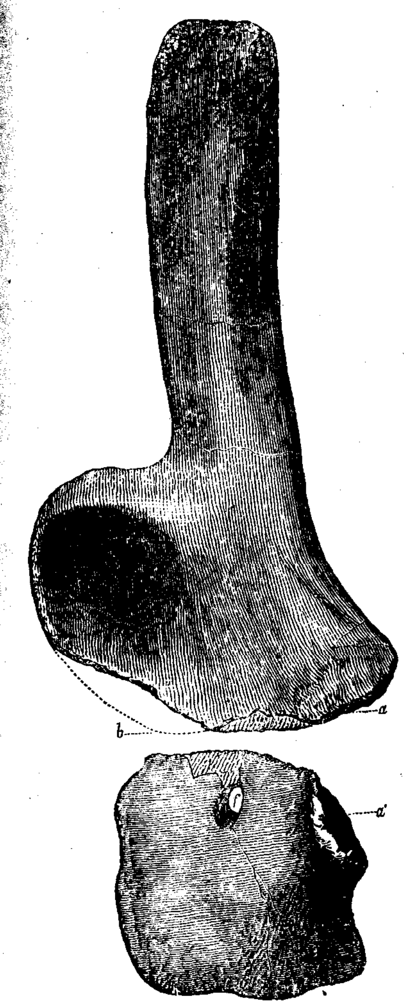

FIG. 1. Scapula and coracoid of *Apatosaurus*, after Marsh.

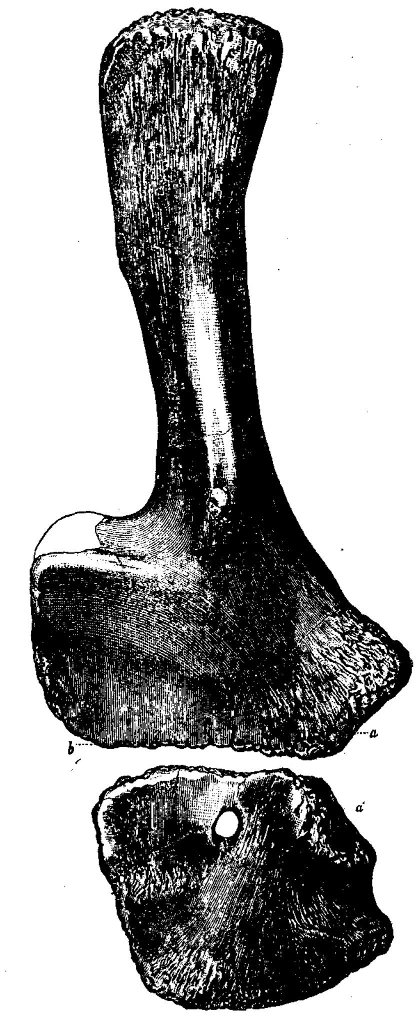

FIG. 2. Scapula and coracoid of "*Brontosaurus*," after Marsh.

The genus *Apatosaurus* Marsh was proposed in 1877 upon a considerable portion of a skeleton, but with brief description only.* Early in 1879 the genus was characterized by the structure of the scapula,

* Am. Jour. Sc., 3d Ser., Vol. xiv, p. 514.

coracoid, and sacrum, and these parts were figured.* In December of the same year the genus *Brontosaurus* was proposed upon an unusually complete specimen briefly described.† Later a more complete description was given and a number of parts figured.‡ Two different restorations were later published.§

The genus *Brontosaurus* was based chiefly upon the structure of the scapula and the presence of five vertebræ in the sacrum. After examining the type specimens of these genera, and making a careful study of the unusually well-preserved specimen described in this paper, the writer is convinced that the Apatosaur specimen is merely a young animal of the form represented in the adult by the Brontosaur specimen. As before pointed out,‖ the imperfectly ossified condition of the scapula, coracoid, and sacrum indicates a young animal. (Figs. 1 and 2.) The presence of but three coalesced vertebræ in the sacrum points to the same conclusion as will appear from a comparative study of sacra offered in this paper. The proportionate size of the two specimens, the shorter shaft and narrow distal end of the scapula, the outline of the coracoid, the open chevrons, the form of the anterior thoracic and the cervical vertebræ, and the structure of the pelvis (Figs. 3 and 4) all display such similarity as one would expect in a young animal of the Brontosaur type. In fact, upon the one occasion in which Professor Marsh compared ¶ these two genera he mentioned the similarity between the scapulæ of their respective types. In view of these facts the two genera may be regarded as synonymous. As the term "Apatosaurus" has priority, "Brontosaurus" will be regarded as a synonym.

The following species have been referred to this genus:

A. ajax Marsh, type of genus, Am. Jour. Sc., (3), xiv, 514, Dec., 1877.

A. grandis Marsh, ibid., (3), xiv, 515, Dec., 1877.
Referred to *Morosaurus*, ibid., (3), xvi, 414, Nov., 1878.

A. laticollis Marsh, ibid., (3), xvii, 88, Jan., 1879.

A. excelsus Marsh, ibid., (3), xvii, 503, Dec., 1879.
(*Brontosaurus excelsus*) this paper.

A. amplus Marsh, ibid., (3), xxi, 421, May, 1881.

Of this number probably not more than two species are valid. *A. ajax* is based upon a specimen too young to admit of specific determination. *A. grandis* is a synonym. *A. laticollis* was described

* Ibid., Vol. xvi, p. 86.
† Ibid., 3d Ser., Vol. xviii, p. 501.
‡ Ibid., 3d Ser., Vol. xxi, p. 417–21.
§ Ibid., 3d Ser., Vol. xxvi, Pl. 1; The Dinosaurs of North America, Pl. XLII.
‖ Am. Jour. Sc., 4th Ser., Vol. xv, p. 305.
¶ The Dinosaurs of North America, U. S. Geolog. Surv., Vol. xvi, p. 168.

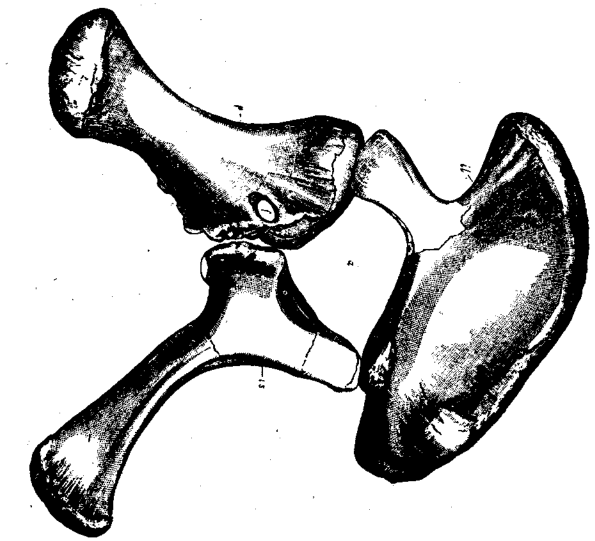

FIG. 3. Pelvis of *Apatosaurus*, after Marsh.

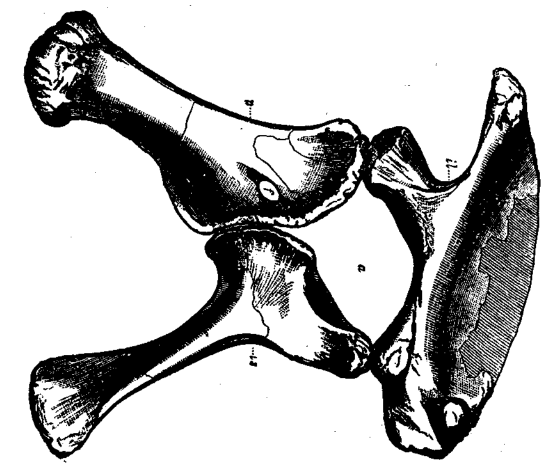

FIG. 4. Pelvis of "*Brontosaurus*," after Marsh.

from a single cervical vertebra which may or may not be identical with the type species. *A. excelsus* is familiar as the type of "*Brontosaurus*," and is based upon a large part of a skeleton. The sixth and the last cervical vertebræ of this specimen as figured by Marsh* show such a similarity to the type of *A. laticollis* as to indicate that the intervening ninth or tenth vertebra would prove identical. However, the present knowledge of the cervical series does not admit of positive identification. *A. amplus* has not been figured and cannot now be determined. The Museum specimen will be regarded as conspecific with the well known Yale specimen and designated as *Apatosaurus excelsus*.

The genus *Apatosaurus* may be distinguished from other members of the Opisthocœlia by the following characteristics: Scapula with shaft and spine almost at right angles; shaft long and slender with slightly expanded distal end; ischium with acetabular surface at right angle to shaft and distal end expanded; sacrum in adult specimens with five ilium-supporting vertebræ; anterior dorsal spines paired, long, and slender; anterior caudal centra with lateral cavities.

DESCRIPTION OF SKELETON.

DORSAL VERTEBRÆ. (Plates XLVI and LII.) The vertebræ lying between the cervical and the sacral regions are all rib-bearing, and hence may be designated by the term "dorsal"; but in the following description they will be referred to as "presacral" and numbered from the sacrum forward in order to afford a definite basis of reckoning, since the fragmentary condition of presacral XI does not admit of its position in the series being determined with absolute certainty. However, there is every reason to believe that this vertebra is the last cervical.

The *dorsal vertebræ* are of the opisthocœlous type, and are all rib-bearing. So much may be said of them as a group—as to other characteristics they represent a continuous transition, passing from the elevated and slender type posteriorly to the depressed and wide-armed type of the anterior dorsal region. In view of this wide difference between the anterior and posterior extremes of the series, it is not surprising that isolated vertebræ have been made the types of three or more different genera. Variation between the extreme types of the dorsal series is especially noticeable in the following four vertebral elements. (1) The centra, (2) the neural spines, (3) the transverse processes, and (4) the capitular facets. In order to bring out their

* Plates XX and XXI, the Dinosaurs of North America.

gradation, the vertebræ will be described by taking up the several elements in turn and tracing them through the entire thoracic series.

The *centra* pass from the less pronounced opisthocœlous type near the sacrum to the pronounced type of the cervical region. In the first presacral the vertical diameter of the centrum is equal to the lateral diameter; as we pass forward in the series the centra become vertically compressed while the lateral measurement remains approximately the same. The articular ends from I to VIII are nearly perpendicular to the axes of the centra; with IX the articular surface begins to incline forward, this feature becoming more and more pronounced until the centra take on the cervical type with presacral XI. The openings of the pleuro-central cavities in the first presacral are almost round and enter the centrum from above downward. With the strengthening of the pedicles and the depression of the centra, these assume a lateral direction. In the anterior members of the series they become elongate axially; in IX and X they are partially replaced by the capitular facet.

In cross section the typical centrum shows an external wall pierced by two lateral foramina leading to the pleuro-central cavities, which are separated by a thin median septum. This arrangement is, however, subject to regional modification. In the first presacrals there are a number of vacuities in the inferior portion of the centrum which do not connect with the lateral fossæ. In I these consist of small cavities within the posterior rim of the centrum; in II the cavities are large and occupy the lower half of the centrum, being separated from the lateral fossæ by a wall two centimeters in thickness.

The *transverse processes* arise from four roots: (1) a horizontal plate which extends laterally from the prezygapophysis; (2) a second horizontal plate which arises from the anterior margin of the postzygapophyses and passing forward unites with the posterior margin of the first; (3) a vertical plate which arises from the base of the pedicle, passes upward and forward, and fusing with the inferior surface of the lateral plate, forms a bracket-like support below; (4) a similar but smaller vertical plate which arises from the lateral surface of the neural spine, passes outward and unites with the superior margin of the horizontal plate, supporting it from above. With the reduction and bifurcation of the spine, the superior root becomes reduced, shifted backward, and in VI joins the posterior root. In IX and X it is absent entirely. With the depression of the capitular facet, a second anterior root makes its appearance in V. This arises from the lateral surface of the capitular process and is noticeable as a slight ridge just below the anterior margin of the horizontal plate. In VI this remains very slight; in VII it is shifted downward forming a median brace between the anterior and the inferior roots; in VIII it appears as an anterior brace to the side of the inferior root; in IX and X it descends quite to the anterior margin of the centrum and forms a second inferior support equal in importance to the first.

The *tubercular facets* are borne low on the extremities of the transverse processes. They are irregularly concave and vary in size according to the strength of the ribs which they bear. In presacrals I to VIII they face outward and slightly downward; in IX and X their direction is altered so as to face more downward than outward.

The *neural spines* undergo a radical transformation in the dorsal region. (Plate XLVI.) The posterior members of the series represent the extreme development of the straight, median spine. From this point to the eleventh presacral, or first cervical, they pass by a regular gradation from the simple to the bifurcate. This change is so regular that no point in the series can properly be designated as "nodal" but at the same time all are transitional. In presacrals I, II, and III the spines are similar in length to the anterior sacral. In IV there is a noticeable shortening supplemented by a slight concavity on the anterior margin of the crest, which marks the first tendency toward bifurcation. In V and VI this concavity is deepened and the spine reduced in the latter to little more than half the length of that in III. At the same time it has increased in breadth and the lateral angles of the crest have become acute and somewhat produced. Each of the lateral plates give rise to two diagonal branches; the median plate is noticeably reduced. In VII the anterior aspect of the spine presents a broad, flattened surface. The median plate is reduced to a mere rugose ridge on the anterior surface; posteriorly it is somewhat more marked. The lateral angles of the crest are extended, forming a pair of lateral processes surmounted by laterally flattened crests. However, the vestigial median plate still furnishes the chief anchorage for the dorsal muscles. In VIII the median concavity descends to a level with the superior margin of the post-zygapophyses. The median plate is reduced to a mere roughening for muscular attachment which persists to the end of the series. Bifurcation may thus be regarded as complete. The spines in IX and X are slight and deeply excavated at their bases by lateral vacuities.

The *post-zygapophyses* are supported inferiorly by a pair of buttresses arising from the posterior surface of the neural arch, laterally by the posterior roots of the transverse processes, and superiorly by a second pair of buttresses descending from the lateral plates of the neural spine. In the posterior dorsal vertebræ the superior buttresses are strong, but with the bifurcation of the spine they become reduced, and are replaced by a second short, stout pair which meet in the median line. In presacral I the articulating surfaces are concave and face downward to articulate with the prezygapophyses of the first sacral; in the succeeding vertebræ they face outward and downward in the form of a wide V. At the point of convergence the articular surfaces are expanded into a prominent hyposphen. This is supported from below by a second pair of buttresses arising from the neural arch. In presacral VII both zygapophyses and hyposphen reach their strongest development. In IX the hyposphen disappears entirely; in X the zygapophyses are more elevated and widely separated.

The *prezygapophyses* are supported chiefly by a single stout pair of buttresses arising from the anterior margin of the pedicles. Their articulating surfaces are directed upward and slightly inward. In the anterior members of the series they are separated by a narrow notch, or hypantrim, into which the hyposphens of the preceding vertebræ fit. In VIII there is a pronounced widening of this notch corresponding with the disappearance of the hyposphen from IX. In IX and X the prezygapophyses are still more widely separated.

The *capitular facet* varies much, both in strength and in position, on the vertebra, as we pass forward in the dorsal series. (Plate LII.) In I the facet is very slight; it arises by three roots from the inferior surface of the prezygapophyses and from the lateral surface of the neural arch. It increases in strength in V and VI, and is slightly depressed by the shortening of the pedicles. In VII the decided shortening of the pedicles brings the inferior border of the facet almost to the margin of the centrum. The facet itself is more than double the size of that in VI. In VIII it is shifted downward so that half of its articular surface springs from the centrum. In IX the facet is borne entirely on the centrum just anterior to the lateral fossa and partially replacing it. In X the transposition is complete, the facet having passed entirely below the anterior end of the lateral fossa. In the last two vertebræ it is also much reduced in size.

MEASUREMENTS OF PRESACRAL VERTEBRÆ IN CENTIMETERS.

PRESACRAL VERTEBRA	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Height over all at median line	1.34	1.31	1.29	1.20	1.06	.88	.72	.58	.53	.49	**.40
Breadth across transverse processes	*.74	*.67	.73	.78	.86	.92	1.01	1.13	1.12	1.14	--
Centrum, length of	.25	.25	*.30	*.26	.28	.29	.29	.33	.36	.37	.44
Centrum, breadth at posterior end	.40	.41	.41	.40	.41	.40	.41	.41	.40	.40	.41
Centrum, vertical diameter at posterior end	.41	.39	.37	.34	.30	.29	.29	.28	.28	.27	.25
Centrum, depth of posterior concavity	.06	.07	.07	.07	.06	.07	.07	.09	.12	.14	.15
Spine, height above centrum in median line	.96	.94	.95	.90	.79	.60	.45	.28	.25	.21	--
Spine, greatest antero-posterior diameter of median plate	.19	.18	.18	.20	.20	.17	.09	--	--	--	--
Spine, length of lateral spines from concavity at median line	--	--	--	--	.13	.19	.29	.43	.46	.40	--
Spine, lateral breadth at crest	.17	.18	.19	.19	.24	.34	.46	.59	.62	--	--
Prezygapophyses, breadth across articulating surfaces	.35	*.33	.35	.35	.34	.35	.44	.54	.58	.57	.59
Prezygapophyses, distance between articulating surfaces	*.01	*.01	.03	.04	.04	*.02	.05	.14	.17	.23	.25
Postzygapophyses, breadth across articulating surfaces	.34	.35	.35	.35	.29	.29	.37	.43	.51	.56	.58
Capitular facet, height of inferior surface above centrum	.20	.24	.22	.18	.19	.19	.06	.09	--	--	--

*Modified by distortion. **Measurement estimated.

THORACIC RIBS.

Eighteen ribs, more or less complete, are preserved with this specimen. Ten of these belonging to the right side form a continuous series in which the first and last are so reduced in size as to indicate that the series is complete. Those of the left side correspond very closely with the right, except that the third and fourth have been carried away entirely. This number of ribs, preserved so nearly in their normal positions, may be regarded as conclusive proof that there were but ten vertebræ in the dorsal series.

In the *first pair* of ribs more than half of the distal ends were eroded away. The head and the tubercle are slender and divergent; the shafts taper toward the distal end and are too slender to have performed any important function. (Plate XLVII.) The second pair of ribs is considerably stronger than the first. Only the proximal half of the right and the head of the left are preserved. At this point the divergence of head and tubercle is most pronounced, the head forming an angle of sixty-five degrees with the shaft. The third and fourth pairs of ribs are the strongest of the series. The articular facets are broad and rugose, and stand at almost a right angle to the shaft. The proximal ends are expanded and massive, bearing trough-like fossæ on their mesial surfaces. The distal ends are missing from both.

The *fifth pair* of ribs is complete and well preserved. The head is more elongate, indicating greater expansion of the thorax at this point. The distal end bears a broad and roughened surface for the attachment of the costal cartilage. The right member of this pair is of interest in having an enlargement in the shaft, due to an imperfectly healed fracture. The adjoining sixth rib has a similar fracture which failed to heal. The sixth pair is marked by a decided reduction in size, a noticeable shortening, and a slender and tapering distal end. The head continues to elongate, the tubercle to shorten. In the seventh and eighth pairs the shafts become shorter and slighter, and the head more elongate. In the ninth the head and tubercle are quite reduced and the shaft is more curved at the proximal end. The tenth pair is reduced to mere rudiments, whose shafts are almost lost. The right one has coössified with the vertebra by the head and tubercle while the distal end has a flattened surface which abutted the crest of the ilium.

MEASUREMENTS OF RIBS.

RIB NUMBER	I	II	III	IV	V	VI	VII	VIII	IX	X
Length	---	---	---	---	2.13	2.07	1.85	1.70	1.26	.62
Breadth across head and tubercle	.430	.510	.500	.440	.405	.420	.360	.310	.250	.240
Breadth of shaft at middle	.080	.095	.130	.130	.125	.085	.090	.085	.080	.060

SACRAL VERTEBRÆ.

The sacrum in this specimen is composed of five vertebræ, coalesced by the centra, zygapophyses, and more or less by the sacral ribs. The second, third, and fourth vertebræ are in addition firmly conjoined by their neural spines, the crests of their neural arches, and the bases of their diapophyses. Their sacral ribs unite distally to form a yoke-like synostosis, which, in the Opisthocœlia, may fittingly be termed the sacricostal yoke. This is approximately symmetrical to the transverse axis of the sacrum and is borne upon the rim of the acetabulum, which constitutes its chief support. These three vertebræ have been described * by Osborn in "Camarasaurus" and by Williston in Morosaurus † as constituting the primitive sacrum. They will therefore be designated in this paper as the primary sacrum, but in the series of vertebræ functional as sacral, or ilium-supporting vertebræ they will be numbered two, three, and four. The first vertebra which functions as a sacral, but varies in the structure of its sacral rib, will be termed the dorso-sacral. In like manner the fifth of the series will be termed the caudo-sacral. (Plate XLVIII.)

The dorso-sacral bears evidence of having united with sacral II by its centrum and zygapophyses before adult age. The sacral ribs show a degree of coössification similar to that between the sacral ribs and the right ilium. The spine remains free, but stands close to the second spine—a condition which would tend to coalition. The caudo-sacral shows even more recent coössification with the primary sacrum. The centra are firmly coössified, the sacral ribs incompletely so; the zygapophyses are conjoined, but little atrophied, the neural spine remains free and isolated. A comparison in structure between this vertebra and the first caudal shows no greater difference than that between caudals I and II.

The centrum in sacral I is not reduced in size and differs from the dorsal centra only in its thicker walls. The anterior end is slightly convex; the lateral cavities open just behind the base of the sacral rib. (Plate XLVIII.) The centra of sacrals II, III, IV are considerably reduced in size and are more firmly united. The pleuro-central cavities open upward, just back of the pedicles. The centrum of sacral V is firmly united with the preceding one, but is not reduced in size and is little excavated by lateral cavities. The posterior surface is quite concave in its lower half, the margin slightly receding above.

The *neural arches* begin with the dorsal type in sacral I; in II, III, and IV they are drawn together antero-posteriorly and conjoined from the neural canal upward, leaving vertically elongate vacuities opening into the enlarged intervertebral chambers of the neural canal. In IV and V the neural arches are shifted forward so as to overhang the intercentral sutures. The prezygapophysial articulation between I and II is atrophied but still in evidence; that between II, III, and IV is lost entirely; between IV and V it has become ankylosed but otherwise little modified. The hyposphen-hypantrum articulation persists as far as sacral V. (Plate L.)

* Bulletin Am. Mus., Vol. x, p. 230.
† Kans. Univ. Quarterly, Vol. vii, p. 173.

The *neural spines* of the sacral vertebræ diminish regularly in length from first to last. The spine of sacral I is similar to that of presacral I, except that the forward curvature is nearer the base. The spines of II, III, and IV are firmly united by their median plates and show from their strength and system of bracing that this was the chief anchorage for dorsal and dorso-caudal muscles. The lateral plates in II are more strongly developed than in any other spine; their anterior buttresses which descend to the prezygapophyses are developed into stout braces to resist antero-lateral strain. The posterior roots have disappeared entirely. The lateral plates of III are almost lost; those of IV are well developed and braced in turn by the posterior root, while the anterior one has disappeared.

The *sacral ribs* take the form of stout, blunt processes firmly ankylosed with the centra and expanded distally to articulate with the ilium. Those of the three primary sacrals are similar in general structure, save that the middle one is reduced in size; they coalesce distally to form the sacricostal yoke. The first and second ribs arise from the mid-lateral surface of the centra; the third has its origin at the anterior end of the centrum. The ribs of the dorso-sacral vertebra arise from the antero-superior margin of the centrum in conjunction with the base of the neural arch. They articulate distally with the anterior surface of the great peduncle of the ilium. The ribs of the caudo-sacral vertebra are similar in origin to those of the true sacrals, but are expended distally into oblique plates, which are united with the diapophyses as in the anterior caudals. In this specimen the ribs are imperfectly united with the sacricostal yoke. They articulate distally with the posterior surface of the lesser peduncle and with the mesial surface of the iliac plate. (Plate XLVIII.)

The *diapophyses* show no essential modification from the thoracic type. They are more or less completely connected with the sacral ribs by a thin vertical plate. On the right side of the museum specimen, where the ilium is conjoined, this plate forms a continuous articular surface, connecting the ribs and diapophyses in sacrals I and II, while in III and IV there remain only slight vacuities. In V, as before mentioned, the diapophyses and ribs are united throughout. In II, III, and IV the merging of the three neural arches, and consequent reduction of space occupied by them in the antero-posterior direction, gives to the diapophyses the appearance of radiating from a common center. This feature is accentuated by the general tendency of sacra to be compressed in this direction while in the matrix, owing to the frailty of the arches as compared with the centra. This also accounts for the usual convexity of the inferior outline of the sacral series which should doubtless be concave.

MEASUREMENTS OF SACRUM.

	M.
Length of five coalesced centra	1.260
Height of sacral I over all	1.350
Height of sacral II over all	1.310
Height of sacral III over all	1.230
Height of sacral IV over all	1.190
Vertical diameter of centrum I at anterior end	.365
Lateral diameter of centrum I at anterior end	.380
Vertical diameter of centrum V at posterior end	.370
Lateral diameter of centrum V at posterior end	.360
Breadth of coalesced spines II, III, and IV at crest	.390
Breadth of coalesced spines II, III, and IV at base	.285
Length of spine above prezygapophysis in I	.780
Length of spine above prezygapophysis in V	.690
Length of sacricostal yoke	.650

MORPHOLOGY OF THE OPISTHOCŒLIAN SACRUM.

The composition of the sacrum in various genera of the Opisthocœlia has been regarded from almost as many points of view as there have been writers on the subject. Marsh looked upon the number of sacral vertebræ as a fixed quantity for each generic group and based many of his genera upon this character. In defining the order "Sauropoda" he characterized the sacrum as composed of not more than four vertebræ. In later classifications the number of sacrals was not given as an ordinal character. Cope placed less stress upon the number of sacral vertebræ, but used it in generic distinctions.

Osborn, in 1898, described the sacrum of "*Camarasaurus*" as follows: "*Camarasaurus* had five sacral vertebræ; three of these constantly coalesced both by centra and neural spines, two others coalesced less constantly and possessed free spines."* Soon after, Williston offered the following more general characterization: "It is very clear that there are three typical vertebræ in all the genera of this family (Camarasauridæ) as well as in the Morosauridæ, if it be a distinct

* Bull. Am. Mus., Vol. x, p. 230.

family, all of which present very distinct points of similarity. It is probable, as evidenced by the separated sacral vertebræ in *Morosaurus lentis* that the condition of ossification varies with age, the middle three uniting earliest, the first next, and the fifth last. The slight union of the fifth might, indeed, be absent in the adult without affording generic or even specific characters."*

A year later Dr. Osborn wrote of the sacrum of *Diplodocus:* "There are four rib-bearing true sacral vertebræ in *Diplodocus* instead of three, as hitherto described by Marsh. The three anterior sacrals, constituting the primitive Dinosaurian sacrum, are firmly united by their neural spines. These three spines coalesce into a single very robust spine showing the diapophysial laminæ separate."

In his recent monograph on *Diplodocus* Mr. Hatcher described two sacra as follows: "The two splendid sacra belonging with skeletons 84 and 94 in our collections are unusually complete. . . . . In each instance the vertebræ are firmly coössified with and give support to the ilia. In 84 the right ilium alone is preserved and this is united with all five of the vertebræ which function as sacral either by means of true sacral ribs or the expanded diapophysial laminæ or by both these elements. All are coössified by their centra and the three median have their spines coalesced. . . . . In skeleton 94, however, there are noticeable certain other more marked differences which are worthy of especial notice as bearing directly upon the nature of the primitive Dinosaurian sacrum. In this skeleton the sacrum is present, with both ilia in position. The centra of the true sacrals are all coössified as in other sacrum. The neural spines of sacrals one and two coalesce and are coössified throughout their entire length as in 84, but the spine of sacral three is quite free from, though closely applied inferiorly to, that of the second sacral. This would seem to indicate that the primitive Dinosaurian sacrum consisted of two rather than three vertebræ, a condition found in the Crocodilia and most other living Reptilia. The fourth sacral in No. 94 bears a free spine and is coössified by its centrum with the third and does not differ in any essential respect from that described by Osborn or from that found to obtain in No. 84 of our collections."

From the above it will be seen that Osborn and Williston agree upon the structure of the primitive sacrum as indicated by "*Camarasaurus*" (Apatosaurus), *Morosaurus*, and *Diplodocus*. This is based upon the tendency of the median three vertebræ to unite by spines and ribs. Hatcher has dissented from this opinion, postulating that the primitive Dinosaurian sacrum consisted of no more than two vertebræ.

* Kans. Univ. Quarterly, Vol. vii, p. 173.

This conclusion is based upon a single sacrum of *Diplodocus;* a second sacrum referred to the same species and described in the same paper agrees with the usual type in having the spines of sacrals II, III, and IV coalesced. The sacrum just described in this paper also agrees in the same particular.

It will be observed that there is a considerable variation in the coössification of various elements in the Opisthocœlian sacrum, which cannot be attributed to age. By comparing the composition of known sacra of *Apatosaurus*, *Diplodocus*, and *Morosaurus*, it will be seen that there is a noticeable similarity in the development of that of the former two, while the latter stands quite aloof. This is well represented by the accompanying diagrammatic figures.

The *Apatosauroid sacrum* is represented by four, possibly five, known specimens. The most primitive composition is found in the young specimen in the Yale University collection, well known as the type of *Apatosaurus*. In this sacrum only the three primary centra with their coalesced ribs are preserved (Fig. 5). A second specimen, described by Dr. Osborn as Camasaurus,* has, according to his description, the three primary centra coalesced by spines and sacral ribs as well as by the centra (Fig. 6). The dorso- and caudo-sacrals are both free; the latter, though structurally a caudal, was functional as an ilium-supporting vertebra. These characteristics as well as the size of the animal indicate that it was not quite adult. A third specimen in the Carnegie Museum figured † by Mr. Hatcher as "*Brontosaurus*," may or may not belong to this genus (Fig. 8). The figure shows that the primary sacrals have their spines coalesced as in the typical adult. The caudo-sacral is firmly conjoined by centrum, ribs, and diapophyses as is the centrum of the dorso-sacral. The first caudal is also conjoined, at least in part.

The unusually well preserved sacrum in the Museum specimen may be taken as a typical representative of the adult of this genus. In this, sacrals II, III, and IV are firmly conjoined by centra, neural arches, sacral ribs, and bases of the diapophyses (Fig. 7). The centra, sacral ribs, diapophyses, and lateral spinous plates are more or less reduced from loss of function. The zygapophyses and zygosphenes are no longer traceable. The dorso-sacral is firmly coalesced by centrum and zygapophyses; the ribs are partially conjoined, the spine is free, but stands close to that of sacral II. The caudo-sacral is a typical anterior caudal coössified by centrum and zygapophyses, and partially by the ribs. The spine is free and isolated. The right ilium

* *Loc. cit.*

† Memoirs of the Carnegie Museum, Pl. x, Fig. 3.

APATOSAUR SERIES.

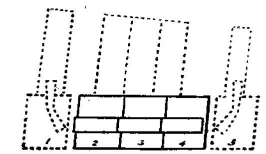

Fig. 5.

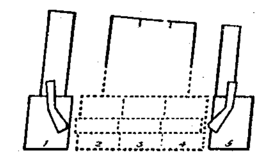

Fig. 6.

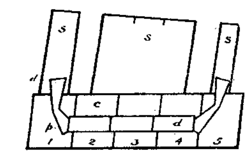

Fig. 7.

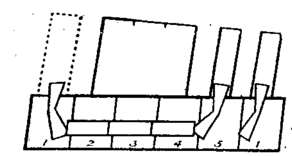

Fig. 8.

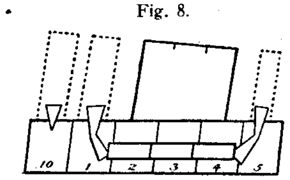

Fig. 9.

DIPLODOCUS SERIES.

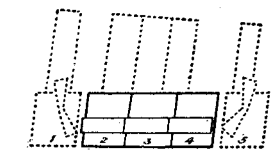

Fig. 10.

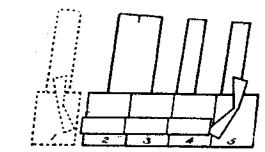

Fig. 11.

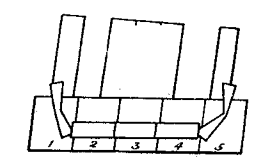

Fig. 12.

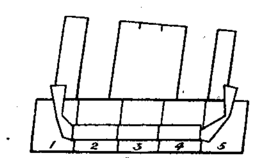

Fig. 13.

MOROSAUR SERIES.

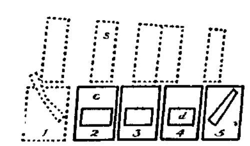

Fig. 14.

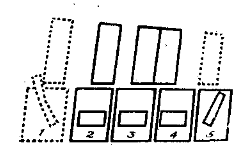

Fig. 15.

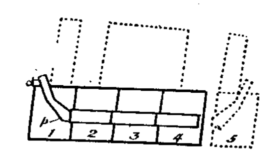

Fig. 16.

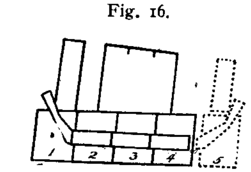

Fig. 17.

Diagrams illustrating the structure of the Opisthocœlian Sacrum.