Article VI.—A COMPLETE SKELETON OF CORYPHODON RADIANS. NOTES UPON THE LOCOMOTION OF THIS ANIMAL.

By HENRY FAIRFIELD OSBORN.

PLATE X.

The chief object of the writer in planning the American Museum Expedition of 1896 was to complete materials for the investigation of the evolution of the Amblypoda, and extend our knowledge of *Coryphodon*. The observations of Cope, Marsh, Osborn, Wortman and Earle have been principally upon scattered and imperfect material, and it seemed of the utmost importance to secure materials sufficient to determine the relations of this animal to its ancestral form, *Pantolambda*, and to its successive form, *Uintatherium*; also the proportions of the body, the positions of its limbs and the number of its vertebræ. Accordingly our party, led by Dr. Wortman, aided by Mr. Granger of the Museum, and Messrs. Brown and Riggs of the University of Kansas, spent the months of April and May in northwestern New Mexico, revisiting the locality where Cope's most complete *Coryphodon*, *C. elephantopus*, had been found. The search here in the 'Coryphodon' or 'Wasatch Beds' was entirely unsuccessful, but fortunately the underlying 'Torrejon Beds' yielded a remarkably complete series of *Pantolambda*. The party moved to the north in June, and devoted July and August to a most energetic exploration of the Big Horn Basin, especially of the exposures on the south side of the Gray Bull River from Brown's Ranch towards the Big Horn River below Otto.

The party soon discovered two skulls, both in the sandstone. The first (No. 2867), upon level A, with four vertebræ and some fragments of limb bones associated with it, the teeth being badly

weathered, has been mounted in our skeleton. The second (No. 2963) was found upon level B, 40 feet higher; it exhibits the form of the top and back of the skull, together with the complete teeth and palate. Shortly afterwards, upon the same level A as No. 2867, the skeleton (No. 2865) was discovered with fifteen ribs and vertebræ, the humerus, ulna, radius and two or three of the sternal bones. This was followed by the discovery on level A of the hind limb (No. 2869), several pairs of jaws, and finally, upon level B, the part of a crushed skeleton (No. 2829), including the skull, jaws, all the ribs and vertebræ in position. This, as Dr. Wortman wrote, made the party absolutely certain of a mount. The four skulls, Nos. 2827, 2867, 2963, 2865, with the associated skeletons, were thus found substantially upon the same geological level, they are in the same stage of evolution, and are found to belong to the classic species *C.* (*Bathmodon*) *radians* Cope, the first known in America.

The party then moved to the overlying Wind River Beds, and discovered a unique skull (No. 2977) of a distinct species, which reverses the natural order of evolution, since the sagittal crest is a little broader than one's finger. This exhibits the desired transition between *Pantolambda* and *Coryphodon*, and represents, in all probability, a persistent primitive type.

Altogether parts of 18 individuals were found in the Wasatch Beds (supplementing the 30 individuals found by Dr. Wortman in 1891), and 7 individuals in the Wind River Beds. The selection of nine individuals for mounting was done with great care as follows: The mounted skull, No. 2867, agrees exactly in size, and is specifically identical with the skull and jaws of No. 5829. The latter (No. 2829), while laterally crushed, had associated with it the right scapula and complete fore-limb, left scapula and parts of left limb which were used in mounting; also all the vertebræ as far back as the pelvis; these vertebræ, while too much crushed to mount, enabled us to determine the formula and select, from series Nos. 2865 and 2863, vertebræ which exhibit the same characters. The latter individual (No. 2863) included the pelvis and hind-limb, thus determining *positively the correct proportions of the entire animal.* The mounting was done with great skill and care by Mr. Hermann.

Description of Skeleton.

Composite of nine individuals, all from the Big Horn Beds, as follows: No. 2867; skull, left humerus, left mtc. I and ectocuneiform; caudals 1–3, 10–11. No. 2867, lower jaw. No. 2829; right scapula and fore-limb complete; left scapula, magnum, trapezium, trapezoid, metacarpals I–V and phalanges. No. 2865; all cervical vertebræ, dorsals and ribs 1–9 complete, 3 phalanges of right pes. No. 2963; dorsals 10–15 and ribs complete, lumbars 1–5 complete, pelvis, left pes (excepting mts. I, III–V, and ectocuneiform). No. 2869; right hind-limb complete (excepting mts. IV–V and 3 phalanges. No. 4329, left ulna, femur and tibia. No. 258; caudals 4, 5, 8. Sternals complete from No. 2825. *Restored:* left radius, left fibula, right mts. IV–V, left mts. III–V, caudals, 6, 7, 9, and 12–22.

In general one is struck by the very large size of the head, formidable front teeth, the shortness of the ribs, the heavy character of the girdles, the heavy limbs, and the semiplantigrade or subdigitigrade condition of the feet. It is probable, as already shown by the writer, that in the hind foot the calcaneum nearly touched the ground in the forward step.

The *skull* presents a very peculiar appearance with its powerful and spreading upper and lower canines, and widely spaced incisors, slender zygomatic arch and broad, flattened cranium. The following characters distinguish this specific type: Premaxillaries short, not reaching nasals; free portion of nasals short; nasals projecting between maxillaries, and then spreading upon inner side of frontal tuberosities; naso-frontal suture disappearing posteriorly; maxillaries occupying a broad area and bulging out opposite the canine alveoli and concave behind; lachrymals not clearly defined; frontals above the orbits supporting two prominent knobs or convexities, confluent with parietals posteriorly; parietals expanding above middle portion of temporal fossa, and lateral parietal crest thickening, as indicative of a rudimentary parietal horn; mid-parietal region depressed and extremely rugose for muscular attachment (*occipito-frontalis*); malars extending to the front of orbit, exhibiting a downward masseteric process slightly behind the orbit, expanding widely but slender in section; postglenoid processes for squamosal rather slender; external auditory meatus widely open, and paroccipital and posttympanic region compressed into a narrow ridge; occiput

low and broad; lower jaws with condyle facing upwards and backwards; prominent depression posteriorly; a mental foramen below first premolar, a second mental foramen below lower canine.

Dentition.—The superior teeth, wanting in this specimen, are perfectly preserved in No. 2829, and agree with the fragmentary type specimen of *Coryphodon* (*B.*) *radians* Cope.

Vertebral formula: C.7, D.15, L.5, S.4.

This remarkably low vertebral formula is ascertained from No. 2829, in which all the dorsals and lumbars are retained in a single block and can be counted with considerable certainty. The formula is very low, but not more so than in *Titanotherium*, in which D. L.=20. The chief characteristic of the vertebral column is the series of low, undifferentiated neural spines, which are ill correlated with the heavy skull.

Cervicals.—Atlas moderately broad with a slightly expanded transverse process, perforated slightly above the base by the vertebrarterial canal. The spine of the axis extends equally forwards and backwards. The remaining cervicals exhibit a gradual development of the inferior lamella, which is well marked in C.6, but lacks the strength exhibited in the larger Perissodactyla. The cervical centra are very short, and the vertebral centra gradually increase in length and depth toward the lumbar region.

The most striking feature of the *dorsal* vertebræ, which is shared by *Phenacodus*, is the great prominence of the transverse process supporting the tubercle of the ribs. This projects widely out from the side of the vertebra in D.1, and gradually recedes to D.11, which is apparently the last vertebra in which the rib tubercle articulates. In all the dorsals the head is placed directly between the adjacent vertebræ from D.1 to D.15. The low spines characteristic of the cervical region extend back as a feature of the dorsals, the vertebræ exhibiting terminal tuberosities for the fascia of the ligamentum nuchæ. The dorsal vertebral spines gradually thicken in antero-posterior diameter; as they pass backwards they decrease in height. In the lumbar region they are cleft on the dorsal line. The lumbars terminate inferiorly in compressed keels.

MEASUREMENTS OF SKELETON.

	FEET AND INCHES.	METERS.	
Length incisors to perpendicular of tail	7′ 9½″	2.38	
Height at withers	3 4½″	1.03	
Fore Limb :			
Scapula	1′ 5″	.43	
Humerus	1′ 3½″	.39	2′ 8½″
Radius	10″	.25	or
Manus, total	7″	.17	.82
Hind Limb :		.71	
Pelvis, transverse	2′ 4″		
Femur	1′ 6½″	.47	2′ 11½″
Tibia	11″	.28	or
Pes, total	6″	.15	.90

These measurements show that the tibia is only an inch longer than the radius, while the femur is three inches longer than the humerus.

The anterior pair of *ribs* is extremely short, the succeeding ribs increase in length and decrease in diameter, passing from a flattened into a trihedral form in D.6 and 7, and finally into an oval form in D.10–15. A characteristic feature of the ribs of D. 6-11 is a pit upon the upper surface just external to the tubercle.

The zygapophyses have horizontal faces as far back as D.15. In D.14 and 15 they turn obliquely upwards, the faces being vertically flattened. In L.1 to L.5 the zygapophyses are sharply concave and nearly vertical in position. The characters of the *caudals* are not certainly known, the few centra being restored from a number of different specimens. We have not ventured to give the tail the remarkably flattened character already described in a specimen found in 1892.

Fore Limb.—The scapula is vertically elongate, terminating in a point superiorly, and distinguished from that of *Uintatherium* by nearly subequal supraspinatus and infraspinatus fossæ. It is partly restored in the mount, but perfectly preserved in No. 2873. The spine rises near the superior border, is slightly thickened and reflected, and passes down into the acromion process, which turns sharply forwards and overhangs the great tuberosity of the

humerus. The humerus is distinguished by the prominent greater tuberosity, which enters inferiorly the prominent and recurved deltoid ridge, extending far down upon the anterior surface, two-thirds the length of the shaft. The characters of this bone are best seen in No. 2780, an animal of the same size.

The entepicondyle is a rugose tuberosity, the ectepicondyle is more elevated on the shaft, and is marked by an anteverted ridge. The forearm is perfectly preserved upon the right side. The radius covers the front face of the humerus, and the distal faces of the ulna and radius are placed obliquely to the transverse axis of the body, facing upwards and throwing the fore feet and toes outwards rather than forwards. In this specimen the cuneiform does not articulate with the fifth metapodial, as observed in certain other specimens. The manus, as above described, is subdigitigrade, the lower surfaces of the proximal ends of the metapodials being slightly raised above the ground. The position of the metapodials in the forward step is, however, much more oblique than in the manus of the Elephant, the lower surfaces being nearer the ground.

The *pelvis* is partly restored in this mount. Its characters are better shown in No. 258. The ilia expand widely, but the anteroinferior border is not extended very far down. The ischia and pubes are strongly developed, and enclose a wide obturator notch.

A very characteristic feature of the skeleton is the long and rather slender form of the femur and the disproportion between the femur and the tibia, which is much greater than that which exists between the humerus and the radius. The great trochanter does not rise to the level of the head. The third trochanter is a long rather low crest, much less strongly marked than in *Pantolambda*, placed on the upper third of the inner side of the shaft. The lesser trochanter is very prominent, and lies slightly below the middle of the shaft. The patella is a very characteristic bone, but there is some doubt as to its position; it appears probable that the slender pointed spine of the patella faces upwards, as the long patella facet is thus made to correspond with the long facet on the inner side of the front face of the trochlea of the femur. The tibia is a very stout bone with a rather low

cnemial crest, and rests by a slightly concave distal face upon the broad flat astragalus. The position of the pes is probably fairly represented in the left right foot, and although it is possible for the astragalus to be brought still nearer to the ground in the long forward step, it appears that in this type plantigradism is not so marked as has been stated by Osborn; probably the different species varied in this respect. As in the fore feet, the median digit faces outward. The astragalus has a well-marked astragalar foramen.

General Appearance of Coryphodon.

The most accurate forecast of the appearance of the animal was that made by Cope[1] in 1874:

"The general appearance of the Coryphodons, as determined by the skeleton, probably resembled the Bears more than any living animals, with the important exceptions that in their feet they were much like the Elephant. To the general proportions of the Bears must be added a tail of medium length. Whether they were covered with hair or not is, of course, uncertain; of their nearest living allies, the Elephants, some were hairy and others naked. The top of the head was doubtless naked posteriorly, and in old animals may have been only covered by a thin epidermis, as in the Crocodiles, thus presenting a rough, impenetrable front to antagonists.

"The movements of the Coryphodons, doubtless, resembled those of the Elephant in its shuffling and ambling gait, and may have been even more awkward, from the inflexibility of the ankle. But, in compensation for the probable lack of speed, these animals were most formidably armed with tusks. These weapons, particularly those of the upper jaw, are more robust than those of the Carnivora, and generally more elongate, and attrition preserved rather than diminished their acuteness. The size of the species varied from that of a Tapir to that of an Ox."

Osborn[2] in 1892 wrote as follows:

"The fact is, the position of the fore and hind feet of Coryphodon is absolutely different. The *fore foot was digitigrade*, like that of the Elephant, the *hind foot was plantigrade*, like that of the Bear. In other words, the carpus was entirely raised from the ground and the manus rested upon the distal ends of the metacarpals and upon the spreading phalanges, while the calcaneum

[1] Vertebrate Palæontology, Vol. IV, Wheeler Survey, p. 203.
[2] Fossil Mammals, of the Wasatch and Wind River Beds, Collection of 1891, Osborn and Wortman, Bull. Am. Mus. Nat. Hist., Sept., 1892, p. 121.

and tarsus rested directly on the ground together with the entire plantar surface of the foot. This substantial difference between the advanced state of evolution of the fore foot and retarded evolution of the hind foot, is of great interest. It is clearly shown in the accompanying figures."

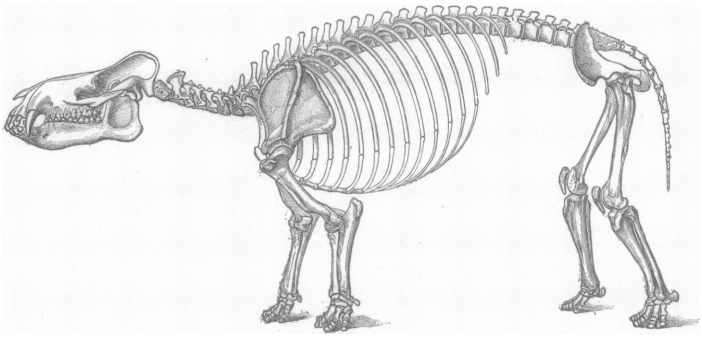


Fig. 1. *Coryphodon hamatus*, as restored by Marsh, 1893. One-twentieth natural size.

In 1893, Marsh,[1] in his description and restoration, presented quite a different conception of the animal as *unguligrade*. In regard to these matters he makes the following statement :

" This restoration is given one-twelfth natural size. The position shown was chosen after careful consideration, and is believed to represent fairly one naturally assumed by the animal in life when standing at rest. The figure represents a fully adult individual, and one of the largest species of the genus which, when alive, was nearly six feet in length and about three feet in height. The basis of this restoration is the type specimen of *Coryphodon hamatus*. This was supplemented by other remains, which appeared to be superficially identical. A large number of such specimens were available, some of them in excellent preservation. For parts of the skeleton where such remains were wanting specimens from nearly allied forms were used, but no serious error can thus result.... The fore feet presented in the present restoration are constructed mainly from the same specimen (that first figured and described by the writer), and the position given in the original figure has been essentially retained.... The position first given to the figure is retained in the restoration after a careful investigation of the whole posterior limbs in a number of well-preserved specimens. In *Dinoceras* the terminal

[1] ' Restoration of Coryphodon,' Amer. Journ. Science, Oct., 1893, p. 324.

phalanges are much larger than in the Elephant, so that they thus bore a greater weight, the digit being undoubtedly free, although a pad may have helped to support the feet. In *Coryphodon* the digits were still more elongate and the terminal phalanges proportionately larger and broader, indicating that they

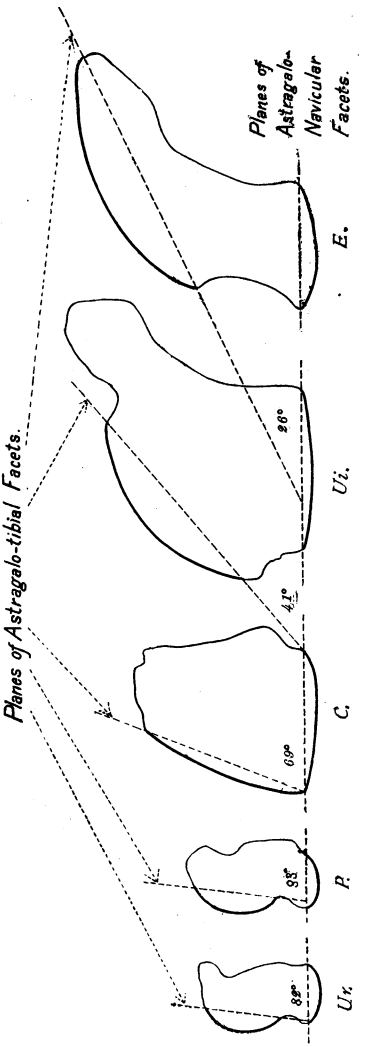


Fig. 2. Diagrams showing the *Angles* between the *Astragalo-tibial* and *Astragalo-navicular* facets, obtained by vertical sections of the Astragalus. *Ur.*, URSUS, plantigrade; angle, 82°. *P.*, PANTOLAMBDA, plantigrade; angle, 83°. *C.*, CORYPHODON, transitional; angle, 69°. *Ui.*, UINTATHERIUM, subdigitigrade; angle, 41°. *E.*, ELEPHAS, digitigrade; angle, 26°.

were covered with hoofs that supported the feet. This would agree with the position given them in the restoration, which coincides with the anatomical structure of the entire hind limb."

This clear statement of Professor Marsh's as to the position of these limbs is consistent with his restoration, in which not only the metapodials but the phalanges are raised from the ground, and the animal is represented as walking upon the tips of its toes, or terminal phalanges, the latter being supported by hoofs. The morphological importance of this restoration is very great. If correct it places *Coryphodon* among the Unguligrada, widely removed from the unquestionably plantigrade *Pantolambda*. Contrary evidence that *Coryphodon*, so far from being unguligrade, was transitional between complete *plantigradism* and *digitigradism*, is given below. Many other important morphological characters are involved in Marsh's restoration, and are now found to be incorrect. The scapula is given a trihedral form, with a very broad angular infraspinatus fossa; the pelvis is extraordinarily reduced; the limbs are elongate and, together with the above-mentioned unguligrade action of the digits, elevated the body very much from the ground. In proportion to the scapula, the humerus, the ulna and the radius are of very great length, and similarly the tibia is only slightly shorter than the femur. The most important character, however, is that assigned to the vertebral column, there being 19 dorsals and, as far as can be determined from the drawing, 6 lumbars, or D. L.=25, a formula exceeding that of the Rhinoceros. The net result of these observations is to give the animal the general appearance and characters of a modern Perissodactyl,[1] with the single important exception of the five digits preserved in the fore and hind feet.

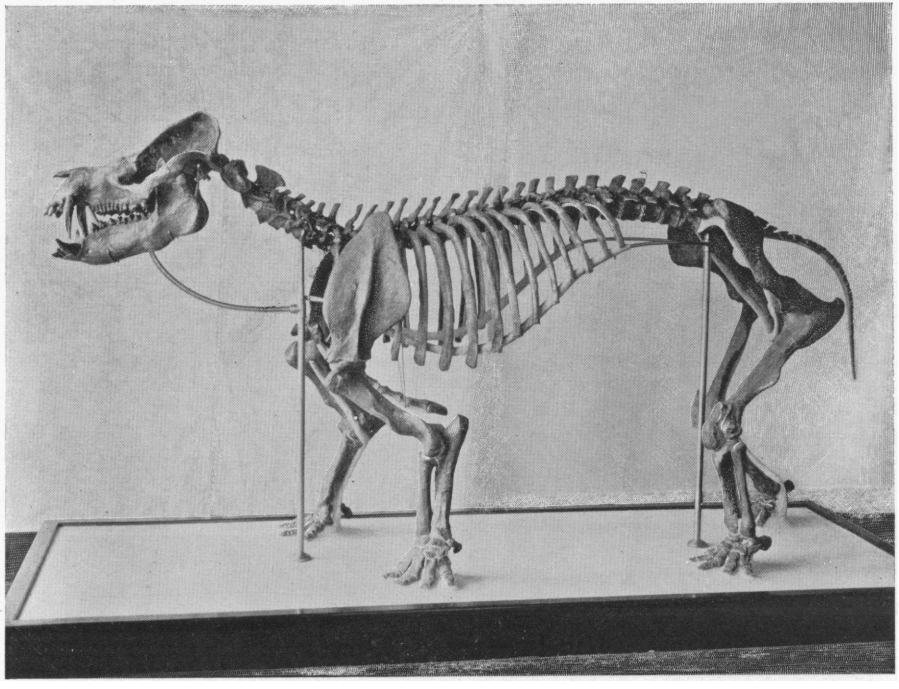
It appears from our more complete material that the difference between the feet was exaggerated by Osborn, as already observed by Marsh. There is no doubt, however, that as seen in the mounted specimen, in the forward step the calcaneum rested very near the ground, being separated merely by a thick plantar pad. The digits of the fore and hind feet have nearly the same relations to the ground. *Both feet are in a somewhat similar stage of tran-*

[1] The Perissodactyl affinities of the animal were dwelt upon in Professor Marsh's earlier papers (Am. Jour. Sc., 1876, page 428; *op. cit.*, 1877, page 84), but were abandoned subsequently ('Dinocerata,' 1884, page 177), in which *Coryphodon* was correctly associated with *Uintatherium* in the Amblydactyla (Amblypoda).

sition between plantigradism and digitigradism. *Pantolambda* has a long tuber-calcis and pes like that of the Bear. *Uintatherium* has a very short tuber-calcis and bore the pes slightly more plantigrade than the Elephant. *Coryphodon* has a tuber-calcis intermediate in length ; in the astragalus the upper facet for the tibia and lower facet for the navicular presents an oblique angle, the astragalus thinning out to a sharp edge in front (whereas in *Uintatherium* these facets are more nearly parallel, and the astragalus is truncate in front). The angles between the tibial and navicular facets of the astragalus, as shown in sections in Fig. 2, afford the most decisive evidence that the pes of *Coryphodon* was intermediate between the nearly plantigrade *Pantolambda* and the sub-digitigrade *Uintatherium.*

Coryphodon had a very short back and short, spreading limbs, with a very clumsy, shuffling gait.

The rudimentary horn observed for the first time in the parietals is prophetic of the great parietal horn of *Uintatherium.* Many other characters of the skull and skeleton are also prophetic, but there is little tendency displayed to reduce the upper incisors or lower canines into the Uintathere type.



MOUNTED SKELETON OF *Coryphodon radians*.
Slightly exceeding one-fifteenth natural size.