Article XII.—ADDITIONAL CHARACTERS OF THE GREAT HERBIVOROUS DINOSAUR CAMARASAU-RUS.

By HENRY FAIRFIELD OSBORN.

WITH THIRTEEN FIGURES IN TEXT.

This gigantic reptile was found in the famous Como Bluffs of Wyoming by Dr. J. L. Wortman, of the Museum party of 1897, and Prof. Wilbur C. Knight, of the University of Wyoming. The Museum number is R. 222. The bones include the left ilium, the ischia and pubes of both sides, the right and left femora, the left tibia and astragalus, the right scapula and coracoid, two shattered cervicals, two complete dorsal vertebræ, two incomplete dorsals, three or four incomplete ribs, coalesced spines of three sacral vertebræ and one sacral centrum, twenty caudals and twelve chevron bones. With the exceptions stated, the bones are in a remarkable state of preservation, having been worked out with exceptional skill by Mr. Granger and others, under the direction of Mr. Hermann.

This is a large individual. The identification is provisional. The measurements, in comparison with those taken from the type of B. excelsus Marsh, are as follows:

		Brontosaurus excelsus.	American Museum No. 222.		
Length	of femur	5 ft. 9 in.	5 ft. 10 in.		
.7	" tibia	3 ft. 6 in.	3 ft. 8 in.		
" "	" pubis	3 ft. 10 in.	3 ft. 10 in.		
" "	" ischium	3 ft. 8 in.	3 ft. 9½ in.		
* *	" scapula	5 ft. 3 in.	5 ft. 7 in.		
"	" coracoid	2 ft. 2½ in.	2 ft. 5 in.		

The new points of greatest importance are :

First.—The discovery of the hitherto unknown characters of the anterior caudal vertebræ.

Second.—The apparent resemblances of Camarasaurus Cope to Amphicalias¹ Cope, to Brontosaurus Marsh, Atlantosaurus Marsh, and Apatosaurus Marsh.

¹This has been anticipated by Marsh (Am. Jour. Sci., Aug., 1881) in his first classification of the Dinosauria, in which *Amphicalias* is bracketed after *Camarasaurus*, and placed in the *Atlantosaurida*. In the final classification of the Dinosauria, however ('The Dinosaurs of North America,' p. 241), *Camarasaurus* and *Amphicalias* are removed to the Morosaurida.

Third.—The observation of structural analogy to certain struthious birds in the anterior dorsals and posterior cervicals.

I. HABITS AND SIZE OF THE ANIMAL IN RELATION TO ITS STRUCTURE.

The estimate given by Marsh of the total length of this animal is nearly or quite 60 feet; the tail is figured at about 24 feet. Since the vertebra believed by Marsh to be the third caudal is probably the 10th or 11th, the tail should be increased to over 30 feet in length, by the addition of at least seven large anterior caudals. The total number of caudals is estimated at 40 as against 37 in *Diplodocus*. Marsh has attributed to *Brontosaurus* 27 precaudal vertebræ, or 13 cervicals and 14 dorso-lumbars. From reasons given below it is probable that there was a larger number of dorso-lumbars, which would still further increase the length of the animal to considerably over 60 feet.

We can only conceive of the Camarasaur as a great wading and swimming quadruped, enjoying a habitat similar to that of the Upper St. John River, Florida, at the present time, namely, a relatively firm bottom gently graded to all depths, supporting a richly luxuriant aquatic vegetation, the river banks bordered by sloping shallows of sand (Colorado, Cañon City Beds) or clays (Wyoming, Como Beds). As imagined by Cope in his picture of Amphicalias ('Century Magazine,' November, 1887), the animal could walk along the bottom, raising the anterior portion of its body. We believe also that it could swim rapidly, propelled by its light but long and powerful tail, which would be useless upon land. The abundance of cartilage around all the limb joints and the non-osseous nature of many of the carpals and tarsals afford positive evidence that the limbs were not continuously subjected to the hard impact of the enormous weight of the body by motion on land. Feeding was done in the water and along the shores. Excursions upon shore were therefore like those of the Alligator, mainly for breeding and egglaying purposes, and they exposed the animal to attack by the Megalosaurs. By means of powerful mid- and posterior-dorsal spines and opisthocœlous vertebræ, the entire anterior part of the

body, while in the water, could be raised or lowered with the great acetabulum acting as a fulcrum, thus presenting an analogy to the Hadrosaurs, which exerted a similar movement upon land. The long neck, similar in structure and almost as flexible as that of an Emeu (*Dromæus*), could thus pass through a prodigious arc in the search for food either under or above water. The neck motion apparently involved the anterior non-spine-bearing dorsals



Fig. 1. Dromæus. Cervicals 13 and 14; dorsals 1 and 2, showing absence of median spines. Dorsal 3, showing large blunt median spine, resembling that of the *Camarasaurus* dorsal, Fig. 11 of this Bulletin, Am. Mus. Coll., No. 607.

as in *Dromæus*, behind which the comparatively inflexible large spine-bearing dorsals rose to maximum height in the sacrum for the insertion of the ligamentum nuchæ and elevator muscles.

The importance of such an hypothesis of function will appear in the following description and discussion, and it applies to all the Cetiosauria, namely, to the *Morosaurus* and *Diplodocus* types as well, which so far as known are uniform with the Camarasaur type in the peculiar bird-like structure of the posterior cervicals and anterior dorsals and in the possession of a very powerful swimming tail.

Ten of the caudals in our specimen afford an interesting illustration of the cause of the distribution of these large skeletons over a considerable surface. The dorsal spines, and in some cases the sides of the centra are found to be deeply gashed with the sharp teeth of a carnivorous Dinosaur. The upper portion of several spines, in fact, is entirely bitten away, the upper surface containing jagged transverse grooves, which prove that the carnivore was of great power, and applied its pointed teeth with strong effect to the gristle and muscles upon the sides of this prodigious tail.

	Centrum, Longitudinal.	Centrum, Transverse.	Centrum, Vertical.	Centrum to top of Spine.	Capitular Pro- cesses Trans- verse.	Tubercular Pro- cesses Trans- verse.	Transverse Processes.	Estimate of Missing Verte- bræ.
Anterior dorsal. Posterior dorsal.	? ?	e310 368	310 340	1050 1280	470 	e864 e715		
First caudal	162	383	335	1075			957	
e 2d caudal	164		e350					<3 & 4
e 5th caudal	168	360	324	892		•••••	e695	< 6 & 7
e 8th caudal	177	340	300	830	• • • • • •		615	io a /
e officaudal	107	333	300	798	• • • • •	••••	622	<10#11
e 12th caudal	179	305	274	712			587	····
e 13th caudal	170	283	200	033		••••	537	
e 14th caudal	173	282	258	598	· • • • · · ·		505	<15
e forn caudal	180	272	248	548		••••	e444	~ 5
e 17th caudal	180	250	228	520	••••	• • • • • •	e395	<18#10
e 2011 caudal ²	105	220	205	1.5	• • • • • •	• · • • • • •	e205	,
e 21st caudal ²	192	210	194	5		• • • • •	172	
e 22d caudal ²	200	202	180		• • • • • •	• • • • • •	137	
$e_{23}u_{1}$ caudal \ldots	198	194	170	1	••••	• • • • • •		
e_{24} th caudal ²	205	184	175	r	••••	••••		100006
$e_2/th caudal2$.	203	171	102	••••	••••	• • • • • •	•••••	~25æ20
e 20th caudal	197	170	155	••••	• • • • • •	••••	••••	100
e_{30} caudal	200	152	140		•••••	· • • • · · ·		~29
e_{26th} caudal ²	203 T8r	140	130	• • • • • •	•••	· • • • • • •	• • • • • •	
e 40 total	105	12/	115	• • • • • •	••••	•••••		< 32@35
• 40 total	•••••			····		• • • • • •	• • • • • •	<37

TABLE I.-MEASUREMENTS OF VERTEBRÆ.

NOTE.-Many interesting facts are brought out by the exact measurements of the caudals given in this Table. The centra decrease steadily in their transverse and vertical diameters, but they increase steadily in the longitudinal diameter as far back as the 26th caudal, then begins a decrease. Thus the estimated 31st caudal measures 203 mm.; the 36th caudal, measuring 185 mm., probably marks the natural decrease towards the tip of the tail. A constant ratio of decrease, however, characterized the dorsal spines.

¹ Measurements agree approximately with supposed 4th caudal, Marsh. ² Summits of spines bitten off and grooved by large cutting teeth.

2. DESCRIPTION OF SKELETON.

The mid-dorsal (Fig. 2) corresponds closely with the supposed 'posterior-dorsal,' described by Marsh as belonging to *Brontosaurus excelsus* (Fig. 12). With the exception of the anterior portion of the centrum and the extremities of the tubercular processes, this vertebra is in a remarkable state of preservation, the neural spine



Fig 2. Camarasaurus. Mid-dorsal. A, anterior view. P, posterior view. Am. Mus. Coll. R. 222. Approximately $\frac{1}{16}$ natural size.

being complete upon the anterior face, and lacking only the upper and lateral portions. It displays the characteristic hyposphen, the complex laminated and excavated condition of the spine, and a pair of small cavities upon the sides of the centra.

The true posterior dorsal (Fig. 3) is a superb vertebra, in nearly perfect preservation, lacking only the anterior portion of the tip of the spine, parts of the extremities of the tubercular processes, and the anterior face of the centrum. It corresponds closely with Cope's type of *Amphicælias altus* (Fig. 13) both in form and measurement, and in the lateral cavities of the centra. It is possible, however, that Cope's type represents a *Diplodocus*. The mid- and posterior-dorsal vertebræ are so different that Cope supposed that they represented different genera, viz., *Camarasaurus* and *Amphicœlias*.



Fig. 3. Camarasaurus. Estimated 5th caudal. Posterior dorsal vertebra. Am. Mus. Coll. R. 222. Approximately $\frac{1}{16}$ natural size.

The sacrum is represented in this specimen by a single large free sacral vertebra, and by the coalesced spines of three sacrals. The significance of these facts will be pointed out later.

The tail of *Camarasaurus* includes a far more powerful and complex series of vertebræ than has been indicated in the figures and descriptions of Marsh.

Immediately behind the sacrum, the first caudal of *Camara-saurus* (Fig. 4) is an entirely unique vertebra, extending laterally into two great transverse plates, which may have come in contact at their extremities with the posterior portions of the ilia. These plates are concave anteriorly. The pre- and post-zygapophyses

are small and obliquely inclined inwards; the anterior face of the spine has a prominent rugose crest, similar to the crest upon the posterior face of the spine, but the latter (posterior crest) sinks between two prominent laminæ, which extend downward to support the post-zygapophyses, pz.



Fig. 4. Camarasaurus. First caudal. A, anterior view. P, posterior view. Am. Mus. Coll. R. 222. Approximately 18 natural size.

Behind this highly specialized vertebra, three vertebræ were probably intercalated, only one of which is preserved in our collection, giving us the transition to the vertebra estimated as the 5th caudal (Fig. 3).

This supposed 5th caudal (Figs. 3, 5) exhibits a marked reduction of the spine as well as of the transverse lamina; the posterior surface of this lamina being excavated by two deep depressions. This vertebra was followed probably by two, which are missing, so that the fourth preserved in our collection is estimated as the 8th caudal (Fig. 5); in this the transverse lamina is still more reduced, and the lateral pockets upon the posterior face are wanting. Behind this is the supposed 9th caudal, which [*June*, 1898.] 15 approaches in its structure that which Marsh has figured as the 4th, but is somewhat more complex. Here follows another interval (Fig. 5), in which would lie the vertebræ described by Marsh as the 4th. (Fig. 6.)

The estimated 12th, 13th and 14th succeed each other with a regular diminution in size, and a steady reduction of the trans-





Fig. 6. Brontosaurus excelsus Supposed 4th caudal vertebra. After Marsh, 1897, Plate xxiv. Approximately 18 natural size.

Fig. 5. Camarasaurus. Anterior caudals. First caudal and 5th, 8th, 9th, 12th caudals as estimated. Am. Mus. Coll. R. 222. Approximately $\frac{1}{10}$ natural size.

verse processes, which gradually transforms into a horizontal plate. The next vertebra preserved is the estimated 16th, which exhibits a very marked reduction in the transverse process, and this disappears entirely in the supposed 20th and 21st, in front of which at least two vertebræ are missing. (See also Note 1, p. 233.)

The missing 16th and 17th vertebræ were probably detached in the manner described above, and the 16 or 20 vertebræ at the end of the tail were also drawn away. In front of the 15th no tooth marks are observed.

3. HISTORICAL NOTES.

Large Cetiosauria have been named from these and similar beds¹ in Colorado, as follows :

No. 1. Titanosaurus montanus Marsh.—Am. Jour. Sc., July, 1877, p. 87. -Golden, Colorado.

No. 2. Camarasaurus supremus Cope.—Pal. Bull. 25, Aug. 23, 1877, Proc. Am. Phil. Soc.-Cañon City, Col.

No. 3. Caulodon diversidens² Cope.—Pal. Bull. 26, p. 193.—Cañon City, Col.

No. 4. Tichosteus lucasanus² Cope.-Pal. Bull. 23, p. 194, Nov. 21, 1877. Proc. Am. Phil. Soc.-Cañon City, Col.

No. 5. Atlantosaurus (Titanosaurus) montanus Marsh.-Am. Jour. Sc., Dec., 1877, p. 514.-Colorado.

No. 6. Apatosaurus ajax Marsh.—Am. Jour. Sc., Dec., 1877.—Colorado.

No. 7. Apatosaurus grandis Marsh.—Am. Jour. Sc., Dec., 1877, p. 515.— Colorado.

No. 8. Amphicalias altus Cope.-Pal. Bull. 26, Dec. 10, 1877. Proc. Am. Phil. Soc.-Cañon City, Col.

No. 9. Amphicalias latus Cope.-Pal. Bull. 26, Dec. 10, 1877. Proc. Am. Phil. Soc.--Cañon City, Col.

No. 10. Symphyrophus musculosus² Cope.-Pal. Bull. 26, p. 246, Jan. 12, 1898.--Cañon Ĉity, Ĉol.

No. 11. Atlantosaurus immanis Marsh.—Am. Jour. Sc., March, 1878, p. 241.--Colorado.

No. 12. Brontosaurus excelsus Marsh.--Am. Jour. Sc., Dec., 1879.--Como, Wyoming.

The rapid and profound transformations in the characters of the vertebræ in different parts of the back bone give these animals an entirely unique position among reptiles, and largely explain the diversities of view as well as the numerous generic references held by different authors, as indicated in the following brief résumé :

(1) The first notice of these animals in American literature was by Marsh,³ under the name of Titanosaurus montanus. This generic name had been shortly before employed by Lydekker.⁴ (2) The second notice was by Cope,⁵ in which the name Camarasaurus was proposed. The species Camarasaurus supremus was based upon a number of dorsal vertebræ from the supposed Dakota Beds of Colorado, near Cañon City. In 18786 these remains were

¹ These beds are equivalent to the Wealden of England, from which many large Dino-saurs have been described, of the same order (Cetiosauria) and possibly representing the

saurs have been described. same genera. ⁹ Never fully characterized or figured. ⁹ Notice of a new and Gigantic Dinosaur, Am. Journ. Sc., July, 1877, p. 88. ⁴ Rec. Geol. Surv. Ind., Vol. IV. p. 38, 1877. ⁶ On a Gigantic Saurian from the Dakota Epoch of Colorado. Pal. Bull., XXVI, Pub-¹⁰ the d Aug. 22, 1877. ¹⁰ The d Aug. 23, 1877.

 ⁶ On the Saurians recently discovered in the Dakota Beds, etc.—Am. Nat., Feb., 1878, p. 71.

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figured. It now appears that the anterior dorsal vertebra (Fig. 2, p. 73, of Cope's article), characterized like the cervicals, by the absence of the median spine, was correctly determined by Cope. In this vertebra the hyposphen is less accented than in the vertebra figured upon the following page (Fig. 5, p. 75), in which the hyposphen is sharply defined, and there is also a median dorsal spine. (5) The fifth notice was by Marsh,¹ in which the name *Atlantosaurus*.



Fig. 7. SACRA OF CETIOSAURIA.

A, Apatosaurus ajax. Three coalesced sacrals. After Marsh, 1897, Plate xvii. B, Atlantosaurus montanus. Three coalesced sacrals and portion of a fourth. After Marsh, 1897, Plate xvii.

C, Brontosaurus excelsus. Five coalesced sacrals. After Marsh, 1897, Plate xxiii. All figures approximately $\frac{1}{20}$ natural size.

was proposed to replace *Titanosaurus*. (6) In the same paper the new genus, *Apatosaurus ajax*, was distinguished by the opisthocœlous cervicals with hollow centra; anterior dorsals with similar characters; posterior lumbars with flat articular faces; sacral vertebræ more solid; anterior caudals biconcave; chevrons not united above. (7) In the same paper the species *A. grandis* is described with the following measurements:

(8) The eighth notice by Cope was based upon characters of the posterior dorsal vertebræ. The vertebra (Fig. 13, p. 80) with a very prominent dorsal spine, re-

¹ Notice of new Dinosaurian Reptiles from the Jurassic Formation. Am. Jour. Sc., Dec., 1877, p. 514.

ferred to Amphicalias altus, agrees closely with that here shown to belong to Camarasaurus. (12) In the twelfth notice (Marsh, 1879) a new type, Brontosaurus excelsus, was defined. Characters : Sacrum composed of five thoroughly coössified vertebræ; in other respects resembling Morosaurus from the Como Beds of Wyoming. The succeeding notices of these animals are fully embraced in Marsh's Memoir, "The Dinosaurs of North America," published in 1897. Here (pp. 166-241) the order Sauropoda and family Atlantosauridæ are described, the latter, however, not including the genus Camarasaurus, which is placed in the Morosauridæ (page 241).

COMPARATIVE MEASUREMENTS OF LIMBS, ARCHES, VERTEBRÆ.

	amara- aurus upremus. ¹	<i>zmara-</i> <i>saurus</i> No. 222, Im. Mus.	mphicæ- ias itus. ¹	patosau- us randis .	rontosau- us xcelsus. ²
Total length of scapula Greatest diameter of coracoid Antero-posterior, ilium Total length of ischium "" pubis "" femur Height of ant-dorsal spine " post-dorsal spine Length, centrum ant-dorsal Median caudal	1517 690 1820 830 275	G 1597 736 1373 1150 1168 1776 1050 1280 	 1060 1930 ³ 1100 	V 2 3	1600 672 1118 1168 1750 948 276

It is a priori improbable that so many different genera of gigantic Saurians of similar size co-existed. It is against the principles of evolution that closely similar types of equal size should occupy the same territory at the



Brontosaurus excelsus. Posterior cervical vertebra. Fig. 8. After Marsh, 1897, Plate xxi. Approximately 18 natural size.

¹ These measurements are given in Cope's second paper upon Camarasaurus. (Am.

Alless measurments are given in Cope's second paper space constraints of the physical second paper space and the physical second paper space the published.
³ Cope gave the length of this femure as 6 feet 4 inches (= 1030), and described it as longer than that of *Camarasaurus*, but in his metric table it is by misprint assigned 1524 mm.

same time. It appears moreover to the writer that the evidence which has been brought forward to demonstrate such an exceptional condition is inadequate and is capable of different interpretation, as follows :

Amphicælias having been shown to be in all probability related to Camarasaurus, the only absolute basis of separation of the remaining types is the number of sacral vertebræ, as in the definitions of Marsh and Cope :

Apatosaurus.Camarasaurus.Atlantosaurus.Brontosaurus.3 sacrals.4 sacrals.4 sacrals.5 sacrals.

This definition does not separate Atlantosaurus from Camarasauius; the type sacrum of Atlantosaurus (Fig. 7B) is, however, fractured anteriorly, and this animal may therefore have pos-



Fig. 9. Apatosaurus ajax. Dorsal vertebra. After Marsh, 1897, Plate xviii. Approximately $\frac{1}{16}$ natural size.

sessed 5 sacrals, like *Brontosaurus* (Fig. 7C).

The three coalesced sacral spines and the single free sacral centrum in our specimen suggest the following hypothesis, namely, that 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.

Such difference in the growth and degree of coalescence is shown to be probable (1) by *Diplodocus*, in which at least three vertebræ coalesce by centra but only two coalesce by spines; (2) by our specimen, No. 222, in which (closely resembling *Brontosaurus* in every other respect) one centrum is free and three spines are coalesced; (3) by the type of *B. excelsus*, in which three spines are coalesced, as figured. (See also Note 2, p. 233.)

The removal to a distance of one or both of the freer sacral vertebræ is quite explained by the fact that these skeletons are

in the great majority of cases very much disturbed and confused before embedding. An instance in point is the loss of all the anterior caudals in Marsh's otherwise excellent *B. excelsus* specimen.

Let us suppose that the three early united vertebræ (of the more primitive Cetiosaur sacrum) were found alone, the others having been detached and lost, we would then have the genus Apatosaurus ; if one of the freer vertebræ had united, we would have the genus Atlantosaurus



Fig. 10. Camarasaurus supremus type. Anterior dorsal vertebra. After Cope. Approximately 18 natural size. Compare Morosaurus, Marsh, 1897, fig. 31, p. 181.

or *Camarasaurus*; if *both* of the freer vertebræ had united we would have *Brontosaurus*.

4. ANTERIOR DORSAL VERTEBRÆ OF THE CETIOSAURS ARE OF AVIAN TYPE.

Anterior dorsals without median spines have been described by Cope in *Camarasaurus* (Fig. 10) and by Marsh in *Apatosaurus* (Fig. 9), *Morosaurus* and *Diplodocus*. This condition seems so general as to constitute almost an ordinal character of the Getiosaurs.

These vertebræ are, moreover, remarkable in resembling those of certain Struthious birds such as *Dromæus* (Fig. 1), in the absence of median spines, in the elevation of lateral spinous processes above the zygapophyses, and in the abrupt development of a median spine upon the third or fourth dorsal.

It is also not improbable that the abrupt transition from vertebræ without median spines to a vertebra with a strong median spine (*Dromæus*, D 3) is paralleled in the blunt spine of the *Camarasaurus* dorsal (Fig. 11), which may well represent D 3 or



Fig. 11. Camarasaurus supremus. Anterior dorsal. Supposed to be the first possessing a median spine. After Cope. Approximately rs natural size.

D4. Behind this would appear the transversely expanded middorsal spines of the *Brontosaurus*¹ (Fig. 12) type, and of our specimen, No. 222 (Fig. 2). Behind this again would appear the posterior dorsal of the Amphicœlias type (Fig. 13) or the still more posterior dorsal of our specimen, No. 222 (Fig. 3).

The difference between these three types of vertebræ (Figs. 9, 12 and 3) is so profound that it seems hardly possible that they could be compressed within the limits of 14 dorso-lumbars—the number which Marsh has figured



Fig. 12.



Fig. 13.

Fig. 12. Brontosaurus excelsus. Dorsal vertebra. After Marsh, 1897, Plate xxi. Approximately $\frac{1}{16}$ natural size. Fig. 13. Posterior dorsal of Amphicalias altus, type. After Cope. Approximately $\frac{1}{16}$ natural size.

 $^{^1}$ This is mistakenly determined by Marsh ('Dinosaurs of North America,' p. 169) as a "posterior dorsal."

in *Brontosaurus*. There were, therefore, in all probability, more dorso-lumbars than 14. Cope has assigned 20 dorso-lumbars to *Camarasaurus*.

So far as habit and function are involved, the transition from the lateral spined to the median spined dorsals, as in *Dromæus*, probably indicates that *Camarasaurus* had a comparatively free anterior dorsal region, consisting of two or more vertebræ, which bore short ribs and moved in all directions with the neck.

The differences in proportion, in length of limb and in other parts subject to age, sex and individual variation noted in these different specimens are undoubtedly superseded by genuine specific differences which mark the Camarasaurs of different geological levels, also by generic differences, which, however, are still to be positively determined by more careful and thorough exploration, and by comparison of the type specimens. The generic name *Camarasaurus* is therefore provisionally employed here.

NOTE I.-CENTRA OF CAUDALS.

There is also great diversity in the caudal centra.

The first caudal centrum is biconvex.

The second to the estimated seventeenth caudal centra are procelous.

The estimated twentieth caudal centrum and all behind it are amphicalous.

NOTE 2.-SIZE SACRUM.

The four sacrals of *Camarasaurus* exhibit exactly the same measurement as the four anterior sacrals of *Brontosaurus*.