THE

AMERICAN JOURNAL OF SCIENCE

[FOURTH SERIES.]

ART. XVIII.—*Entelodonts in the Marsh Collection;* by EDWARD LEFFINGWELL TROXELL. With Plate III.

[Contributions from the Othniel Charles Marsh Publication Fund, Peabody Museum, Yale University, New Haven, Connecticut.]

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GENERAL SUMMARY.

The purpose of such a paper is to put at the disposal of science the fine collection of entelodonts in the Peabody Museum. The known species are listed and the standing and a brief description of each are given, as well as a list of the new species proposed at this time. In the discussion of the teeth and bony processes on the skull and mandibles, it is reasoned that the latter were for muscle attachment, and facilitated the movements of the jaws in eating and may also have supported cheek pouches. The anterior mental processes may well have guarded the points of the canines, as in the sabre-toothed cats, or in *Dinoceras*.

The great diversity of the material did not permit the reference of every specimen to a known species, nor did the fragmentary material warrant making a new species for each strange specimen. It was found most practicable, therefore, to group allied specimens, even though at times widely different, in order to emphasize their relationship and to arrange the whole in a systematic way.

Summary of Measurements

	A. clavus clavus holotype mm.	*A. clavus darbyi* holotype mm.	*A.* sp. No. 10286 mm.	*A. crassum* paratype mm.
Skull length, condyles to incisor border	392	430	....	....
Width across muzzle at alveolus of P^2	58.0	62.0	....	....
Width of rami back of anterior tubercles	45.4	....	....	49.0
Depth of ramus at P_2	46.6	....	56.0	60.0
Depth of ramus at M_2	51.6	61.7	68.0	72.3
Diameter of P^4, transverse	21.0	21.8	24.6	....
Diameter of P^4, ant.-post.	21.0	18.2	24.3	....
Diameter of M^2, transverse	24.7	25.3	28.4	....
Diameter of M^2, ant.-post.	24.3	24.0	27.0	....
Upper premolar length	103.0	114.0	....	....
Upper molar length	67.6	67.0	81.0	....
Diameter of P_4, transverse	12.8	14.8	16.2	....
Diameter of P_4, ant.-post.	28.8	25.0	30.5	29.0
Diameter of M_2, transverse	17.9	18.4	20.5	22.0
Diameter of M_2, ant.-post.	24.9	23.6	26.0	26.0
Lower premolar length	112.0	....	141.5	135.0
Lower molar length	71.7	70.5	75.9	76.0

	A. marshi holotype mm.	*P. potens* holotype mm.	*M. zygomaticus* genoholotype mm.	*M. latidens* holotype mm.	*Chærodon caninus* genoholotype mm.
Skull length, condyles to incisor border	540	....	760	....	610
Width across muzzle at alveolus of P^2	80.6	....	96.0	80.0	85.5
Width of rami back of anterior tubercles	64.6	78.0	....	75.0	62.0
Depth of ramus at P_2	62.0	92.0	....	74.0	83.0
Depth of ramus at M_2	75.0	109.0	....	76.0	83.0
Diameter of P^4, transverse..	27.8	....	34.0	39.0	34.6
Diameter of P^4, ant.-post...	28.6	....	31.0	35.0	30.0
Diameter of M^2, transverse.	32.3	....	42.5	45.0	43.0
Diameter of M^2, ant.-post..	29.3	....	40.0	42.2	36.0
Upper premolar length	130.0	....	186.0	....	155.0
Upper molar length	82.8	....	112.0	117.0	105.0
Diameter of P_4, transverse..	18.4	?23.0	*33.5	29.0	27.0
Diameter of P_4, ant.-post...	34.0	41.4	*53.0	44.0	35.0
Diameter of M_2, transverse.	23.8	28.6	*39.5	34.7	31.0
Diameter of M_2, ant.-post..	30.4	35.4	*54.0	43.0	35.5
Lower premolar length	149.0	200.0	....	189.0	166.0
Lower molar length	88.4	108.5	....	126.5	107.0

* *Ammodon leidyanus*, holotype and paratype.

Two new genera, four new species, and one new subspecies have been made in order to establish certain new features not heretofore known in the Entelodontidæ. The concluding sections of the paper are concerned with the detailed description of the types and the more important specimens in the collection.

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PART I. MORPHOLOGY AND TAXONOMY.

INTRODUCTION.

Purpose of the present paper.—The development of our knowledge of the group of giant pigs called entelodonts has been so well given, especially by Scott (1898) and by Peterson (1909), that it is not worth while for us to repeat its general history, but in the great amount of material in the Yale Museum there are several specimens of unusual importance, some of which are entirely unknown to the scientific public, and some are but imperfectly known or have even been misrepresented in the literature, and so it seems necessary to go over this phase of the work again. There is a double purpose in presenting a paper on this material, namely, that of increasing the value of the specimens themselves, forming as they do a part of the interesting collection which Professor Marsh brought together in the early days of his paleontological work; but more especially, by detailed descriptions and drawings, to lay more broadly the foundation on which to study these animals in the future. The fine drawings are due to the artistic skill of Mr. R. Weber.

It is especially fitting, at the beginning of my work here as a member of the Peabody Museum staff, to express my gratitude to the two men, Professor Schuchert and Professor Lull, my former instructors, who have been most generous in their sympathy and assistance, and who now offer me every advantage in carrying on the work of my choice. To my congenial associates and myself the whole Marsh collection is thrown open for study and description under circumstances most propitious.

With reference to the group of entelodonts in particular, some of the Marsh specimens are entirely new, some of them had never been carefully studied before, and most of the material had never been completely prepared. In several instances, well known specimens have been further developed so that now new features are observed, giving evidence which contradicts some of the conclusions of former studies. The present paper treats almost exclusively the fossils in the Marsh Collection of the Peabody Museum at Yale.

In earlier paleontological writings, types were made on single molars or on a fragment of bone without teeth. In attempting to use these fragmentary types as guides, it becomes very evident that we cannot depend upon the characters shown by a single tooth or other small part of the fossil; we must know a large part of the skull; we should know the whole skeleton.

Status of species.—There were some twelve or fourteen species referred from time to time to *Entelodon* (*Elotherium,* see Peterson 1909, p. 43) and finally to the true American forms *Archæotherium, Pelonax, Ammodon, Dinohyus,* etc.; of these, recent authors recognize but few. Following is a list of the Oligocene forms commonly seen in the literature:

Entelodon magnus Aymard 1846. *E. coarctatus* Cope 1889. *E. calkinsi* (Sinclair) 1905. *Archæotherium mortoni* Leidy 1850. *A. robustum* Leidy 1852. *A. ingens* (Leidy) 1856. *A. superbum* (Leidy) 1868. *A. imperator* (Leidy) 1873. *A. crassum* (Marsh) 1873. *A. clavus* (Marsh) 1884. *Pelonax ramosus* Cope 1874. *P. potens*

(Marsh) 1893. *P. bathrodon* (Marsh) 1893. *Dæodon shoshonensis* Cope 1878. *Ammodon leidyanus* (Marsh) 1893 (Miocene). *Dinohyus hollandi* Peterson 1905 (Miocene).

Let us note the status of each of these.

Entelodon magnus Aymard is an interesting specimen of which the skull and lower jaws and other skeletal material constitute the first fossil of the sort found; for many years no distinctions between it and the American forms were noted.

Entelodon coarctatus Cope is undoubtedly quite distinct from any other American species, and from the observations which follow[1] it is apparent that if any of our entelodonts are closely related to *E. magnus* of France, it is this specimen described so long ago by Professor Cope.

Entelodon calkinsi (Sinclair), referred by Peterson (1909, pp. 64-65) to the strange genus *Dæodon,* in this paper is put under the new genus *Chœrodon.* The specimen was found in the John Day beds of Oregon; it is discussed more fully in connection with *Chœrodon caninus,* genoholotype, on a later page.

Archæotherium mortoni Leidy was the first species found in America. The type specimen consisted of a

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[1] These two species are shown to be similar from the subjoined table of ratios: P_2 of *E. coarctatus* is relatively rather small as indicated by the ratio 66.9 per cent, while both P_3 and P_4 are comparatively large, with the ratios 80 and 80.6 per cent. The relation of P_3 and P_4 in each case is identical.

Other resemblances between the two are: the very small diastemata or their absence between the premolars, the first premolar small and single-rooted, crowns of premolars wrinkled and compressed, with cutting edges fore and aft. The main known differences between the two species are: the relatively larger size in general and of P_2 in particular, and the seemingly rougher teeth and well developed cingula of *E. magnus.* These differences certainly can not mark a greater variation than that of species, and so we would replace the American form under the old name of *Entelodon.*

RATIOS FROM MEASUREMENTS TAKEN FROM THE DRAWINGS OF COPE AND PETERSON.

	E. coarctatus mm.	Ratio %	*E. magnus* mm.
Length of molar premolar series......	167.1	74.0	226.0
Length of three lower molars..........	71.5	75.8	94.4
Height of enamel on crown of P_1	15.8	73.1	21.6
Height of enamel on crown of P_2	18.2	66.9	27.2
Height of enamel on crown of P_3	25.4	80.0	32.0
Height of enamel on crown of P_4	20.0	80.6	24.8

fragment of the skull with two premolars. Although the first description was almost as fragmentary as the fossil, we do find some accurate measurements, and later there were published some drawings. Peterson has discovered at the Carnegie Museum some excellent skulls which he identifies as *A. mortoni,* and has thus put the specific name on a more solid foundation.

Archæotherium robustum Leidy. This species was made on rather an important specimen in the collection of Doctor Owen, from the John Day region, and the name may some day be revived by a careful study of the original material, the location of which is not known at present. Peterson in his memoir makes no mention of this species, which Leidy himself tells us is no doubt the male individual of *A. mortoni.*

Archæotherium ingens (Leidy). The drawing published by Leidy in 1869 is by him "referred" to the species made in 1856; whether that may be interpreted to mean the same actual specimen we can not be sure. Peterson says that the type is not now known, and Leidy himself stated that he was "prepared to admit that these larger fossil remains may have pertained to robust males of *Elotherium mortoni.*" The type specimen represents "a huge species, indicated by several mutilated canines, the anterior extremity of a lower jaw without teeth, and the crown of an inferior molar tooth."

Archæotherium superbum (Leidy) is like the last species; of it Peterson says the "type is altogether inadequate"; furthermore the geological age and present location also are unknown, and in his estimation the name becomes a thing simply of historical interest.

Archæotherium imperator (Leidy) is represented by fragments which are unsuitable as types and Peterson states that they "should therefore be regarded only as an historical record of the first report of the existence of entelodonts in the John Day formation."

Archæotherium crassum (Marsh) was founded on two skeletons in the Yale Museum concerning which there is considerable misunderstanding; it is certain that the complete zygomatic arch, fig. 9, with associated skeletal parts (Cat. No. 12020)[2] is one of the specimens, of the features of which Professor Marsh says: "The most striking of

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[2] Catalogue numbers cited refer to specimens in the Yale Fossil Vertebrate Collection in the Peabody Museum.

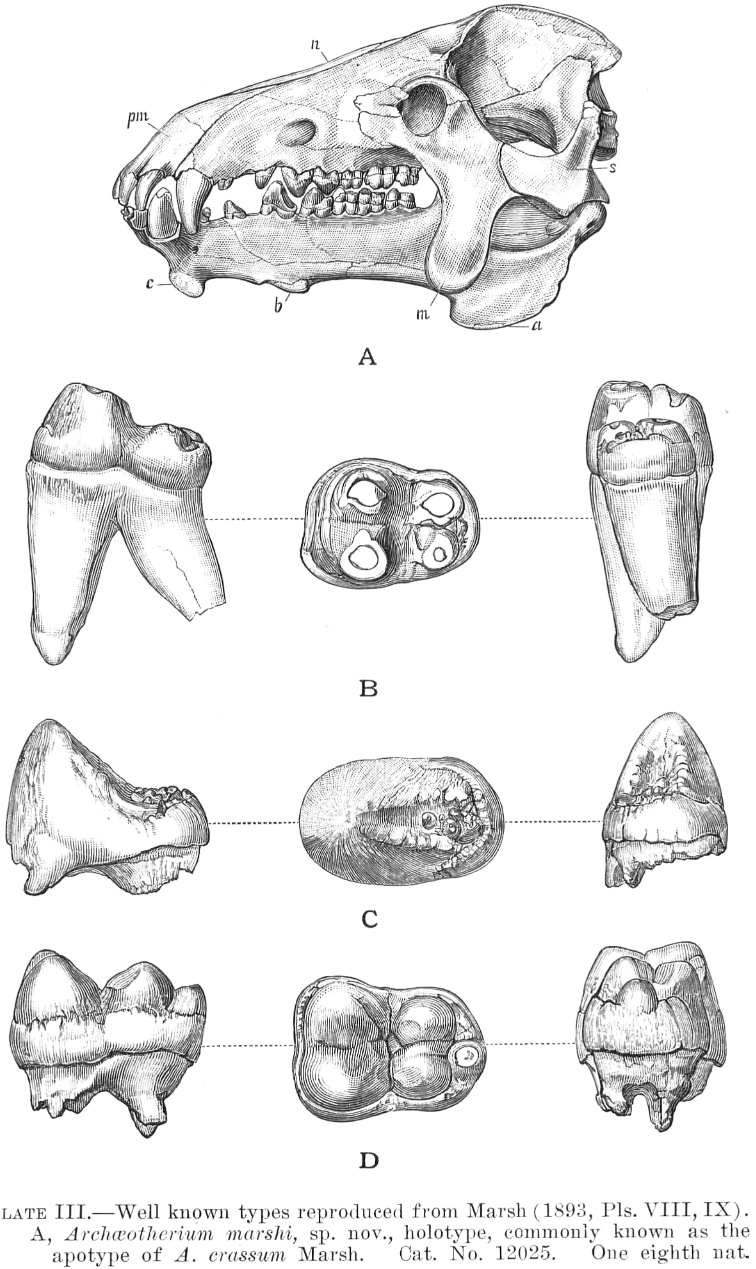

Plate III.—Well known types reproduced from Marsh (1893, Pls. VIII, IX).

A, *Archæotherium marshi*, sp. nov., holotype, commonly known as the apotype of *A. crassum* Marsh. Cat. No. 12025. One eighth nat. size.

B, *Pelonax bathrodon* (Marsh). Holotype. Cat. No. 12030. Three views of third lower molar. One half nat. size.

C, *Ammodon leidyanus* (Marsh). Views of genoholotype, P_4, Cat. No. 12040; and D, paratype, M_3, Cat. No. 12041. Both one-half nat. size.

these is a very long process descending from the malar bone and giving attachment to the masseter muscle.'' This was the first report of this very odd character in one of the entelodonts. On a later page in this paper the type is figured and the description amplified in the hope that we may find material comparable to it. It should be carefully noted that most of the description of this species by Marsh, Peterson, and others has been made from an apotype,[3] specimen No. 12025 (see Pl. III, A), which is found in many respects to be different from the original and is here made the type of a new species, *A. marshi.*

Archæotherium clavus (Marsh) was considered by Peterson to be a subspecies of *A. mortoni,* but dûe to the fact that the skull has now been completely freed from the matrix, showing the teeth and other parts (figs. 1-3), heretofore unknown features will be pointed out which it is believed will reinstate the name as that of a full and separate species. The holotype is Cat. No. 12035 of the Yale collection.

Pelonax ramosus Cope is a genus and species made on the great size of the tubercles on the lower jaw and on the single-rooted premolars, I and II. It is based on the ramus of a mandible of a very large animal of which the skull, according to Cope, would have measured nearly 2½ feet in length.

Pelonax potens (Marsh) Peterson (figs. 13, 14) is a peculiar species, with very heavy mental tubercles, single-rooted first premolar, and, unlike the type of the genus, with a double-rooted, though small, second premolar. The type specimen consists of the lower jaws with the fourth premolar and the three molars of one side. It is No. 12042 of the Yale Museum collection.

Pelonax bathrodon (Marsh) Peterson (Pl. III, B), has for its type a single lower third molar which, roughly estimated from the dimensions given by Cope in his original description, is about 3 mm. less in length than the corresponding tooth of *P. ramosus.* The specimen is indistinguishable from Cope's description of *P. ramosus* and is inadequate as a type. It is Cat. No. 12030 of the Yale collection.

Dæodon shoshonensis Cope is known by the body of the ramus of a very large animal. The extreme width and

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[3] See Schuchert, C., and Buckman, S. S., Science, n. s., 21, 899, 1905.

the absence of the mental tubercles are characters found elsewhere only in specimens of *Dinohyus.*

Ammodon leidyanus (Marsh) (Pl. III, C) was a species made by Professor Marsh on two teeth from the Miocene of New Jersey, and probably represents the largest of the entelodonts known. It is only mentioned here with the Oligocene forms because of its connection with the larger species. The holotype is Cat. No. 12040, and the paratype Cat. No. 12041, of the Yale collection.

Dinohyus hollandi Peterson is a very large Miocene species of which the whole skeleton is known. It is so fully and completely described by the author in his interesting memoir that any further mention here would be superfluous.

To the species already listed, the following new designations will be added in later pages, based on characters summarized under their respective groupings:

Archæotherium marshi, sp. nov., figs. 10-12.
A. clavus darbyi, subsp. nov., figs. 4-8.
Megachœrus zygomaticus, gen. et sp. nov., figs. 15, 16.
M. latidens, sp. nov., figs. 17, 18.
Chœrodon caninus, gen. et sp. nov., figs. 19, 20.

THE BONY PROCESSES IN RELATION TO THE TEETH AND MUSCLES.

The teeth are so constructed that they interlock throughout; the long separation of the incisors from each other and from the canines, to make way for the opposing teeth, is noteworthy, but the premolars also interlock: P_4 fits into the inner side of $P^{3.4}$ in a triangular pocket; the posterior shelf of P_4 comes in contact with the top of the fourth upper premolar. This strong cutting machine, represented by the formula $P\frac{3.4}{3.4}$, was well adapted to nipping off a particularly tough root, done by a backward, inward shearing of the lower jaw; and to fortify the teeth for this backward pressure, the lower premolars face in that direction, while the upper teeth are set at an angle facing forward.

The molars are constructed to mash the food, which probably consisted of bulbs and roots torn up by the canines and cut off and into short lengths by the premolars. The high cusps of M_2 and M_3 fit in between the cones respectively of $M^{1.2}$ and $M^{2.3}$; there is just room enough for the cones of the uppers, between each set of the high anterior cusps on the lower molars.

The actual movement of the teeth, beginning in front, was a shearing inward of the lower premolars, graduated into the shearing, grinding, crushing of the anterior molars, each one in turn from before backward; and finally the movement was ended when M_3, facing slightly inward, came fairly against the face of M^3 turned at an angle outward. This movement of the jaws may be judged from the wear between adjacent teeth, showing the slight movement of a tooth in the jaw with respect to the others, and also from the wear on the inner sides of the upper molars and on the outer side of the lower; in the latter case it amounts sometimes to the shearing off of a large portion of the side of the tooth.

The incisors are not only worn on the ends but are notched posteriorly, probably by lateral motion of the opposing teeth. The canines are generally worn off at the tips at right angles. Always the upper canine is worn flat anteriorly and it in turn wears a diagonal groove on the posterior side of the lower canine. On the anterior face of C^1, specimen No. 10286, there is a horizontal notch probably resulting from transverse movement against the tip of the lower canine.

In none of the specimens at hand is there evidence of wear by roots drawn across the base of the tooth such as is reported by Scott.

These apparent movements of the teeth and the lower jaw may offer a clue as to the purpose of the mental tubercles. Writers have hesitated to speculate, even, about the use of the many processes found on the skulls of the entelodonts. Peterson (1909, p. 144) "believed . . . that these processes, at least in the genus Dinohyus, existed for the attachment of muscles in order to give required strength to this portion of the head." Cope (1874A, p. 504), in speaking of the great tubercle on the lower jaw of *Pelonax ramosus,* says: "The posterior edge is acute and the extremity very rugose as though for the attachment of a horny or cartilaginous cap or apex." Later (1888, p. 1089) he compared the "osseous projections" to the "wattles in old males of the recent hog. In the *E. ramosum* these tuberosities become processes, and the anterior ones especially are so long that when the chin was stretched, hog-like, on the mud, it was raised well above the surface, allowing the passage underneath of water or of small animals."

Without commenting on this idea of Professor Cope, let us examine other hypotheses, perhaps equally fantastic. When we compare the skulls with those of *Hippopotamus,* we wonder whether they might have had large thick lips, somewhat prehensile, which the tubercles by their wide extent aided in movement: to pull the lips away from the long teeth before biting and to draw the corners of the mouth forward in order to fold long reeds and grasses into the teeth.

There is a striking similarity between the anterior mental tubercle in *A. clavus clavus* and the protecting flange for the canine in some of the ancient sabre-tooth cats and in the Dinocerata, in that it forms a recess with a bony projection beneath. In some of the species of *Archæotherium,* and more especially in *Pelonax,* these guards are very extensive. In *Pelonax* we do not know the canines, but I imagine they were not so developed as to require such a very long sheath for their protection. The correlation between the wide-reaching tubercles and the widespread points of the upper canines, especially where the body of the ramus becomes smaller and the symphysis shorter, is well illustrated in *A. marshi* (fig. 12), where we find the points of the canines separated a distance about equal to the width of the tubercles.

The posterior mental processes were undoubtedly for muscle attachment, and because they are generally curved backward, we assume that the pull of the tendon was from that direction or from above. Two possibilities present themselves: first, from comparison with the dog (these entelodonts resemble the carnivores in many respects), we presume there was a muscle, homologous to the occipito-mandibularis, having its origin on the paroccipitals, or, in these animals, on the outer extremity of the temporal, and its insertion on the ventral border of the ramus, whose purpose it was to open the mouth or drop the jaws. Secondly, there may have been a muscle corresponding to the buccinator which in the dog is inserted low on the ventral border of the ramus and has its origin on the maxilla. In the Entelodontidæ a muscle of similar nature may have had its origin on the dependent process of the jugal, its insertion on one or both of the mental processes, and may have served the purpose, first, of a cheek muscle to press the food between the teeth, or again to give the mandible the strong backward motion, referred to on a previous page, in the process of mastication.

There is the additional possibility that these lateral extensions from the face and jaws supported cheek pouches or ''muscular walls'' comparable to those ascribed to the Ceratopsia by Professor Lull,[4] for retaining large quantities of food within the mouth before it was ready to be swallowed.

The dependent process from the jugal arch, in all probability, gave origin to the masseter muscle which generally arises from the jugal and is inserted broadly on the wide angle of the ramus. From the tip of the process the fibres of the muscle might have given the forward, the backward, and even a sideward movement to the mandible, for, judging from the wear on the teeth and the form of the molars, there was a definite transverse motion.

The condyles of the ramus permitted an unusual freedom of movement to the jaws in nearly every direction, including the opening to a wide angle, but the various hypothetical muscles would have fortified against pulling the condyles out of the shallow glenoid cavity. In the enormously developed jugal of *M. zygomaticus* (fig. 15), it is important to notice that the process extends backward so that its outer, posterior edge almost parallels the border of the angle of the ramus. Whatever may have been the original purpose of this dependent process, it is evident that these animals profited by its use until it reached the enormous size shown in this species, probably the last of its race.

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[4] Lull, R. S., U. S. Geol. Survey, Mon. 49, p. 194, 1907.

TO BE CONTINUED.