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STRUCTURE AND RELATIONSHIPS OF OPISTHOCŒLIAN DINOSAURS.

PART II.

THE BRACHIOSAURIDÆ

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CHICAGO, U. S. A.
September 1, 1904

STRUCTURE AND RELATIONSHIPS OF OPISTHOCŒLIAN DINOSAURS.

PART II.

THE BRACHIOSAURIDÆ.

BY E. S. RIGGS.

The genus *Brachiosaurus* was recently described* by the writer from the humerus, femur, coracoid, and such parts of the sacrum and vertebral centra as could be seen before the specimen had been removed from the matrix. During the past winter the sacral and presacral vertebræ, which had been badly damaged by weathering, have been reconstructed with great care and patience by Messrs. J. B. Abbott and C. T. Kline. As these parts have one after another been worked out, the unusual character of this animal, which was first indicated by the extraordinary proportions of the humerus, has become more and more evident. So different is its structure from that of other members of the Opisthocœlia that the writer feels justified in placing it in a new family. The Brachiosauridæ is, therefore, proposed as a family group, to include this genus together with the smaller and more primitive form recently described by Hatcher under the name *Haplocanthosaurus.*

The family characters so far observed are: *Humerus as long as femur; neural spines of vertebræ simple; dorsal vertebræ more than ten.* Other characters equally distinctive will doubtless develop as these animals become better known. The following key will aid in determining members of this group:

Opisthocœlian dinosaurs with fore leg longer than hind; vertebral spines simple throughout; number of dorsal vertebræ more than ten: Family Brachiosauridæ.

(*a*) *Size medium; dorsal vertebræ fourteen; centra not elongate; neural arch unusually elevated, diapophyses directed obliquely upward and outward, hyposphene-hypantrum articulation moderately developed: Genus Haplocanthosaurus.*

(*b*) *Size large; neural arches not unusually elevated, spines increasing in length from sacrum to mid-dorsal region, hyposphene-hypantrum*

*Am. Jour. Sci., Ser. 4, vol. 15, p. 299.

articulation unusually developed, centra of dorsal vertebræ elongate: Genus Brachiosaurus.

The type specimen of *Brachiosaurus* as now prepared for exhibition, consists of the sacrum, seven presacral and two anterior caudal vertebræ, the right humerus, coracoid, ilium, and femur, and a number of ribs more or less complete. It was collected by the Museum paleontological expedition of 1900 from the Grand River valley of western Colorado. (Pate LXXI.) When found, the vertebral column was lying with spines downward and the vertebræ were but little displaced from their normal relations. The ventral surface of the sacrum, the ilium, and the anterior caudal vertebræ were exposed, and had suffered more or less from weathering.

At the seventh presacral vertebra the thin clay stratum in which the specimen was imbedded "pinched out," and was replaced by a massive layer of sandstone with coarse sand and pebbles at the base. This, together with the uniform displacement of the ribs, humerus, and coracoid to the left and the presence of an isolated ilium of *Diplodocus*, which had the appearance of having been drifted up against the broken vertebral series, indicated that the anterior portion of the skeleton had been carried away by the invasion of a water-current after the specimen had been partially covered with sediments.

The humerus and coracoid were displaced some ten feet to the left, and when found the distal end of the former was exposed at the surface, broken and displaced. When the fragments had been gathered up and fitted to the portion still in the matrix the bone measured almost seven feet in length. This length so much exceeded that of any humerus previously known, that the writer at the time believed it to be a crushed and distorted femur. Had it not been for the unusual size of the ribs found associated with it, the specimen would have been discarded as an Apatosaur, too poorly preserved to be of value.

The conclusion that the bone in question was a distorted femur was given additional weight by the discovery soon after of a well-preserved femur of almost identical length, associated with the ilium and sacrum. But later, when the two leg bones were removed from the matrix and carefully compared in the laboratory, the identity of the humerus was at once established by the structure of the head as well as by the clearly defined deltoid area from which the deltoid crest had been broken away and lost. From figures 3 and 4, Plate LXXIV, the characteristic structure of the opisthocœlian humerus will at once be recognized.

DORSAL VERTEBRÆ.

The seven dorsal vertebræ preserved in the specimen were found in a series, and but little displaced from their relative positions. The centra and transverse processes are considerably distorted by the compression to which they have been subjected. These distortions have been corrected in the specimen as far as was practicable, but no effort has been made to further correct them in the drawings. (Plate LXXII.) The vertebræ are distinguished by the lightly constructed and elongate centrum with its large lateral cavity, and by the single neural spines, short in the posterior members of the series, but becoming more and more elongate anteriorly. Equally distinctive is the unusual development of the hyposphene-hypantrum articulation. The whole structure suggests lightness and flexibility attained with an evident sacrifice of that strength which is everywhere apparent in the unwieldy *Apatosaurus*.

The number of vertebræ in the dorsal series cannot, of course, be determined from this specimen. Reasoning from certain similarities between this genus and *Haplocanthosaurus*, in which the number has been determined as fourteen,* we may expect a more numerous series than characterizes *Apatosaurus* and *Diplodocus*. As this number must for the present remain conjectural, however, the vertebræ will be referred to as presacral and numbered from the sacrum forward.

The first presacral vertebra may be distinguished, as in all opisthocœlians so far as the writer has observed, by the massive postzygapophyses which overhang the posterior end of the centrum, by the low stout spine and the short centrum† with small lateral cavities or pleurantra. From this point forward, both the centra and spines rapidly elongate, the diapophyses become more and more expanded, but, contrary to all that might be expected, the zygapophyses become reduced almost to insignificance.

The *centrum* in the dorsal vertebræ is opisthocœlous in type, but less pronouncedly so in the anterior members of the series than is common in the mid-dorsal region of most forms. In the first presacral the centrum is similar in length to that of *Apatosaurus*, but in the preceding vertebræ it rapidly increases in length. The pleurantrum is of moderate size; the anterior end of the centrum is truncate, with a slight convexity above the middle: the posterior end, now badly distorted, was doubtless uniformly concave. The second cen-

*Memoirs of the Carnegie Museum, vol. 2, No. 1.

†In the preliminary description of this genus the writer, estimating from the specimens still in the matrix, characterized the posterior dorsal centra as longer than wide. Closer examination shows that this is not true of the last dorsal.

trum takes on a more typical opisthocœlous outline. From this point forward the centra increase slightly in length, the pleuracœle enlarges, and the general structure displays even greater lightness. A cross-section shows an internal arrangement very similar to that of *Apatosaurus* (*Brontosaurus*) as figured by Marsh.

However, the lateral cavities are larger, and the peripheral walls thinner than have been observed by the writer in that genus. The median septum is so fragile as to be lost entirely in some of the vertebræ.

The *neural arch* is unusually slight in this genus. Its posterior surface is narrow and rounded; anteriorly it is produced into two laterally directed ridges which descend from the base of the prezygapophyses to the anterior rim of the centrum. Inclosed by these ridges and by the buttresses supporting the prezygapophyses is a deep fossa, into the lower margin of which the neural foramen opens.

The *transverse processes* in presacrals I to III and in V are broken and lost. In those vertebræ in which they are preserved, these processes have been too much distorted to admit of their direction being determined with certainty. In the posterior members of the series they were evidently much reduced. In IV a single transverse process is preserved which is little more conspicuous than the tubercular facet. In VI and VII these processes rapidly increase in length. They arise from four roots very much as do those of the posterior dorsals in *Apatosaurus*. They are broad at the base antero-posteriorly, rugose on the anterior margin, and recurved at the distal end.

The *capitular facets* for the rib attachment are borne high above the centrum throughout the present series. In presacrals I and II there is little evidence as to their position, but in III a well-developed facet is preserved. From this point forward the facets are borne by the lateral surface of the prezygapophyses as well as the anterior margin of the transverse process, and are supported by a buttress descending to the anterior margin of the neural arch. The zygapophyses, together with the hyposphene-hypantrum articulation constitute one of the distinguishing features of the vertebræ of this genus. Throughout the dorsal series, so far as known, the zygapophyses are narrow and placed close to the median line. There is no evidence of dichotomy in the anterior dorsal region as observed in *Apatosaurus*, *Camarasaurus*, *Morosaurus*, and *Diplodocus*. The weakness in the zygapophyses is compensated by the strength of the hyposphene-hypantrum articulation. The articular surfaces of the former are directed horizontally. The mesial surface of the prezygapophysis curves rapidly downward and is continuous with the vertical articular surface of the hyposphene. Similarly the articular surface of the postzygapophysis is continuous with that of the hypantrum. The two form a firmly interlocking joint capable of resisting lateral strain. The hypantrum is also slightly expanded inferiorly so as to prevent a downward displacement of the prezygapophyses.

The *prezygapophyses* are supported by a single pair of buttresses, which also form the anterior margin of the neural arch, and by the anterior plate of the transverse process. The postzygapophyses are supported from above by a pair of stout buttresses which descend from the postero-lateral margin of the spine; laterally they are supported by the posterior root of the transverse process and inferiorly by a pair of buttresses arising from the posterior margin of the neural arch and attaching to the anterior surface of the hypantrum. In the sixth and seventh presacrals this support is strengthened by passing to the inferior surface of the hypantrum.

The *neural spines* in this genus are single and median so far as known, and there is no reason to doubt that they continue so throughout the dorsal series. Unlike those of any other known members of the Opisthocœlia, the spines are short in the first presacrals, and become more and more elongate as far as the middle thoracic region. They are made up of the usual median plate expanded at the crest into a rugose knob and roughened on the anterior and posterior margins for the attachment of interspinous ligaments. They are flanked at the anterior and posterior margins respectively by a pair of greater and lesser lateral plates. The posterior plates arise from the superior root of the prezygapophyses, pass upward along the lateral border of the median plate near the posterior margin, and form a stout lateral support to the crest. The anterior lateral plates arise similarly from the base of the prezygapophyses and strengthen the anterior border of the median plate. In presacral I the spine is low, massive, and strongly reinforced by buttresses arising from the postzygapophyses. In II it is noticeably higher and less firmly braced. In IV and V the base of the spine becomes broadened anterio-posteriorly by the diverging roots of the lateral plates. A lateral vacuity appears between the posterior and inferior roots of the transverse process and the base of the postero-lateral spinous plate. In VI and VII the spine becomes more elongate and somewhat more slender.

MEASUREMENTS OF PRESACRAL VERTEBRÆ IN METERS.

PRESACRAL VERTEBRA.	I.	II.	III.	IV.	V.	VI.	VII.
Height over all	.76	.80	.84	.86	.88	.90	.91
Breadth across transverse processes				.60**		.78	.90
Centrum, length of	.27	.35	.38	.39	.42	.44	.43
Centrum, breadth of posterior end	.30*	.31	.31	.30	.31	.30	.30
Centrum, vertical diameter at posterior end	.26	.28	.29	.28	.26	.27	.27
Centrum, depth of posterior concavity	.05	.07	.08	.09	.08	.08	.08
Centrum, length of pleurantrum	.10	.16	.18	.18	.19	.19	.22
Centrum, breadth of pleurantrum	.07	.07	.07	.06*	.08	.10	.09
Spine, height above prezygapophyses	.26	.29	.31	.33	.37	.41	.43
Spine, lateral diameter at crest	.11*	.18	.20	.28	.22*	.19*	.21
Prezygapophyses, breadth across articular surfaces	.19	.21	.18	.18	.16	.16	.17
Prezygapophyses, distance between articular surfaces	.05	.04	.04	.04	.04	.04	.04
Hyposphene, depth of articular surface	.06	.06	.08	.07	.08	.08	.07

*Modified by distortion.
** Estimated.

SACRUM.

The sacrum of *Brachiosaurus* is at once distinguished from that of the other large opisthocœlian dinosaurs by its unusual breadth across the sacral ribs as compared with its length and the height of its component vertebræ. (Plate LXXIII.) The specimen under consideration has been damaged somewhat by compression, but more seriously by later exposure to weathering at the surface. As a result, the neural arches of sacrals II–IV inclusive were too badly damaged to be restored; and with them the centra above the lateral cavities. With these exceptions their structure can be determined with certainty.

The sacrum is made up of five ilium-supporting vertebræ instead of four, as originally described,* all of which are firmly coössified by their centra and the distal ends of their sacral ribs. Sacrals I to IV are coalesced by their zygapophyses and the base of their diapophyses, and sacrals II and III by their spines. As in the typical opisthocœlian sacrum† the ribs of sacrals II, III, and IV enter into

*Am. Jour. Sci., 4th Ser., vol. 15, p. 303.
†This publication, GEO. SER., vol. ii, No. 4, p. 180.

the composition of the sacricostal yoke and may be regarded as comprising the primary sacrum. The dorso-sacral is highly specialized, but its support of the acetabulum is a secondary function. The caudo-sacral is functional as an ilium-supporting vertebra, though its caudal affinities are still clearly marked.

The *centrum* of sacral I is somewhat shorter than that of the last dorsal, and is irregularly convex on the anterior end. The pleurantral foramina are almost closed by the expanded sacral ribs. The centrum of sacral II is similar in length to that of I, but is laterally expanded to meet the unusual development of its sacral rib. There is no evidence of a pleurantrum. The centra of III and IV are less expanded laterally, and bear traces of the pleurantral foramen. That of V bears no trace of the lateral cavities. Its posterior end may have been convex above and concave below, as is the typical structure, although this feature cannot be determined with certainty.

The *sacral rib* in I is developed into a broad, winglike appendage, whose primary elements can scarcely be traced. It arises from the upper half of the centrum anterior to the much-reduced pleurantrum and from the lateral surface of the neural arch. The capitular portion passes backward, joins the rib of sacral II, and articulates with the mesial surface of the greater peduncle. The tubercular element is fused with the distal end of the diapophyses so that it is impossible to determine where the one ends and the other begins. It is probable, however, that the tubercular portion of the rib is represented by the rugose end only. It attaches to the crest of the ilium above and in front of the base of the greater peduncle.

The second pair of sacral ribs are by far the strongest of the series. The proximal ends are greatly expanded and attach to the whole lateral surface of centrum II as well as to the posterior half of centrum I. The shaft is constricted at the middle, and the distal end is expanded to enter into the composition of the sacricostal yoke. The third pair of ribs are much reduced in size. They arise from the anterior half of centrum III in common with the posterior margin of the second pair. The shaft is slight, but the distal end is expanded to form the middle section of the yoke. The fourth pair arise from the anterior two-thirds of the centrum. From the superior margins of ribs II, III, and IV broad plates arise to connect with the corresponding diapophyses. The fifth pair of sacral ribs arise from the mid-lateral surface of the centrum, and passing diagonally forward, unite with the distal ends of the fourth pair in supporting the lesser peduncle of the ilium. These bear traces of the primary caudal structure although they are modified as ilium-supporting elements.

The *diapophyses*, like the sacral ribs, are remarkable for their unusual length and slenderness. The first pair arise from the lateral surface of the spine and the stout prezygapophyses. Their distal ends unite with the sacral ribs in forming the great lateral plates. The second and third pairs arise in common from the fused spines of sacrals II and III. Distally they diverge to unite with the iliac crest. The fourth pair arise independently; they are directed diagonally backward and attach to the border of the ilium above the lesser peduncle. Midway between the base of the diapophyses and the attachment with the ilium there is a marked rugosity which suggests that the diapophysis may terminate at that point and the distal portion be made up of the tubercular portion of the rib. This could be determined only from the study of a very young specimen.

The *sacral spines* are remarkably short and blunt. In structure they are made up of a thickened median plate expanded at the crest to form a blunt knob, and flanked in the anterior three by a slight pair of lateral spinous plates. The first is free, but stands close to the second. In structure it resembles the posterior dorsal, though its lateral plates have almost disappeared. The second and third spines are so firmly united as to show no trace of the line of fusion. Their lateral plates arise from the middle of their respective surfaces. The fourth and fifth take on the caudal type of structure, which consists of a median plate expanded into a simple knob at the crest. The fourth stands quite close to the third; the fifth is isolated. All have marked rugosities on the anterior and posterior margins for the interspinous ligaments.

MEASUREMENTS OF SACRUM.

	M.
Length of five sacral centra	.95
Breadth across second pair of sacral ribs	1.05
Breadth across fifth pair of sacral ribs	.98
Height of first sacral vertebra	.64*
Height of third sacral vertebra	.60*
Height of fifth sacral vertebra	.53*
Length of centrum I	.19
Length of centrum II	.18
Length of centrum III	.15
Length of centrum IV	.22
Length of centrum V	.21

* Dimension modified by distortion.

CAUDAL VERTEBRÆ.

Two anterior caudal vertebræ were found in close apposition with the posterior end of the sacrum. The first has been so distorted in a diagonal direction that the structure of its centrum and zygapophyses can scarcely be determined. The second (Figs. 1 and 2, Plate LXXV) has suffered less from distortion, and is otherwise fairly well preserved. The centra are in general amphicœlous. The anterior end of the first is concave in its lower half, but is so badly distorted that it does not show whether or not it had the characteristic convexity usually found in the upper half of the first centrum. The posterior end is slightly concave, a feature which the crushing has tended to lessen. In the second caudal the anterior end is uniformly concave, the posterior end slightly more so. There is no trace of the lateral cavities found in almost all the opisthocœlians. It cannot be determined whether or not these vertebræ were chevron-bearing.

The *neural arches* are massive, broad on the anterior surface, but drawn to a rounded angle about the posterior opening of the neural foramen. Laterally there are traces of a slight ridge leading downward from the prezygapophyses to the base of the transverse process.

The *zygapophyses* are slight for a vertebra of such dimensions; the anterior pair has been pushed upward by compressure. The articular facets normally face inward and slightly upward. The posterior pair in the second caudal bears distinct evidence of a hyposphene.

The *neural spines* are characteristically simple. They are laterally compressed at the base and expanded at the crest into a roughened knob. The anterior and posterior margins bear the strong rugosities for interspinous ligamental attachments which persist throughout the vertebral series.

The *caudal ribs* are equally simple. The capitular element is represented by a stout process arising from the lateral surface of the centrum above the middle. It is vertically compressed and apparently expanded into a rounded end. No trace of the tubercular element is to be seen.

MEASUREMENTS OF CAUDAL VERTEBRÆ.

	Caudal I.	Caudal II.
Height over all	.61*	.59
Centrum, length of	.16	.15
Depth of anterior end	.28*	.29
Breadth of anterior end	.33	.31
Breadth across transverse processes	.56*	.48
Spine, height above zygapophyses	.18	.17
Antero-posterior diameter	.10	.10
Lateral diameter at crest	.11	.09

*Dimension modified by distortion.

The *ilia* are represented by the right bone, which has lost its greater peduncle, but is otherwise quite well preserved, and a badly weathered left, which, fortunately, has the greater peduncle preserved. The right bone has been modified by a distortion which has depressed the whole posterior half, straightened the superior border, distorted the acetabulum, and reduced the depth in the supra-acetabular region. It is figured from a lateral view without correction, other than the restoration of the greater peduncle from a comparison with that of the left. (Fig. 3, Plate LXXV.)

The important feature of the ilium is the unusual development of the pre-acetabular portion. The greater peduncle is near the middle; the anterior half is expanded into a broad but rather thin plate, most of which stands anterior to the attachment of the first sacral rib. At the point of greatest eminence the crest is thickened for the attachment of the first diapophysis. The anterior border is much more rounded than it is in any of the other large dinosaurs. At the anterio-inferior angle the border is quite thick and roughened for muscular attachment. This roughening continues one-third of the way from the angle to the point of attachment for the first sacral diapophysis, where it disappears and the border becomes thin and rounded. The crest continues very thin to a point over the middle of the acetabulum, where it again becomes stronger and rugose. This continues to the posterior angle, which is much thickened, and offers the usual broad surface for the origin of lateral caudal muscles.

The acetabulum is distorted by the depression of its arch. It presents to the head of the femur a broad and rounded surface, which terminates at either end in the peduncles. Its superior surface takes the form of an arch which juts far beyond the iliac wall on the mesial side, and presents a concave surface for the support of the sacricostal yoke. The attachment for the first diapophysis is a triangular fossa bounded by two ridges which descend from the crest and converge at a point seven or eight inches below. From this point a rounded ridge passes obliquely downward and backward to the base of the greater peduncle. The points of attachment of the second and third diapophyses are very slight; no trace of a fourth appears. The fifth has a strong attachment at the thickened crest above the lesser peduncle. The plates connecting the diapophyses with the sacral ribs do not attach to the iliac wall as in *Apatosaurus*.

THORACIC RIBS.

The unusual length of the ribs, as well as the breadth of the head and tubercle and the strength of the shaft, bears evidence of the immense thorax of this animal. One of the more slender ribs from the mid-thoracic region measures fully nine feet (2.745 m.) in length. Another has a shaft eight inches (.204 m.) in breadth. The head and tubercle are almost equally developed and widely separated to give the firm attachments rendered necessary by the great length of the ribs. (Fig. 5, Plate LXXV.) In some instances the attachment is strengthened by a second tubercle on the inferior surface of the head similar to that figured by Marsh on the cervical vertebræ of *Apatosaurus*. The anterior surface of the shaft below the head is perforated by a large foramen which leads to an internal cavity. On account of the elevation of the capitular facet on the vertebræ, the head and tubercle are borne almost on a level. By reason of this the flattened surface of the proximal end passes insensibly into the lateral surface of the shaft without that twist common to the ribs in animals of this group.

LEG BONES.

The *humerus* is somewhat crushed antero-posteriorly and twisted so that the head and distal end are brought into the same plane. The surface of the distal end has flaked away in the process of weathering to a firm chalcedony core. (Fig. 1.) In relative slenderness the humerus is approached more nearly by that of *Diplodocus* than that of any other well-known American dinosaur. The head is considerably expanded, forming a rounded prominence especially conspicuous on the posterior surface. The great tuberosity is stout and rugose; its proximal surface meets the lateral margin of the shaft in a pronounced angle. This angle is not produced posteriorly to inclose a fossa as in *Morosaurus*. The inner border below the head is drawn out into a rather thin margin, though roughened for muscular attachment. The deltoid crest is partially broken away, but was evidently quite prominent. (Fig. 4, Plate LXXIV.) Its base forms with the anterior surface of the shaft a broad and shallow concavity. Mid-

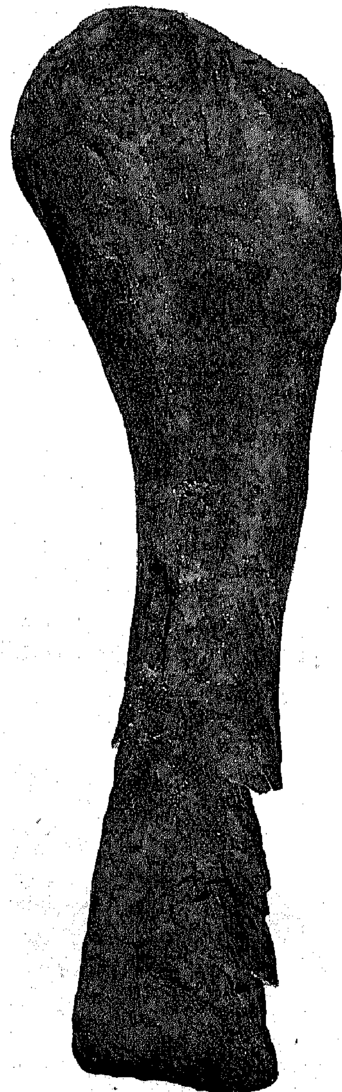


Fig. 1. Posterior view of right humerus of *Brachiosaurus altithorax*, 1/10 natural size.

way between the deltoid crest and the great tuberosity is a second rugose surface evidently for the insertion of other shoulder muscles. The ectepicondylar ridge is entirely lost, owing to the weathering to which the distal end has been subjected. The direction of the bone fibres on the lateral margin indicates that it may have been quite prominent. All traces of rugosity have likewise disappeared from the distal end, indicating that the humerus was probably some inches longer than it now stands.

The *coracoid* is a larger, but less massive, bone than that of *Apatosaurus*. (Fig. 4, Plate LXXV.) It is elongate antero-posteriorly, rounded on its inferior margin, and straight at the scapular articulation. The glenoid articular surface is directed outward as well as backward, a feature observed in no other opisthocœlian genus. The postero-inferior surface is thick and rugose for epicoracoidal attachment near the glenoid cavity, from which it is separated by a narrow notch only. The posterior border becomes gradually thinner, and its rugose character disappears midway between the glenoid cavity and the anterior scapular angle. The emargination noticeable in the specimen at this point is due to crushing from contact with the head of the humerus while in the matrix.

The *femur* is well preserved, though somewhat compressed antero-posteriorly. (Figs. 1 and 2, Plate LXXIV.) Regardless of its great length, this bone is almost as stout in the shaft as that of *Apatosaurus*, though the articular ends are proportionally less expanded. The lateral surface of the shaft has a prominent convexity one-fourth of its entire length below the great trochanter. A marked rugosity, probably for the insertion of one of the gluteal muscles, extends downward from the great trochanter to this point. As in all opisthocœlians the fourth trochanter forms a rugose prominence on the posterior internal margin of the shaft above the middle.

MEASUREMENTS OF THE LEG BONES.	M.
Humerus, length of parallel to axis	2.04
Greatest breadth of proximal end	.65
Thickness of head antero-posteriorly	.28
Least breadth of middle shaft	.24
Distance from angle of great tuberosity to upper margin of deltoid crest	.51
Femur, length parallel to axis	2.03
Breadth of head and great trochanter	.59
Breadth of shaft at fourth trochanter	.43
Breadth at distal end	.58
Distance from head to upper margin of fourth trochanter	.78
Coracoid, greatest breadth	.87
Inferior border to scalpular margin	.54
Glenoid margin to foramen	.34
Ilium, greatest length	1.24
Breadth of preacetabular plate	.53
Base of great peduncle to anterior angle	.40
Length of great peduncle	
Depth over acetabulum (estimated)	.45
Lateral breadth of acetabular wall	.16
Thickness of plate at antero-inferior angle	.08
Thickness of crest above great peduncle	.025
Thickness of posterior angle	.12

RELATIONSHIPS.

In proposing the genus *Brachiosaurus* from the characters presented by the leg bones and sacral centra of this specimen, the writer had some doubt as to the possible relations with the imperfectly described genus *Camarasaurus*. However, a recent examination, through the courtesy of Dr. Osborn, of the type specimen as it is being prepared for exhibition in the American Museum, at once set at rest all such doubts. The massive structure of the vertebræ and the distinctly Morosaur-like spines of that genus have nothing in common with the slenderly constructed and elongate centrum and the single median spines of *Brachiosaurus*. Relationship with the tall and slender posterior dorsal vertebra which constitutes the type of *Amphicœlias* is equally impossible.

Of all the American opisthocœlia the only known form which may be regarded as closely related to this genus is *Haplocantho-*

saurus, recently described* by Hatcher. These two genera display certain structural affinities common to no other North American group. The most important of these are: (1) the single median spines which persist throughout the vertebral column in the above-named genus and which appear to have been equally persistent in *Brachiosaurus;* (2) the unusual breadth of the sacrum in comparison with its length and the height of its component vertebræ; (3) the simple structure of the anterior caudal vertebræ; (4) the great expansion of the preacetabular portion of the ilium. In addition to these, are to be considered the presence of fourteen dorsal vertebræ as described by Hatcher in *Haplocanthosaurus*, and the unusual length of the humerus in *Brachiosaurus*. Recent developments with regard to the number of vertebræ in *Diplodocus*† and in *Apatosaurus*‡ might throw some doubt upon this point were it not that the genera under consideration evidently belong to a distinct phylogenetic line, and that Hatcher has made a strong case in favor of fourteen dorsal vertebræ in his genus. The vertebral formula in *Brachiosaurus* cannot, of course, be determined from the interrupted series preserved in the type specimen. It is most probable that the number will prove to be the same as in *Haplocanthosaurus*, although the elongation of the dorsal centra might suggest that a reduction had taken place in this form.

Of the two genera, it will be observed that *Haplocanthosaurus* is much the smaller and comparatively primitive, while *Brachiosaurus* is a long-limbed and highly specialized type. Points of generic difference are abundant. The first and most evident of these is one of size, which is well indicated by the comparative length of femora. That of *Haplocanthosaurus* measures about fifty inches, while in *Brachiosaurus* the same bone measures fully eighty. More important differences are to be found in the relative height of the neural arches, the development of the hyposphene-hypantrum articulation, and the length of the centra in the dorsal vertebræ.

In the smaller genus the vertebral pedicles are peculiarly attenuate, giving to the neural arch the extraordinary elevation pointed out by Hatcher, and to the neural canal the unusually great vertical diameter. In the larger and more highly specialized *Brachiosaurus* there is no evidence whatever of this characteristic. The pedicles are broad antero-posteriorly, narrow and rounded on the posterior margin instead of being produced into an angle, as in the smaller form, and the neural canal is but little deeper than wide.

*Memoirs of the Carnegie Museum, vol. ii, No. 1.
†Memoirs of the Carnegie Museum, vol. i, No. 1, p. 29.
‡This publication, GEOL. SER., vol. ii, No. 4, p. 196.

It will be observed that in *Haplocanthosaurus* the zygapophyses are about as strong as those of *Morosaurus*, and extend a like distance from the median line. Their articular surfaces are plane and directed slightly upward as well as laterally. The hyposphene has a moderate development. In *Brachiosaurus*, on the other hand, there is a marked crowding together of the zygapophyses at the median line, especially in the mid-dorsal region, and an unusual development of the hyposphene-hypantrum articulation. The articular surfaces of the zygapophyses are directed laterally and are slightly curved, so that the postzygapophyses embrace the anterior pair. The centra of the dorsal vertebræ in the larger genus are, with the exception of the last, much more elongate and more thinly walled than in the smaller form. The sacral ribs also show a much higher degree of specialization. In *Haplocanthosaurus* they arise uniformly from the anterior end of the centra and show but little variation in strength throughout the series. In the larger animal, however, the second pair are greatly expanded, as has been described above, while the third pair are correspondingly reduced in size. There is also a much greater relative expansion of the thoracic cavity, as is shown by the comparative length of the anterior ribs.

The neural spines of *Brachiosaurus*, so far as preserved, present the same type of structure as do those of *Haplocanthosaurus*, but while those of the latter genus reach their greatest length at the third presacral and begin to diminish with the sixth, those of the former increase regularly to the seventh. There is also a more pronounced shortening of the neural spines and transverse processes of the anterior caudals in *Brachiosaurus*, indicating a reduction of the caudal series, consistent with the cephalad specialization of this form.

In most of the above noted differences, *Haplocanthosaurus* presents a more primitive structure, from which *Brachiosaurus* might well be derived. However, the elevation of the neural arches and the upward direction of the diapophyses in the smaller form present a degree of specialization which precludes this possibility. A very similar condition exists in *Stegosaurus*, probably as an adaptation to the support of its dermal armor. While it is hardly possible that such an armor could have existed in this form without having been preserved in one or the other of the two specimens described by Hatcher, the elongation may have resulted from a like muscular development, or it may be due to acquired aquatic habits, as such a tendency is found in certain cetaceans. To assume that the dorsal pedicles had attained such an elevation and were again reduced to the low, broad structure found in *Brachiosaurus*, would be inconsistent with all laws of organic development. We must, therefore, conclude that the two forms have arisen from a common ancestry, probably somewhere in the lowermost Jurassic, and that while the *Haplocanthosaurus* phylum remained in general conservative, it reached a high degree of specialization in this one particular. *Brachiosaurus*, on the other hand, is a somewhat later representative of the more highly specialized line which had taken to purely terrestrial habits.

These conclusions are in accord with the evidence to be derived from the relative age of the horizons in which these fossils are found. While there is little reliable stratigraphic data for comparison between the eastern and western Colorado localities, the evidence which has been adduced would indicate that *Brachiosaurus* comes from a horizon at least one hundred feet above the Cañon City quarry. However, various species of *Apatosaurus* and *Morosaurus* are found in the same horizons with both forms, so that the difference in time alone is not sufficient to account for the differences between these two related forms. We must, therefore, attribute these differences chiefly to digressive development.

PROBABLE HABITS.

The habits of the Opisthocœlia have been regarded as semi-aquatic or at least marsh-dwelling. This conception was based largely upon the structure of the teeth, which are fitted for masticating soft, succulent vegetation, and upon the ponderous bulk of the animals which seemed best suited for aquatic locomotion. It is true that the massive structure of the vertebræ in such forms as *Apatosaurus ajax* bears some resemblances to the vertebræ in cetaceans. However, the writer has failed to discover in the skeletal structure of aquatic or semi-aquatic animals, either reptilian or mammalian, any of that fluting and hollowing of the vertebræ which have been interpreted as evidence of aquatic habits in the Opisthocœlia. This same effort at lightening the skeleton was regarded by an earlier English writer as evidence of aërial habits!

That which appears to the present writer to afford most reliable evidence as to habits is the structure of foot and limb. As pointed out by Hatcher, there is no evidence among opisthocœlians of that shortening or angulation of limb, or the broadening of foot, which is common to amphibious animals. Nor is there anything in the structure of the opisthocœlians which is not found in some terrestrial forms. The straight hind leg occurs in quadrupeds only among those forms which inhabit the uplands. Familiar instances of parallel development of this character are found in the proboscidea, dinocerata, etc. The short, stout metapodials and blunted phalanges characteristic of the Opisthocœlia would be as ill adapted for propulsion in water or upon marsh lands as are those of the elephant. The reduction in the number of claws offers further evidence along this line, and finds a parallel in the great ground sloths. In short, if the foot structure of these animals indicates anything, it indicates specialization for terrestrial locomotion.

In the genus *Brachiosaurus* there are very different proportions of fore and hind leg, of pelvis and thorax and tail, from those of the usual type of opisthocœlian dinosaurs. To harmonize with them we may expect that decided differences existed in the head and neck. The foot structure in *Apatosaurus* and *Diplodocus* may, as before stated, be regarded as highly specialized, but the length and slenderness of limb, the deep thorax, the broad sacrum, the expanded ilium, and the abbreviated tail of *Brachiōsaurus* all point to a greater agility and a much better adaptation to terrestrial habits than is found in any other representative of the Opisthocœlia.

The varying structure of the dorsal vertebræ in the larger dinosaurs offers some interesting problems as to the habits of the animals. In some genera a relation between the length of the dorsal spines and the breadth of the zygapophyses is noticeable. We may well assume, with other writers, that the heavier forms, such as *Apatosaurus* and *Diplodocus*, which are provided with long spines in the sacral and posterior dorsal region, were adapted to rearing up on the hind legs as is represented in the conventional mounted skeleton of *Megatherium*. In these forms we find that the body is short and therefore well adapted to this habit. *Morasaurus* and *Camarasaurus* are less perfectly adapted to such a habit by reason of their shorter spines, but might well have been capable of assuming the upright position. The slender shaft of the ischium in the former genus could have hardly afforded sufficient support in the sitting posture. In all of these, however, it will be observed that the zygapophyses are strong and placed far apart, especially in the anterior dorsal region of *Apatosaurus*. Their separation is doubtless directly due to the bifurcate spines, but that arrangement was a concomitant of the development of a median set of dorsal muscles whose function it was to elevate the anterior portion of the body. The unusually strong zygapophyses served to support and control the ponderous shoulders and neck when the upright position was assumed. All of this bespeaks great mobility of the anterior portion of the body.

In *Haplocanthosaurus* we have noticed that the spines are short posteriorly, but reach their greatest length at the middle of the dorsal series. Together with this arrangement we find a more generalized structure of the zygapophyses and hyposphene, such as was noticed in *Morosaurus*. The former are moderately broad, but are nowhere placed far apart; the latter has a slightly greater development than in the above-mentioned genus. In *Brachiosaurus*, the zygapophyses reach the extreme reduction and the hyposphene-hypantrum articulation reaches the extreme development. The zygapophyses are crowded together near the median line in a way which would render impossible any considerable lateral movement of the body. The hyposphene articulation is well constructed to prevent lateral displacement. The strong thoracic ribs with widely divergent head and tubercle firmly anchored in the same horizontal plane doubtless added greatly to the strength of the vertebral column in this region. In this we recognize the rigid quadrupedal structure of the vertebral column.

From the above considerations it will be seen that *Brachiosaurus* is the culminating type of a phylum, distinct from anything hitherto known in America. Its length of limb and bodily proportions show that it was fitted for purely quadrupedal movements. Though the structure of the feet and lower legs is unknown, there is every reason for believing that the animal was specialized in terrestrial habits. This fact would restrict its range to grounds where conditions were less favorable for its preservation and so account for its remaining so long undiscovered.

SUMMARY.

The following conclusions are reached in this paper:

1. The genus *Brachiosaurus*, together with the smaller related form, *Haplocanthosaurus*, should be placed in a new family of the opisthocœlia for which the name *Brachiosauridæ* is here proposed.

2. The distinguishing characters of this family, so far as known, are: Humerus as long as femur; neural spines of the vertebræ simple; dorsal vertebræ numbering more than ten.

3. *Brachiosaurus* is a highly specialized form, related to, but not directly descending from, *Haplocanthosaurus*.

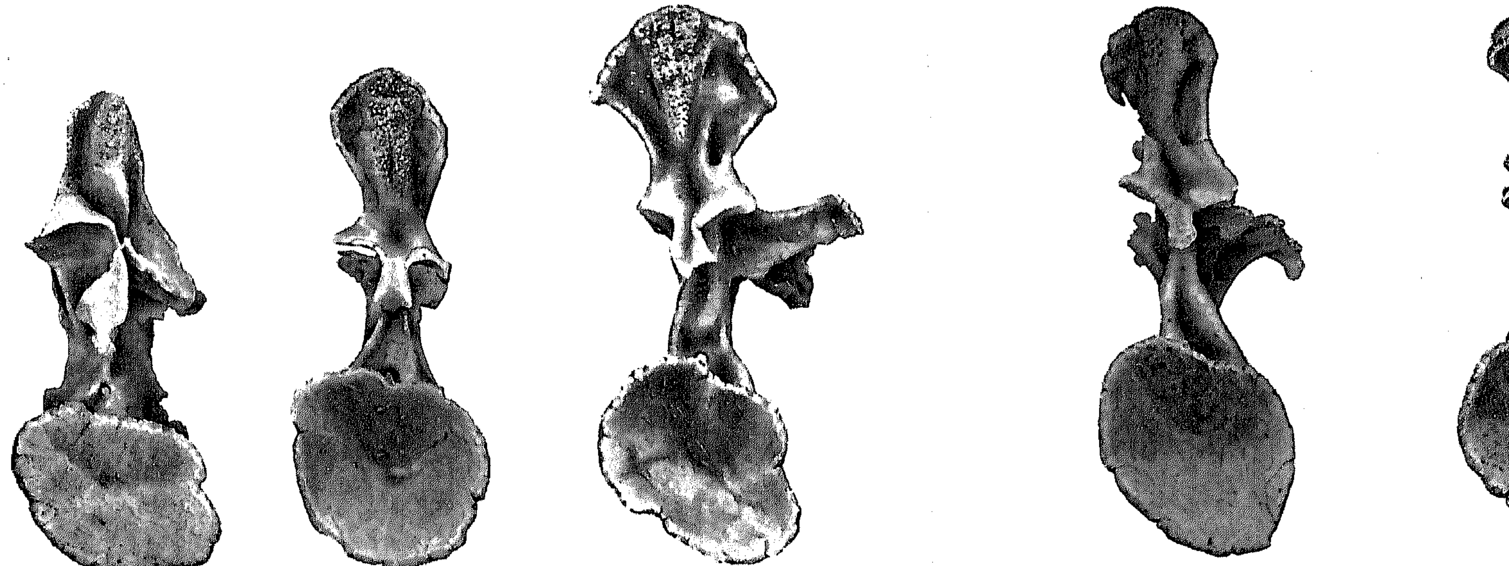
4. The known characters which distinguish *Brachiosaurus* are: Its large size, immense thorax, highly specialized hyposphene-hypantrum articulation of the vertebræ, low, broad structure of the vertebral pedicles, and the unusual breadth of the sacrum.

5. While *Morosaurus*, *Apatosaurus*, and *Diplodocus* are, by reason of their elevated sacral spines and strong dorsal vertebræ, fitted for assuming the upright position, the short sacral spines and heavy fore

legs of *Brachiosaurus* indicate that its habits of locomotion were entirely quadrupedal.

6. The foot structure in most opisthocœlians furnishes unmistakable evidence of terrestrial habits. The length of fore limb and bodily proportions of *Brachiosaurus* show that this form was more highly specialized for terrestrial habits than any other known member of this order.

Dinosaur Quarry No. 13 near Grand Junction, Colorado. The dorsal vertebræ, sacrum, ilium, and ribs of the type specimen of *Brachiosaurus* ar[illegible]tion as found.



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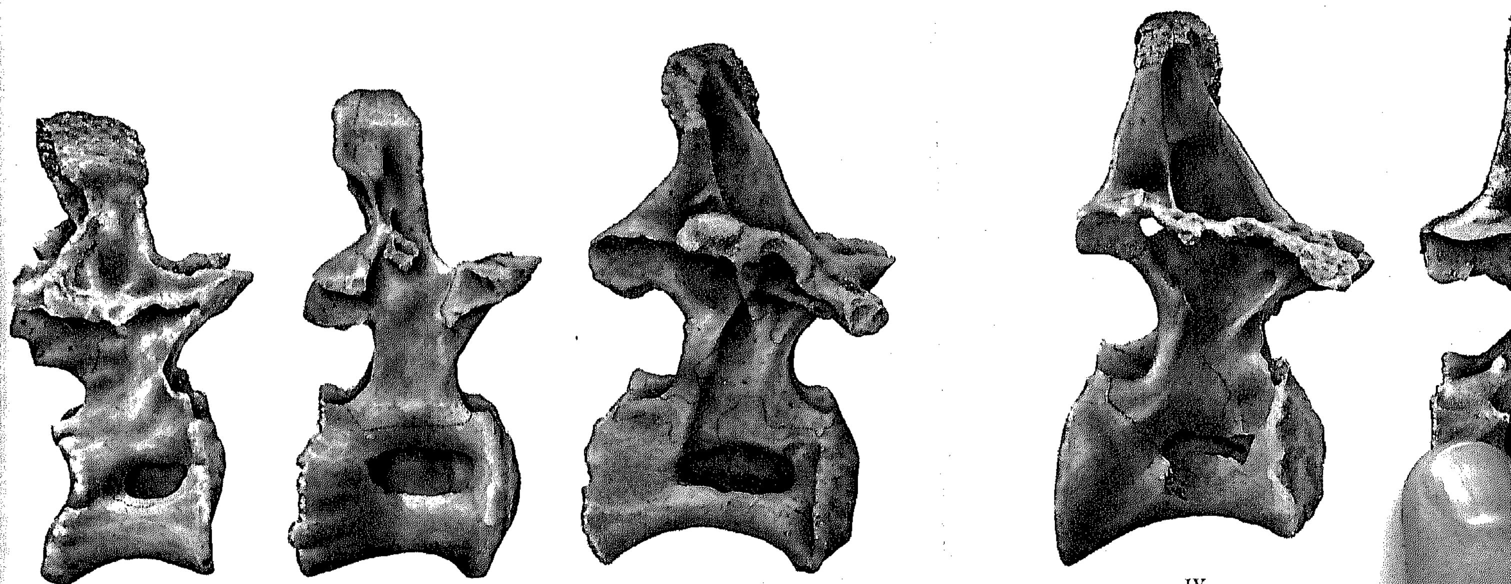

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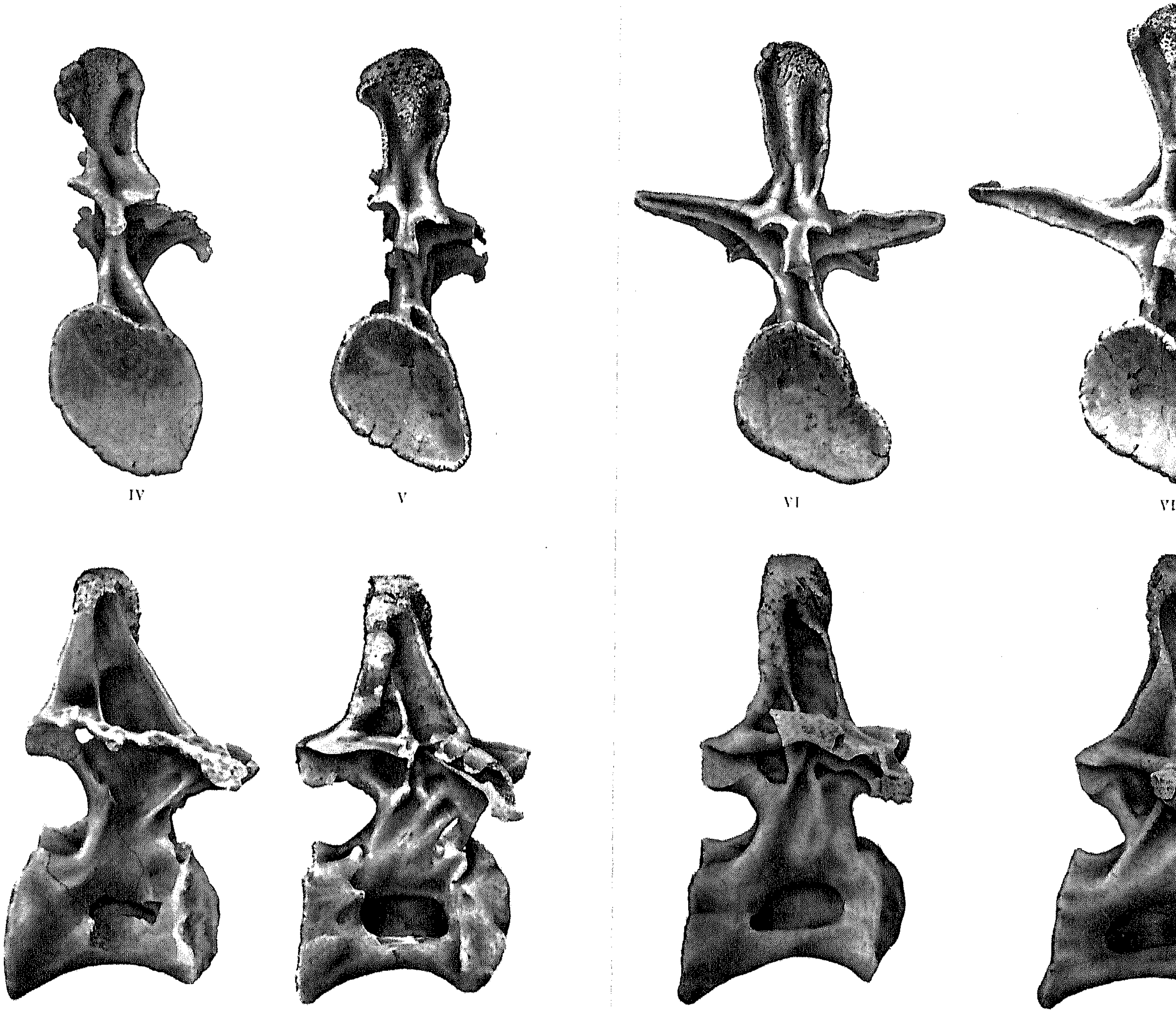
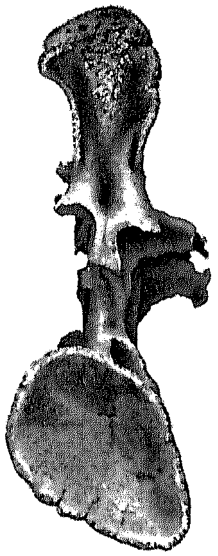
Lateral and posterior views of the first seven presacral



l and posterior views of the first seven presacral vertebræ of *Brachiosaurus altithorax*. All 1/12 natural size.



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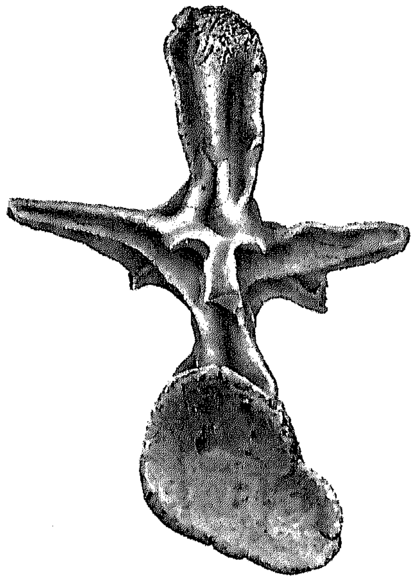

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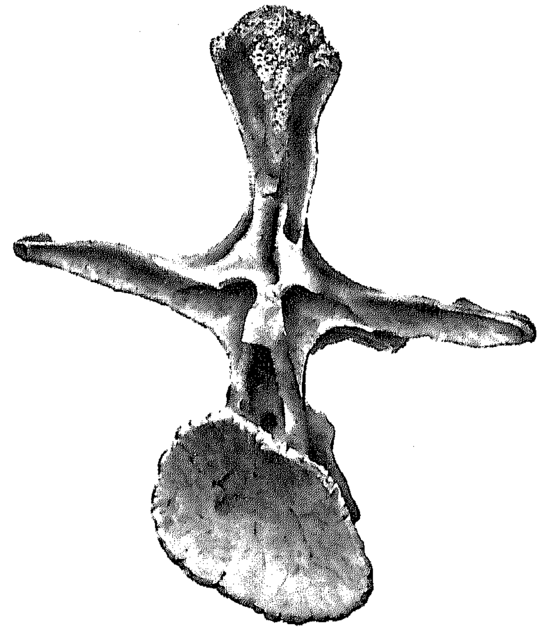

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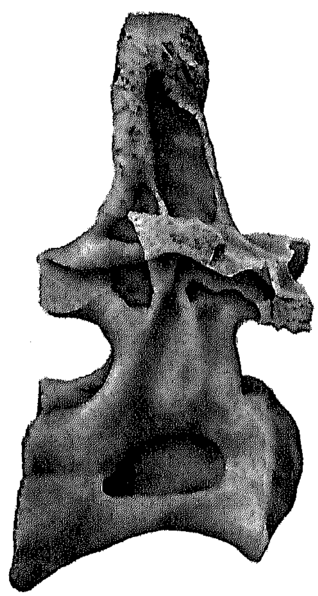
V



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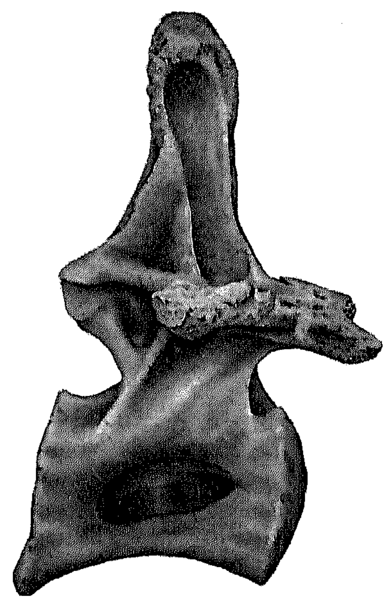


VII

en presacral vertebræ of *Brachiosaurus altithorax*. All $\frac{1}{12}$ natural size.

PLATE LXXIII.

BRACHIOSAURUS ALTITHORAX.

FIG. 1. Lateral view of sacrum, 1/12 natural size. Anterior end at right.
FIG. 2. Inferior view of same, 1/12 natural size. Anterior end below.

Fig. 1

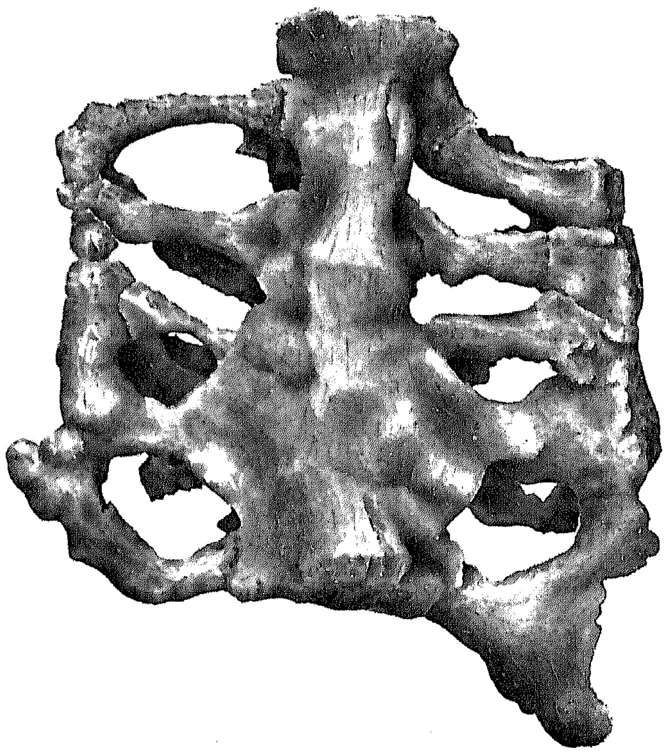


Fig. 2

PLATE LXXIV.

BRACHIOSAURUS ALTITHORAX.

FIG. 1. Head end view of right femur.
FIG. 2. Anterior view of same.
FIG. 3. Head end view of right humerus.
FIG. 4. Anterior view of same.
All 1/14 natural size.

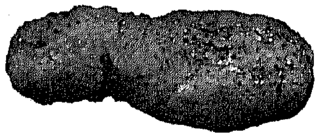


FIG. 1

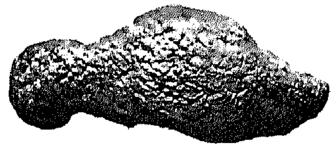


FIG. 3

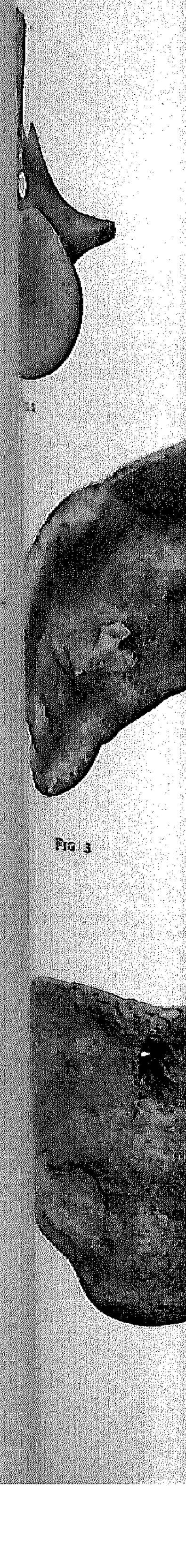
FIG. 2

FIG. 4

PLATE LXXV.

BRACHIOSAURUS ALTITHORAX.

FIG. 1. Posterior view of second caudal vertebra.
FIG. 2. Lateral view of same.
FIG. 3. Lateral view of right ilium.
FIG. 4. Lateral view of left coracoid.
FIG. 5. Mesio-anterior view of the head of a thoracic rib.
All about 1/12 natural size.



l vertebra.

of a thoracic rib.

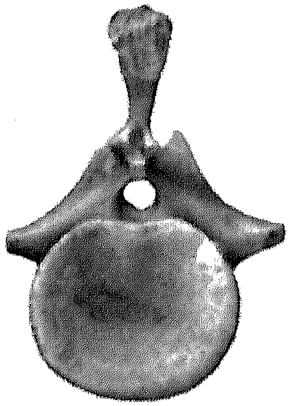


Fig. 1

Fig. 2

Fig. 3

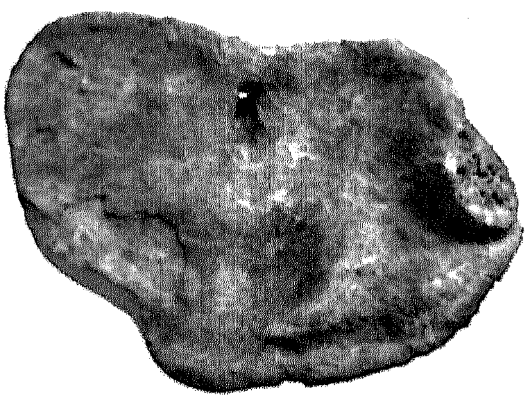


Fig. 4

Fig. 5