

Article XI. — EVOLUTION OF THE AMBLYPODA.
PART I. TALIGRADA AND PANTODONTA.

By HENRY FAIRFIELD OSBORN.

TWENTY-NINE TEXT FIGURES.

The Amblypoda constitute a sharply distinguished order of Ungulates which probably sprang from the Creodonta during the Cretaceous period and extended through the Eocene period in three great stages of evolution known as the suborders Taligrada, Pantodonta and Dinocerata, the latter entirely confined to North America.

They are arrested or persistently archaic in structure throughout, but especially in the brain, the triangular teeth, and the pentadactyl feet. The morphological problems involved in the skeleton and teeth, and the phylogenetic problems involved in the succession and extinction of the main and collateral lines, form the main subjects of this essay.

The American Museum has sent out a series of expeditions after remains of the Amblypoda: First, into the Wasatch of Wyoming, 1891; second, into the Bridger and Washakie Basins, 1893 and 1895; third, into the Torrejon, 1892 and 1896; fourth, into the Wasatch of New Mexico, and Big Horn Mountains of Wyoming, 1896. We have thus succeeded in bringing together invaluable material for the history of this remarkable group from the time it issued in the Creodont-like *Pantolambda*, of the Torrejon Beds until it became extinct in the largest Uintatheres of the Upper Washakie and Middle Uinta Beds.

Several very important results are obtained:

First.—The evidence can be clearly stated as to the succession of the known types of Pantolambdidae, Coryphodontidae and Uintatheridae. Many prophetic or ordinal characters are now observed in the earliest types; certain species of *Coryphodon* are found to show the rudimentary parietal horns and the incisiform

lower canines of the Uintatheres, but no known species leads directly into *Uintatherium*.

Second.—It is now demonstrable that the Periptychidæ belong in this group as a *bunodont division*, which probably arose and diverged in the Cretaceous period.

Third.—The nearly complete skeleton of *Pantolambda bathmodon*, the most archaic type of Ungulate known, places almost upon the firm basis of fact Cope's hypothesis, that the Ungulates sprang from the Creodont division of the Unguiculates.

Fourth.—A fairly complete systematic revision of the entire group is rendered possible.

The writer desires to express at the outset his indebtedness to Dr. J. L. Wortman for his energetic and intelligent supervision in the field of these various expeditions, assisted by Mr. Walter Granger, Mr. Barnum Brown and others; to Dr. W. D. Matthew for the skill and care with which the very fragmentary skeletons of *Pantolambda* have been put together, and for critical assistance in the diagnosis of specific types. Also to the various preparators and draughtsmen of the department.

I.—ORIGIN OF THE AMBLYPODA.

A. THE CRETACEOUS TRITUBERCULATE MOLAR.

Hypothetical Upper Cretaceous Ancestors.—In describing the Laramie mammals in 1893 the writer¹ directed attention to the resemblance which certain isolated upper and lower molars bore to the teeth of the Periptychidæ, especially to *Ectoconus* and *Haploconus*. The figures of these teeth are here reproduced.

In *C* (*Synconodon*), the crowns are laterally compressed, thus bringing the primary proto-, para- and metacones, both of the trigon and trigonid, very close together. This compression of the primary cones is also true of *F* (*Ectoconodon*), in which type the outer wall is reinforced as in *Ectoconus* by accessory tubercles.

¹ Osborn, 'Upper Cretaceous Mammals,' Bull. Am. Mus. Nat. Hist., Vol. V, pp. 325-329.

This compression is an essential character of the Periptychidæ. The upper and lower molars of *Protolambda*, *Hl*, *A* and *Al*, on the other hand, resemble those of the Pantolambdidae.

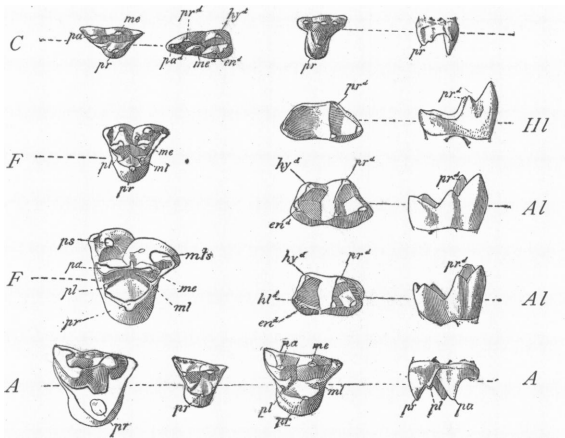


Fig. 1. LARAMIE TRITUBERCULATES.

C. Synconodon sexicuspis. Upper and lower molar types. Nos. 2218, 2220. Am. Mus. Coll.

F. Ectoconodon petersoni. Upper molar types. Nos. 2224, 2223. Am. Mus. Coll.

A. Protolambda hatcheri. Upper molar types. Nos. 2201-3. Am. Mus. Coll.

Lower molars *Hl*, *Al* (possibly correlated), Nos. 2241, 2230, 2231. Am. Mus. Coll.

These types may now be defined as follows :

Synconodon, gen. nov.

Type.—Isolated upper and lower molars. Am. Mus. Coll., Nos. 2218, 2220.

Definition.—Molars long and narrow. Trigons laterally compressed, primary cones approximated. Talonid well developed.

S. sexicuspis, sp. nov.

Definition.—Talonid of lower molars with three cusps, hypoconid, hypoconulid, entoconid. Type as above. Fig. 1, *C*.

Ectoconodon, gen. nov.

Type.—Isolated superior molars. Loc., Laramie. Am. Mus. Coll., Nos. 2223, 2224.

Definition.—Superior molars very broad. Trigon laterally compressed. Two external prominent cones (parastyle and metastyle), reinforcing the outer wall of the crown.

E. petersoni, sp. nov.

Superior molars with conules and a rudimentary mesostyle. Type as above. Fig. 1, *F*.

Protolambda,¹ gen. nov.

Type.—Four isolated upper molars. Loc., Laramie. Am. Mus. Coll., Nos. 2201-3.

Definition.—Superior molars with open trigon and elongate outer wall. Paracone and metacone laterally compressed. Conules subrescenscent. Parastyle prominent.

P. hatcheri,² sp. nov.

With rudimentary spur, metastyle on posterior external border.

Type, as above. Fig. 1, A.

The lower molars III and AI, in Fig. 1, probably are associated with this type.

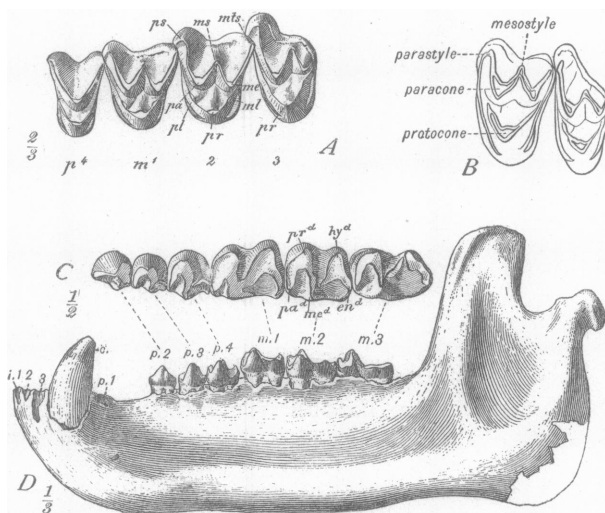


Fig. 2. *Pantolambda cavirictus*. A, superior molars, No. 963; B, diagram of same; C, inferior molars, crown view, No. 3961; D, lower jaw, type of *P. cavirictus*. Am. Mus. Coll.

These types are quite distinct from the trituberculates described by Marsh³ from the Laramie, namely, *Didelphops*, *Cimolestes*, *Pedomys*, *Telacodon*, *Batodon*, so far as these are known.

These animals are defined and placed here *hypothetically* merely to show that *in the Upper Cretaceous are found types of upper and lower teeth capable of giving origin to the teeth of the Amblypoda*.

¹ Having a type of tooth antecedent to that of *Pantolambda*.

² Dedicated to Mr. J. B. Hatcher, the well-known writer and explorer.

³ Discovery of Cretaceous Mammalia, Pts. I, II, III, Am. Jour. Sci., July, 1889, to Mch., 1892.

EVOLUTION OF THE MOLARS IN THE AMBLYPODA.

The upper and lower molars of the Periptychidæ are purely bunodont, characterized by a compressed trigon, the development of accessory external cusps, and crescentic internal cusps upon the superior premolars. The latter recall the teeth of *Pantolambda*. *Ectoconus* is the only type in which the lower premolars tend to become molariform.

The *Pantolambda* superior molar (Fig. 2 *A*) shows a crescentic disposition of the three primary cones, which are, however, closely approximated as in the Periptychidæ, the outer wall of the crown extending widely into the parastyle. The lower molar shows a lofty trigon distinguished by the marked elevation of the metaconid, and a talonid best shown in Fig. 2 *D*. No true hypoconulid is developed. From the entoconid a spur extends forwards and inwards, to which the designation 'entoconid 2' may be given, as seen in Fig. 3. This little cusp becomes a very important feature of the crown in *Bathyopsis* and *Uintatherium*.

The *Coryphodon* superior molar (Fig. 4), as homologized by Cope, Earle and the writer, exhibits a protoloph and an ectoloph consisting of a greatly reduced paracone, a vestigial mesostyle and strongly crescentic metacone. In the last superior molar these ectoloph elements are transformed into a single oblique lophoid crest. The inferior *Coryphodon* molar (Fig. 3) shows a greatly elevated protoconid, an enlarged metaconid and depressed paraconid. The talonid consists of a hypoconid, entoconid and a low spur, the entoconid 2, prophesied in *Pantolambda*.

From this, the *Bathyopsis* and *Uintatherium* lower molar is readily derived, as shown in Fig. 3, simply by the fission of the metaconid into the metastylid, *mld*, and further reduction of the paraconid and entoconid 2. This fission is an ad-

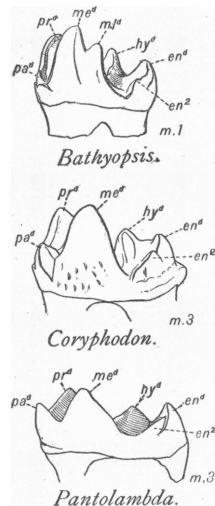


Fig. 3. Lower molars, Amblypoda. Diagrams showing evolution of crown. Not to scale.

pld protoconid; *pad* paraconid; *me* metaconid; *mld* metastylid; *hy* hypoconid; *en* entoconid; *en.2* entoconid 2.

ditional analogy with the Horse molar to those which the writer has already pointed out.

The superior molar of *Bathyopsis* is unknown. That of *Uintatherium* probably represents, as Cope supposed,

the ectoloph swung around so as to form with the protoloph a V opening outwards. Just internal to the apex of the V the hypococone is often developed.

We thus observe a set of profound changes resulting finally in the unique lophodont crown of *Uintatherium*.

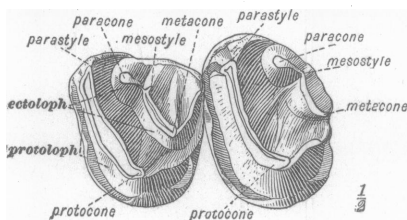


Fig. 4. Upper molars of *Coryphodon testis*, showing primary and secondary elements. Am. Mus. Coll., No. 274.

B. EVOLUTION OF THE UNGULATE FOOT FROM THE CREODONT TYPE.

Cope's famous generalization as to the serial character of the primitive ungulate foot, supported and extended by Osborn, has been recently disputed by Matthew (1897, p. 320) upon the very strong ground that most of the earliest, *i. e.*, basal Eocene, feet are non-serial or displaced; so far as known, both the Creodont carpus and tarsus are certainly non-serial. Cope's generalization

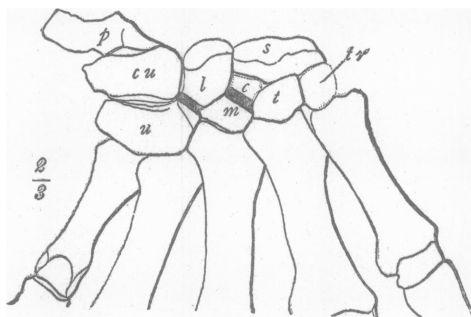


Fig. 5. Creodont carpus (*Dissacus carnifex*), heavy lines showing hypothetical protungulate displacement.

therefore appears to be non-consistent with his own theory that the Ungulates sprang from Creodonts.

The evidence *as to the earliest types* stands thus :

	<i>Creodonta.</i>	<i>Amblypoda.</i>	<i>Condylarthra.</i>	<i>Meniscotherium.</i>
Carpus	Non-serial.	Non-serial.	Non-serial.	Non-serial.
Tarsus	Non-serial.	Non-serial.	Serial.	Serial.

Carpus.—Matthew's conclusion is important as concentrating our attention upon the *interlocking* or *alternating* (lunar on unciform, scapho-centrale on magnum) carpus of such a Creodont type as *Dissacus* (Fig. 5), from which the *carpus* of the *Amblypoda* and *Condylarthra*, and probably of all Ungulata, may be derived.

The manner in which this was probably effected is :

<i>Amblypoda.</i>	<i>Condylarthra.</i>
Absorption or coalescence of centrale.	Absorption or coalescence of centrale.
Lunar remaining on unciform.	Magnum greatly enlarged and spreading beneath lunar, which is thus separated from unciform.
Magnum somewhat enlarged.	

The *enlargement of the magnum*, as observed in both *Amblypoda* and *Condylarthra*, would tend to *readjust* the primitive Creodont interlocking or displaced arrangement, and, especially where the weight is concentrated on the median toes, give us the *secondarily serial Phenacodus* type.

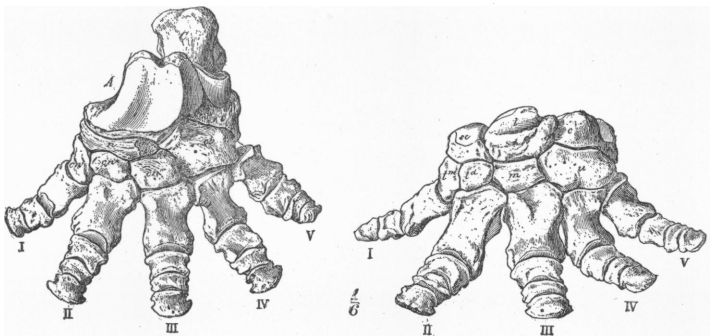


Fig. 6. Pes and Manus of *Coryphodon testis*, viewed from above, showing enlarged magnum. Am. Mus. Coll., No. 258.

Tarsus.—In the tarsus the case is different; while the non-serial Amblypod (*Pantolambda*) tarsus can be directly derived from the Creodont, the serial Condylarth tarsus probably arose from an unknown serial Creodont. Hence a double or parallel derivation of the two-hoofed orders, as follows:

<i>Protungulate</i>	Persistent atypical displacement in	Carpus secondarily serial. Tarsus persistently serial.	Carpus and tarsus typically displaced.
<i>Creodonta.</i>	carpus and tarsus.		
Tarsus interlocking, } <i>Amblypoda.</i>		
Carpus interlocking. }	} <i>Condylarthra</i> <i>Diplarthra.</i>		
Tarsus serial.			

Other characters of the primitive foot are given in the following synopsis, also upon pages 184, 187, 188, 216 of this Bulletin:

2.—SYNOPSIS OF THE EVOLUTION OF THE AMBLY- PODA.

The subjoined table brings out the three important laws of phylogeny as applied to taxonomy:

First.—The *persistent primitive* characters (*P.p.*) are also the *ordinal characters*, which serve to separate this phylum from the Condylarthra, Proboscidea, Hyracoidea, Diplarthra and other ungulate orders.

Second.—The *primitive* (*Pr.*) *progressive*, (*Pg.*) and *retrogressive* characters (*Re.*) constitute the *subordinal characters*.

Third.—Among the above characters are innumerable characters both in skull, limb and foot structure in which the Amblypoda *parallel* certain Perissodactyla, Artiodactyla and Proboscidea. The latter are mainly approached in the adaptations to great body weight, which first misled Cope to place this group with the Proboscideans.

Primitive [*Pr.*], Persistent primitive [*P.p.*], Progressive [*Pg.*] and Retrogressive [*Re.*] Characters.

	<i>Taligrada.</i>	<i>Pantodonta.</i>	<i>Dinocerata.</i>
SKULL.	<p><i>P.p.</i> Brain small, olfactory lobes large, hemispheres smooth, cerebellum exposed.</p> <p><i>Pr.</i> No air cavities. Sagittal crest. Frontoparietal sutures open.</p> <p><i>P.p.</i> Anterior nares terminal.</p> <p><i>Pr.</i> Premaxillæ separate, reaching nasals.</p> <p><i>Pr.</i> Maxillaries smooth.</p> <p>Frontals smooth.</p> <p><i>Pr.</i> Parietals smooth.</p> <p><i>Pr.</i> Nasals smooth, extending between orbits.</p> <p><i>P.p.</i> Mastoid (periotic) widely exposed, perforate, bordering auditory meatus.</p> <p><i>Pr.</i> No alisphenoid canal.</p> <p><i>P.p.</i> Zygomatic arches slender.</p> <p><i>Pr.</i> Mandibular condyle elevated, facing upwards.</p>	<p>The same.</p> <p><i>Pg.</i> Extensive air cavities. Cranium flattened. Frontoparietal sutures closed.</p> <p>The same.</p> <p>Premaxillæ grooved above, separate, not reaching nasals.</p> <p>The same.</p> <p><i>Pg.</i> Frontals with supraorbital knobs.</p> <p><i>Pg.</i> Rudimentary parietal horns.</p> <p>The same, shortened, extending between orbits.</p> <p>The same, much compressed.</p> <p>The same.</p> <p>The same.</p> <p>Condyle elevated, facing obliquely.</p>	<p>The same.</p> <p>The same.</p> <p>The same.</p> <p><i>Re.</i> Premaxillæ divergent, edentulous, reaching nasals.</p> <p><i>Pg.</i> Maxillaries with horns.</p> <p>The same.</p> <p>Large parietal horns.</p> <p><i>Pr.</i> Nasals with rudimentary horns; reduced in length.</p> <p>The same, widely exposed and perforate, bordering auditory meatus.</p> <p><i>Pg.</i> An alisphenoid canal.</p> <p>The same.</p> <p><i>Pg.</i> Condyle depressed, facing backwards.</p>
DENTITION.	<p><i>Pg.</i> Molars triangular (tritubercular), selenodont.</p> <p><i>Pr.</i> Paracone complete.</p> <p>Superior premolars composed of two crescents, unlike molars.</p> <p><i>Pr.</i> Superior incisors present.</p> <p><i>Pr.</i> Canines round, normal.</p>	<p>Molars triangular, selenolophodont.</p> <p><i>Pg.</i> Paracone reduced.</p> <p>The same.</p> <p>The same present.</p> <p><i>Pg.</i> Canines round, trihedral, or compressed, enlarged.</p> <p>The same.</p>	<p>Molars triangular, lophodont.</p> <p><i>Re.</i> Paracone wanting.</p> <p>Superior premolars submolariform.</p> <p><i>Re.</i> The same absent, or vestigial.</p> <p><i>Pg.</i> Superior canines lance-shaped. Inferior, incisiform.</p> <p>The same.</p>
VERTEBRÆ.	<p><i>Pr.</i> Cervicals short, dorsals and lumbers with short spines.</p>	<p>The same.</p>	<p>The same.</p>

	<i>Taligrada.</i> <i>Continued.</i>	<i>Pantodonta.</i> <i>Continued.</i>	<i>Dinocerata.</i> <i>Continued.</i>
VERTEBRÆ.	<i>Pr.</i> D. L. — ?. Sacrales unknown.	<i>Pr.</i> D.=15, L.=5. Sacrales unknown.	D. L.=? Sacrales = 4.
RIBS.	<i>Pr.</i> Very short.	The same.	The same.
ARCHES.	<i>Pr.</i> Scapula acuminate, fossæ subequal. <i>Pr.</i> Ilium acuminate.	<i>Pg.</i> The same, infraspinatus fossæ somewhat enlarged. <i>Pg.</i> Ilium, border expanded.	<i>Pg.</i> Scapula triangular; infraspinatus fossæ greatly enlarged. The same.
FORE-LIMB.	<i>Pr.</i> Bent outwards at elbow : manus everted.	The same.	<i>Pg.</i> Straight, or vertical at elbow.
HUMERUS.	<i>Pr.</i> An entepicondylar foramen. <i>Pr.</i> Prominent deltoid and ectepicondylar (supinator) crests.	<i>Pg.</i> No entepicondylar foramen. <i>Pg.</i> Entepicondyle somewhat reduced.	The same. The same.
RADIUS AND ULNA.	<i>Pr.</i> Subequal. <i>Pr.</i> Ulna, posterior border convex.	The same. <i>Pg.</i> The same, concave.	The same. The same, concave.
CARPUS.	<i>Pr.</i> Lunar resting upon cuneiform. <i>Pr.</i> An os centrale. <i>Pr.</i> Magnum small. <i>Pr.</i> Plantigrade.	The same. <i>Pg.</i> Os centrale united. <i>Pg.</i> Magnum larger. <i>Pg.</i> Sub-digitigrade.	The same. The same. The same. Digitigrade.
FEMUR.	<i>Pr.</i> Prominent third trochanter.	<i>Re.</i> Reduced third trochanter.	No third trochanter.
TIBIA.	<i>Pp.</i> Rudimentary spine and cnemial crest. Femoral facets, approximate.	The same. The same, approximate.	The same. The same, confluent.
FIBULA.	<i>Pr.</i> Articulating with calcaneum.	The same.	<i>Pg.</i> Not articulating with calcaneum.
TARSUS.	<i>Pr.</i> A tibiale. <i>Pr.</i> Mesocuneiform small. <i>Pr.</i> Astragalus with neck.	<i>Pg.</i> A tibiale, variable. <i>Pg.</i> The same, enlarged. <i>Pg.</i> Astragalus without neck.	A tibiale, variable. The same, enlarged. The same.

	<i>Taligrada.</i> <i>Continued.</i>	<i>Pantodonta.</i> <i>Continued.</i>	<i>Dinocerata.</i> <i>Continued.</i>
TARSUS.	<p><i>P.p.</i> Astragalar foramen.</p> <p><i>Pr.</i> An astragalo-cuboidal facet.</p> <p><i>Pr.</i> Astragalo-tibial facet very limited and facing obliquely outwards.</p> <p><i>Pr.</i> A calcaneo-fibular facet.</p> <p><i>Pr.</i> Mts. V. curved with prominent 'peroneus brevis' process.</p> <p><i>Pr.</i> Plantigrade.</p>	<p>The same, variable.</p> <p>The same.</p> <p><i>Pg.</i> The same, extended, horizontal, approaching astragalo-navicular facet anteriorly.</p> <p>The same.</p> <p><i>Pg.</i> The same straight, process reduced.</p> <p><i>Pg.</i> Subdigitigrade.</p>	<p>The same, variable.</p> <p>The same.</p> <p><i>Pg.</i> The same, extended, horizontal, separated from astragalo-navicular facet anteriorly.</p> <p><i>Pg.</i> No calcaneo-fibular facet.</p> <p>The same, straight; process vestigial.</p> <p><i>Pg.</i> Digitigrade.</p>
FEET.	<i>Pr.</i> Pentadactyle and isodactyle.	The same.	The same.

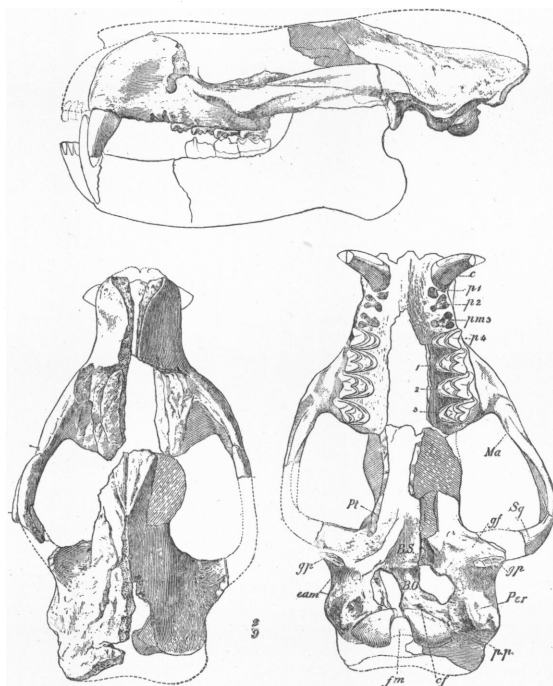


Fig. 7. *Pantolambda cavirictus*. Cotype. Lateral, inferior and superior views of cranium. Am. Mus. Coll., No. 963.

3.—SYSTEMATIC REVISION.

Order AMBLYPODA *Cope*.

Most primitive order of Ungulates known. *Brain* very small, with smooth cerebral hemispheres, large olfactory lobes and exposed cerebellum. *Dentition* brachyodont: Superior molars triangular (tritubercular, bunodont, selenodont, lophodont), rarely with functional hypocone. *Feet* pentadactyl, isodactyl; plantigrade (as in Bear) to subdigitigrade (as in Elephant). *Displacement* in carpus (unlike Diplarthra); lunar resting on unciform only; in tarsus (like Diplarthra), astragalus resting on cuboid. A tibiale tarsi. Astragalus perforated or grooved.

The three suborders are very widely separated.

SUBORDINAL CHARACTERS.

<i>Taligrada</i> Cope.	<i>Pantodonta</i> Cope.	<i>Dinocerata</i> Marsh.
<i>Dentition.</i>		
Typical Eutherian formula.	The same.	No superior incisors.
Molars tritubercular selenodont.	Lopho-selenodont.	Lophodont.
Premolars simple, with two crescents.	Premolars simple, two crescents.	Premolars submolariform.
<i>Skull.</i>		
Nasals, frontals and parietals smooth. A sagittal crest. No alisphenoid canal; no air cavities.	Rudimentary parietal horns. Cranium flattened. No alisphenoid canal. Air cavities.	Nasal, maxillary and parietal horns. Cranium flattened. An alisphenoid canal. Air cavities.
<i>Limbs.</i>		
Plantigrade. An entepicondylar foramen. A 3d trochanter. An os-centrale. Fibula articulating with calcaneum. Astragalus with neck.	Semi-plantigrade. No entepicondylar foramen. A 3d trochanter. No os-centrale. Fibula articulating with calcaneum. Astragalus without neck.	Sub-digitigrade. Entepicondylar foramen. A 3d trochanter. Os-centrale wanting. Fibula not articulating with calcaneum. Astragalus without neck.

Suborder TALIGRADA *Cope.*

Family PERIPTYCHIDÆ *Cope.*

Molars bunodont, primitive triangle compressed in superior molars; secondary internal cusps developed (protostyle and hypocone). Lower molars with hypoconulid. Third and fourth upper and lower premolars enlarged.

Family PANTOLAMBIDIDÆ¹ *Cope.*

Molars selenodont, primitive triangle less compressed. Lower molars without hypoconulid. No secondary internal cusps.

Family PERIPTYCHIDÆ *Cope.*

In 1892 (op. cit., p. 47) Osborn pointed out that *Periptychus* is distinguished from the order Condylarthra (in which it had been placed by Cope) first, because the *tarsus is not serial*, there being a displacement of the astragalus upon the cuboid; second,

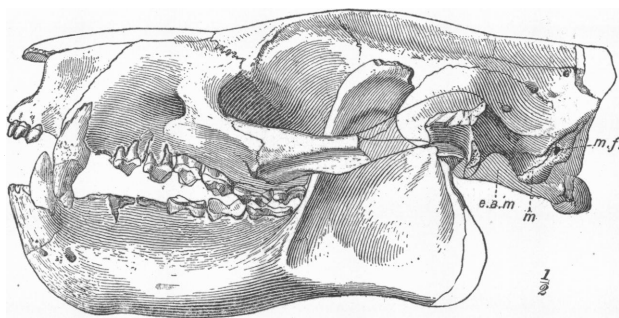


Fig 8. *Pantolambda bathmodon*. Lateral view of skull, showing wide exposure of mastoid. Composition of Nos. 2550 and 2549, Am. Mus. Coll.

because it has the *strictly trigonal molar* of the Amblypoda. In 1897² Cope adopted this view and removed the Periptychidæ to the Amblypoda. The close comparison of *Pantolambda* and *Periptychus* given below fully confirms this step. The condition of the upper premolars as composed of two crescents and (unlike

¹ See Osborn and Earle, 1892, p. 49.

² Am. Nat., 1897, p. 335. Matthew has, however, retained the Periptychidæ in the Condylarthra.

the Condylarthra) with little or no tendency to acquire the molar pattern, is essentially similar in the two families.

Subfamily ANISONCHINÆ *O.&E.*

Smaller forms. ? Arboreal.
Superior molars with conules suppressed or wanting. Paraconid reduced or wanting. Astragalus short and wide,¹ with deeper trochlea.

Subfamily PERIPTYCHINÆ *O.&E.*

Larger forms. ? Terrestrial.
Superior molars well developed. Paraconid strong. Astragalus with shallower trochlea.²

The genera and species of Periptychidæ, as recently revised by Matthew,³ are given in the following geological table.

	Cretaceous.	Basal Eocene.		Lower Eocene.			Middle Eocene.			
	Laramie.	Puerco.	Torrejon.	Wasatch.			Wind River.	Bridger.		
				Lower.	Middle	Upper.		Bridger.	Washakie.	Uinta, A and B.
UINTATHERIIDÆ								×	×	×
BATHYOPSIDÆ							×			
CORYPHODONTIDÆ				×	×	×	×			
PANTOLAMBIDÆ.										
Pantolambda cavirocketus			×							
“ bathmodon			×							
PERIPTYCHIDÆ.										
Ectoconus ditrigonus		×								
Periptychus rhabdodon			×							
“ carinidens			×							
“ coarctatus		×								
Conacodon entoconus		×								
“ cophater		×								
Haploconus lineatus			×							
“ corniculatus			×							
Anisonchus sectorius			×							
“ gillianus		×								
Hemithlæus kowalevskianus		×								
INCERTÆ SEDIS.										
Ectoconodon		×								
Synconodon		×								
Protolambda		×								

¹ Matthew, Bull. Am. Mus. Nat. Hist., 1897, p. 297.² Op. cit., p. 265.

Family PANTOLAMBIDIDÆ Cope.

Genus *Pantolambda* Cope.

Dentition typical. First upper premolar one-rooted. Second, third and fourth three-rooted, with internal cones. Canines rounded.

P. bathmodon.

Type: Mandibular ramus, No. 3956.
Smaller size. Both dental series continuous.

P. caviroctus.

Type: Jaw, No. 3961.
Larger size. First lower premolar close to canine and separated from second by a wide diastema. Premolars reduced in size.

*P. caviroctus*¹ Cope.

The type lower jaw, described and figured by Cope (Am. Nat., Vol. XVIII, p. 1111) is peculiar in the close apposition of the first lower premolar to the canine, and the wide diastema behind it. This is the largest type known and the diastema is probably prophetic of the diastema invariably observed in *Coryphodon*, (Fig. 2).

The skull (Fig. 7) was mistakenly described by Osborn and Earle in 1895 (1895,² p. 43) as *P. bathmodon*. It differs in its much greater size from *P. bathmodon*, and in the absence of diastemata from the *P. caviroctus* jaw. Unlike *Coryphodon* the upper canines are mainly worn upon the inner posterior surface.

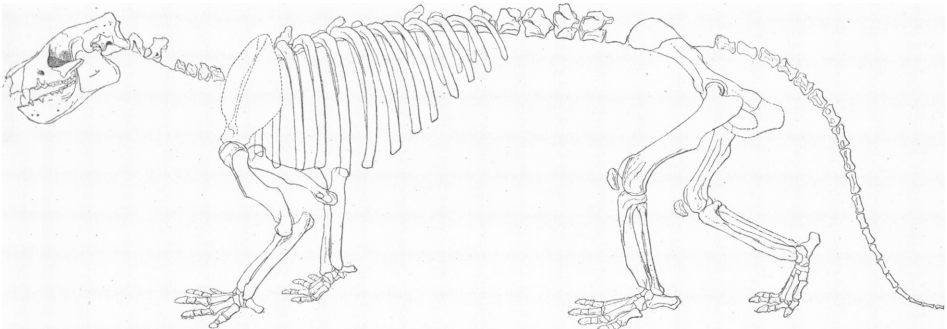


Fig. 9. Skeleton of *Pantolambda bathmodon*. Scapula wholly, pelvis partly restored. Composition from several individuals. One-eighth natural size.

¹ Am. Nat., Vol. XVII, 1883, p. 968.

² Am. Nat., Vol. XVI, 1882, p. 418.

***P. bathmodon*¹ Cope.**

The composition skeleton of *P. bathmodon* measures 2 feet 9 inches (830 mm.) from the premaxillaries to the back of the ischiac symphysis, and 1 foot 1¾ inches at the withers. It is thus about the size and proportions of a large Wolverine (*Gulo luscus*).

Excepting in the selenodont teeth, it typifies the *hypothetical Protungulate*, being more primitive than either *Euprotogonia* or *Phenacodus*. The step is that of the Bear, the feet very broad and spreading, the wrist and ankle being slightly raised off the ground, and the phalanges terminating in hoofs.

The vertebræ preserved (Nos. 2549, 2551) indicate a short neck (C. 6 = 10 mm.) as in *Periptychus*, and a back increasing in strength and power as we pass towards the lumbar region. Thus the dorsals are short anteriorly (D. 5 = 15 mm., No. 2549) and indicate less separation of the zygapophysial and rib-tubercle facets than in *Phenacodus*. The lumbar (L. 4 = 25 mm., No. 2549) are longer; unlike most Creodonts they present horizontal rather than vertical zygapophysial facets. The tail is long and powerful.

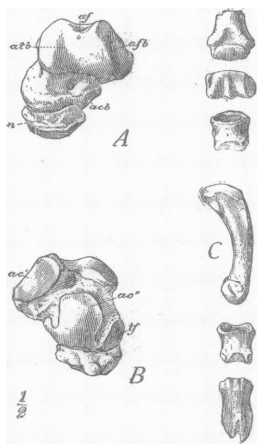


Fig. 10. *Pantolambda bathmodon*. Astragalus, metacarpal III and phalanges. Am. Mus., Cope Coll., No. 3957.

PRIMITIVE OR PROTUNGULATE CHARACTERS.—Among the *persistent primitive* or Creodont characters of *Pantolambda* are the following:

Brain small, olfactory lobes large, hemispheres smooth. Skull with a sagittal crest; terminal anterior nares; nasals very long and expanding posteriorly; mastoid (periotic) widely exposed and forming lower posterior border of external auditory meatus; tympanic bones rudimentary; zygomatic arches slender; no alisphenoid canal; basi-cranial foramina separate.

Dentition typical; no diastemata; molars tritubercular, incisors small, cylindrical; canines rounded. Girdles: scapula unknown; ilium acuminate as in *Phenacodus*.

¹ See Cope, Am. Nat., Vol. XVII, p. 406.

Fore-limb strongly bent outwards at elbow (as in Creodonta and Carnivora), manus everted. Humerus with powerful deltoid, pronator (entepicondylar) and supinator (ectepicondylar) crests; ulna with a convex posterior border; carpus with an os centrale, an extremely small magnum and short trapezoid, causing the metacarpal IV to be inserted proximally between the trapezoid and magnum (Fig. 12).

Hind-limb straight, with three trochanters upon the femur (Fig. 11). Tibia with a rudimentary spine, a very long cnemial crest (Fig. 11) and femoral facets approximate. Tibia (Fig. 11) articulating with calcaneum. Probably an *os-tibiale* (Fig. 12). Mesocuneiform short (analogous to trapezoid in the carpus), so that metatarsal IV articulates between ento- and ectocuneiforms (analogous to metacarpal IV). Articulation between tibia and astragalus slanting obliquely inwards, very limited in extent, bounded posteriorly

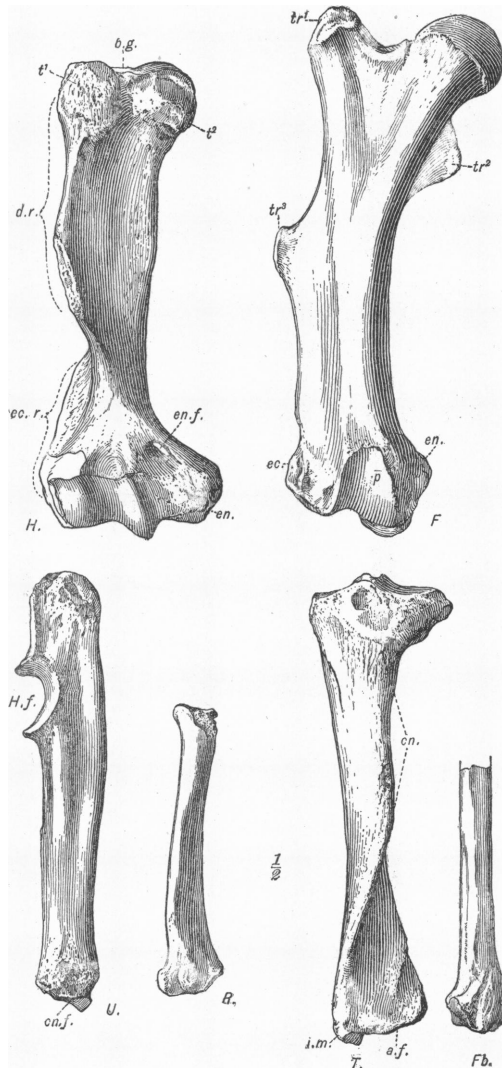


Fig. 11. *Pantolambda bathmodon*. Anterior view of fore and hind limbs, showing powerful development of crests and trochanters as in the Creodonta. Humerus, No. 2549. Femur, No. 2523 (2551, 2549). Tibia, No. 2551. Ulna, Nos. 2550, 2547. Radius, No. 2547 (2546). Am. Mus. Coll.

by astragalar foramen which issues posteriorly between the ectal and sustentacular facets (Fig. 12) (as in Creodonta). Astragalo-navicular head broad convex; two astragalo-calcaneal facets only. Fifth metatarsal curved with a prominent external tuberosity for the *peroneus brevis* muscle, as in the Bear.

All these osteological characters are shared by Periplychus, so far as the skeleton of the latter genus is known; (the carpus of *Periplychus* is unknown). The skull, vertebræ and proportions of the limb bones in the two types are remarkably similar.

ORDINAL OR AMBLYPOD CHARACTERS.—*Primitive ordinal characters.* It will be observed in the definition of the Amblypoda, p. 180, that many of these above-described primitive characters persist throughout the evolution of the order, and therefore rank as *ordinal*.

MEASUREMENTS : SKULL, TEETH, SKELETON.

	P. BATHMODON.		P. CAVIRICTUS.	
	Mus. Nos.	Mm.	Mus. Nos.	Mm.
Skull, condyles to premaxillaries . . est.	2548	157	963	est. 272
Molar-premolar series, superior		055	"	088
inferior	2550	060	3961	118
Lower jaw, symphysis to angle	2550	126	"	est. 251
Fore-limb : Humerus, total length	2549	124		
Radius, "	2547	083		
Manus, "	"	081		
Hind-limb : Femur, "	2551	148		
Tibia, "	"	119		
Pes, "	"	109	3963	184
Ilium, total length, as restored	"	111		
width		031		
RESTORED SKELETON.				
Skull to perpendicular of ischiac symphysis		830		
Height at shoulder blade		350		
ilium		332		

SPECIALIZED ORDINAL CHARACTERS.—There are, however, many structures in *Pantolambda* which amply affirm Cope's view, that *Pantolambda* is the ancestral type of the great lower and middle Eocene forms. These are : the separation of the premaxillæ

in the median line (as in *Coryphodon* and *Uintatherium*), the widely exposed mastoid (as in *Uintatherium*); the nasals extending far back between orbits (as in *Coryphodon*); the molars triangular and selenodont leading to the *Coryphodon* type. The scapula is unknown, probably acuminate as in *Periptychus*. The most striking likenesses to *Coryphodon* in the fore-limb are in the muscular crests of the humerus, the outward flexure of the elbow, the displacement of the lunar upon the unciform.

STRUCTURE OF THE FEET IN PANTOLAMBDA.

Both manus and pes are of exceptional interest. The terminal phalanges are hoof-bearing.

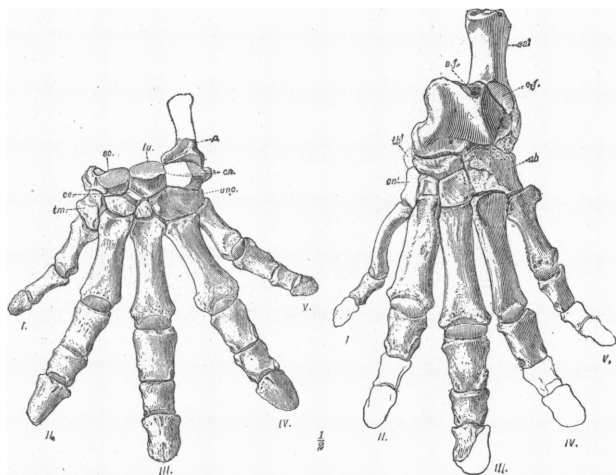


Fig. 12. *Pantolambda bathmodon*. Superior view of carpus No. 2546, partly restored, and tarsus (composition No. 2551), showing essential Creodont structures. Coll. Am. Mus. Nat. Hist.

Fore-foot.—As carefully put together by Dr. Matthew (see Fig. 12), the manus certainly possessed a separate *centrale*. Other exceptional features are the curvature of Mtc.I and the proportions of the distal carpals.

<i>Pantolambda bathmodon</i> }	Magnum smallest. 4 mm.	Trapezoid intermediate. 9 mm.	Trapezium large. 16 mm.
<i>Coryphodon testis</i> }	Magnum large. 37 mm.	Trapezoid smallest. 30 mm.	Trapezium largest. 40 mm.

These proportions show that the evolution of the carpus in the Amblypoda marks an *enlargement of the magnum* and *trapezium* and absorption or coalescence of the *centrale*.

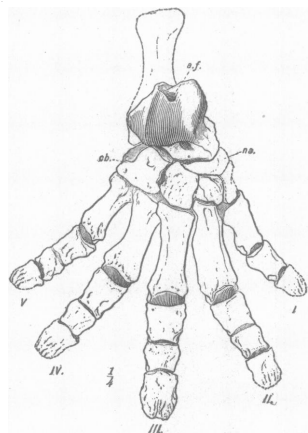


Fig. 13. *Pantolambda cavirictus*. Right pes, directly from above. No. 3963, Am. Mus. Coll.

Hind-foot.—The very large pes, probably belonging to *P. cavirictus* (No. 3963), and small pes of *P. bathmodon* (No. 2550) agree in the many primitive characters enumerated in the Table, p. 178. Analogous to the manus we find a curved first metapodial (Mts. I). As in *Periptychus* and in *Ursus* the fifth metapodial bears a prominent process for the *peroneus brevis* abductors. As in most Creodonts the cuboid is wedge-shaped proximally for the calcaneum and astragalus, and the astragalo-tibial facet faces obliquely inwards (instead of upwards as in *Coryphodon*); this facet is very narrow, bounded by the astragalar foramen posteriorly and

a deep pit anteriorly. A very important feature in this species is the thinning out of the inner side of the navicular, bringing the ectocuneiform almost into contact with the astragalus.

Comparative Measurements.

	<i>P. bathmodon.</i> MM.	<i>P. cavirictus.</i> MM.
Astragalus, greatest diameter.....	20	44
Tarsals, transverse measurement.....	33	68
Metatarsal I.....	23	35
“ II.....	34	Est. 60
“ III.....	40	61
“ IV.....	36	60
“ V.....	28	50

Suborder PANTODONTA *Cope*.

The Pantodonta or Coryphodontia are distinguished by a very great increase in size, the large development of the upper and

lower canines, the lopho-selenodont molar teeth, and the broad-topped skulls. These and other advances upon the *Pantolambda* type were effected in the interval between the deposition of the Torrejon or Upper Puerco and the Wasatch Beds.

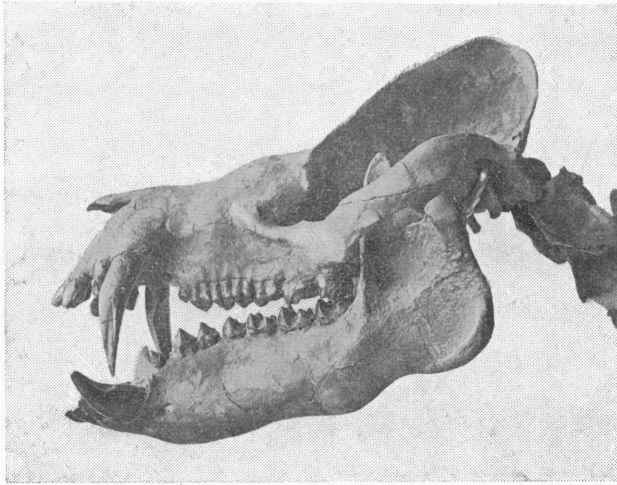


Fig. 14. Skull of *Coryphodon testis*. Male specimen, No. 2867, as mounted in skeleton. Lower jaw, No. 2872. Am. Mus. Coll. The back part of the skull is elevated by distortion.

REVISION AND CRITERIA OF SPECIES.

Twenty-one species were named by Cope, with as little regard for the laws of individual variation as for the association of skeletons with teeth or of jaws with skulls. It is *a priori* improbable that such numerous species should have coexisted, considering that all the collections come from a few levels and a single geographical region. Our knowledge of large living quadrupeds, such as the African Rhinoceros, shows that rarely more than two species of one genus coexist, and these have different local feeding habits. The writer has found the same to be true of the Eocene Titanotheres of Wyoming. Earle's revision of the species (1892), therefore, marked a valuable advance but left much to be done, owing to his lack of comparative material at the time.

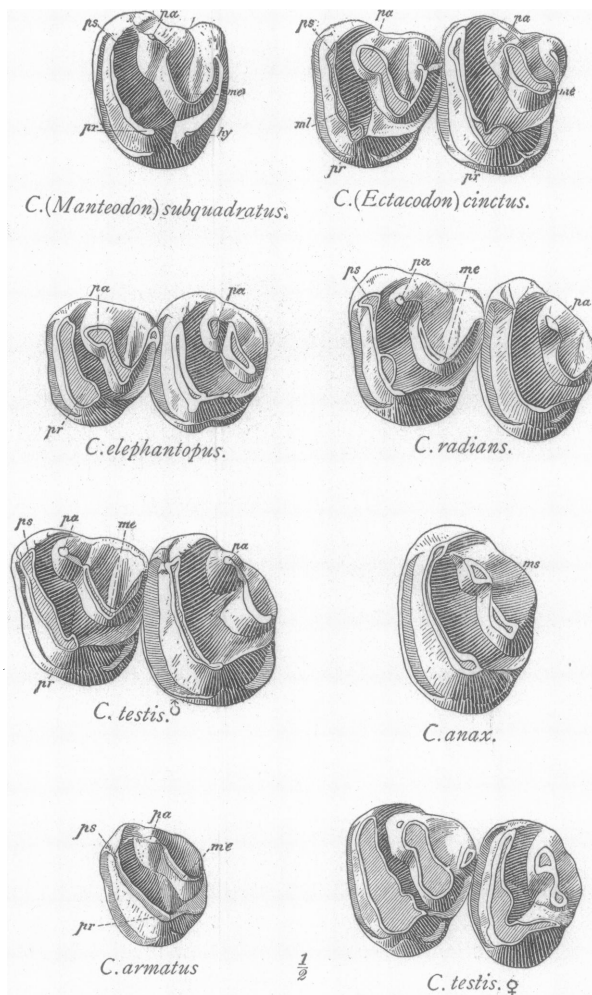


Fig. 15. Typical upper molars. *C. subquadratus*, type; *C. cinctus*, type; *C. elephantopus*, cotype; *C. radians*, type; *C. testis*, male, No. 274; *C. anax*, type; *C. armatus*; *C. testis*, type, female. All in the Am. Mus. Coll.

Altogether there are about thirteen distinct species known at present, which are distributed as in the following Table.

	WASATCH.						WIND RIVER.
	N. M.	WYOMING.					WYOMING.
	New Mexico.	Evanston.	Black Buttes.	Gray Bull, Big Horn Mts.	Clark's Fork.	Buffalo Basin, Big Horn Mts.	Wind River Mts.
SERIES I.							
<i>C. wortmani</i>							×
SERIES II.							
<i>C. testis</i>				×			
" <i>repandus</i>				×			
" <i>marginatus</i>				×			
" <i>cinctus</i>				×			
" <i>semicinctus</i>		×					
" <i>lobatus</i>	×			×			
" <i>anax</i>				×			
" <i>pachypus</i>						×	
" <i>elephantopus</i>	×					×	
" <i>cuspidatus</i>	×						
" <i>obliquus</i>	×			×			
" <i>latipes</i>		×					
" <i>latidens</i>	×						
" <i>ventanus</i>							×
SERIES III.							
<i>C. armatus</i>			×			×	
" <i>simus</i>	×						
" <i>molestus</i>	×						
" <i>lomas</i>	×						
INCERTÆ SEDIS.							
<i>C. radians</i>		×		×			
" <i>hamatus</i>		×					
" <i>subquadratus</i>				×			
" <i>curvicristis</i>				×			
" <i>singularis</i>							×

MOLAR TYPES.—It is essential, first, to clearly conceive the correlated changes taking place in the upper and lower molar teeth, as shown in the accompanying figures and diagrams.

In the *upper molars* :

1. *Pantolambda* (Fig. 2) exhibits the triangular upper molar ancestral to *Coryphodon*, ectoloph (with crescentic cones and meso-style) at *right angles* to protoloph

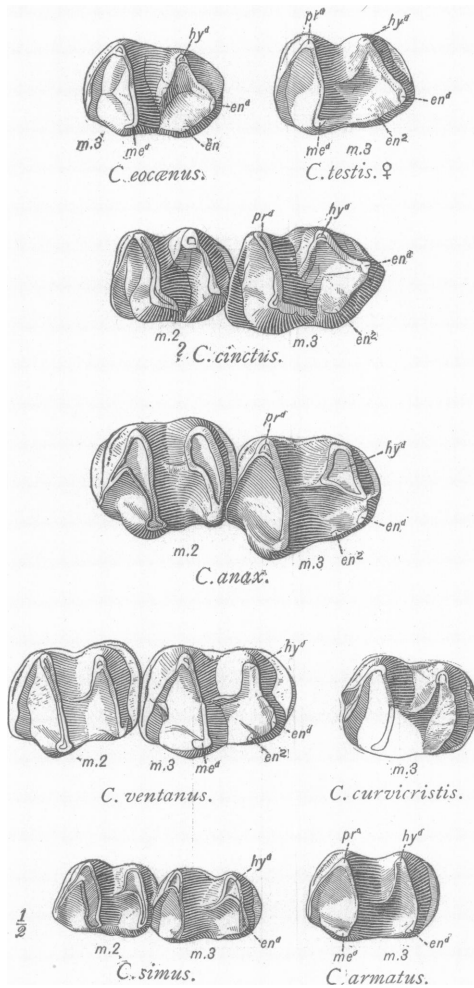


Fig. 16. Typical lower molars. *C. eocænus*, cast of Owen's type. *C. testis*. *C. cinctus*, variety, with triangular heel, No. 4329. *C. lobatus*, typical lower molar, No. 4305. *C. ventanus*, type, No. 2970. *C. curvicristis*, type, No. 4326. *C. simus*, No. 2563. *C. armatus*, type, No. 4316. All in the Am. Mus. Coll.

third cusp (entoconid 2) degenerate; crests *less oblique*, *C. testis*.

3. *Final stage*, a bilobed heel (hypoconid, entoconid), entoconid 2 absent, crests *transverse*, *C. simus*. A tooth exactly of the Tapir or Lophiodon type.

2. *C. radians* presents an intermediate stage, ectoloph (with crescents and meso-style disappearing) *oblique* to protoloph (Fig. 15).

3. *C. armatus* presents a final stage, oval crown, ectoloph (a slightly concave crest) *parallel* to protoloph (Fig. 15).

The second upper molar slowly goes through the same phases as the third, and both approach the *Uintatherium* pattern.

In the *third lower molar* various species of *Coryphodon* exhibit (Fig. 16):

1. *Primitive stage*, a trilobed heel (hypoconid, entoconid, entoconid 2); crests *oblique*, heel with three main cusps, *C. eocænus*.

2. *Intermediate stage*, a heel with two main cusps (hypoconid, entoconid),

Thus the crests of the upper and lower molars slowly become transverse, and simultaneously also preserve their mutual interlocking shear; the stages, 1, 2 and 3, in each being probably correlated.

It is, however, extremely difficult to determine the species by these principles alone, because the hypolophid, or posterior crest, of the third lower molar seems to be highly variable, not in its *obliquity of angle*, but in the greater or less development of the *entoconid 2*, as frequently seen upon opposite sides of the same jaws (*e. g.*, Nos. 2868 and 4321).

CUTTING TEETH.—The *canines* aid us: the primitive form is *round* (persisting in *C. wortmani*) as in *Pantolambda*; the intermediate form is *triangular* and antero-posteriorly compressed (*C. testis*, *C. ventanus*); the final form is flattened and laterally compressed (*C. armatus*), paralleling the *Uintatherium* type, because the long axis of the blade is longitudinal.

SKULL.—When fully known, the top of the skull will prove highly distinctive. At present we know only the comparatively primitive crested type (Fig. 18 B), and the flattened type (Fig. 18 C), which approaches *Uintatherium*.

[May, 1898.]

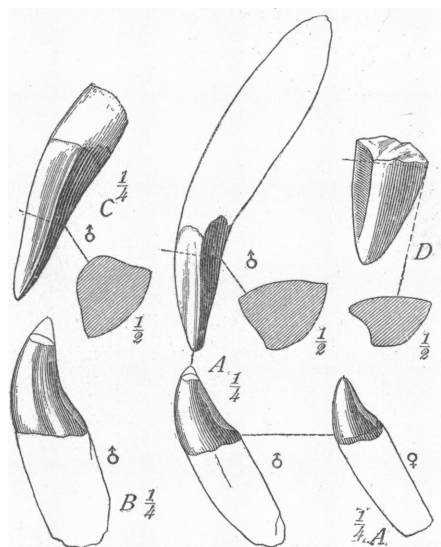


Fig. 17. Upper and lower canines, lateral views and sections. A, *Coryphodon testis*, ♂, male upper and lower canines, No. 274. ♀, female lower canine. B, *C. anax*, male lower canine, No. 4328. C, *C. ventanus*, male upper canine, No. 2970. D, *C. armatus*, upper canine and section, No. 4315. This very small canine is upon double the scale of the other teeth.

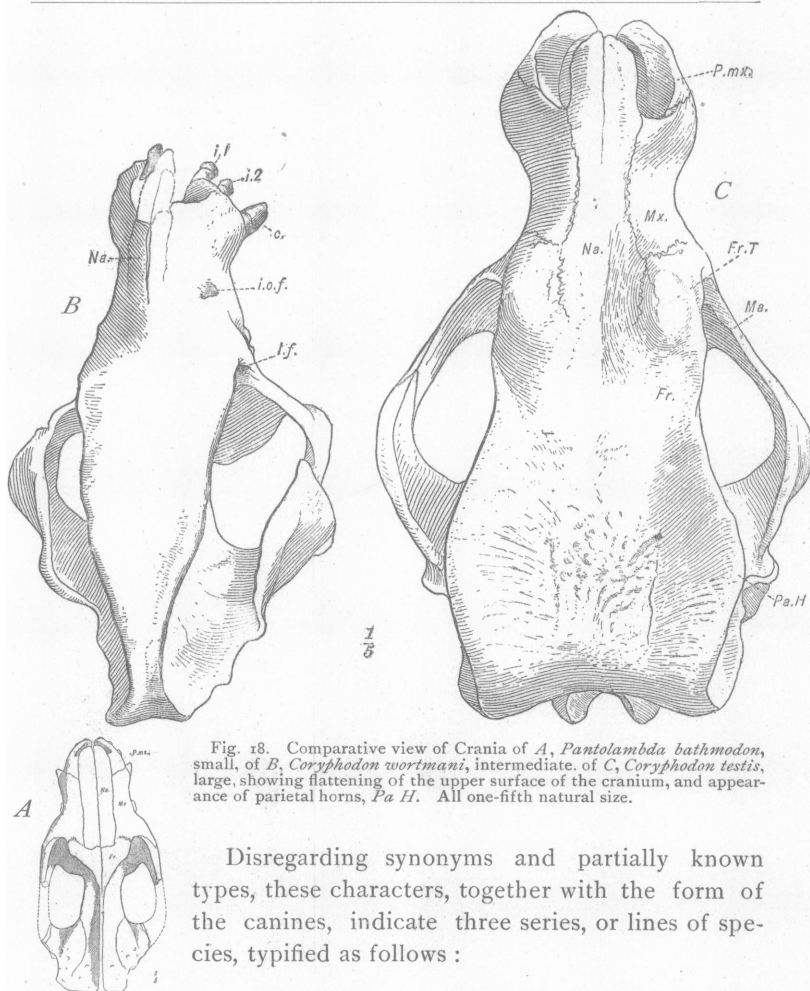


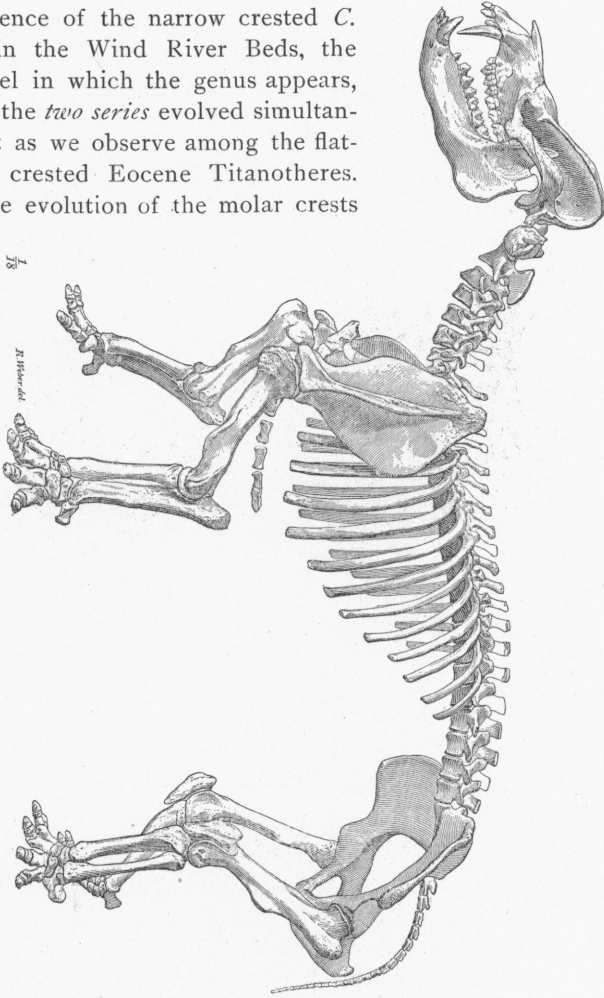
Fig. 18. Comparative view of Crania of *A*, *Pantolambda bathmodon*, small, of *B*, *Coryphodon wortmani*, intermediate, of *C*, *Coryphodon testis*, large, showing flattening of the upper surface of the cranium, and appearance of parietal horns, *Pa. H.* All one-fifth natural size.

Disregarding synonyms and partially known types, these characters, together with the form of the canines, indicate three series, or lines of species, typified as follows :

Levels.	Series I.	Series II.	Series III.
	Primitive. Narrow crested skull. Canines rounded.	Specialized. Broad crested skulls. Canines triangular. Second lower incisors enlarged; third ditto reduced. Lower molar crests oblique to transverse. $M_{\bar{3}}$ trilobate to bilobate.	Specialized. Medium crested skulls. Canines laterally compressed, grooved. Molar crests nearly or quite transverse. $M_{\bar{3}}$ bilobate.
Wind River	<i>C. wortmani</i> .		
Wasatch...	<i>C. elephantopus</i>	<i>C. armatus</i> .

The presence of the narrow crested *C. wortmani* in the Wind River Beds, the highest level in which the genus appears, shows that the *two series* evolved simultaneously, just as we observe among the flattened and crested Eocene Titanotheres. In each the evolution of the molar crests

Fig. 18a. *Coryphodon testis*. Mounted skeleton in the American Museum of Natural History.



from *oblique* to *transverse* angles, with degeneration of the entonoid, loss of crescents, etc., was apparently parallel.

The *sex* characters, as clearly shown in numerous specimens of *C. testis*, are : Males larger, with powerful upper and lower canines ; females smaller, with smaller upper and lower canines. (See Fig. 17.)

Among the specific or variable characters in the skeleton are the presence or absence (compare Earle) of the tibiale facet, of the astragalar foramen, and of the articulation of the cuneiform with Mtc. V, which variation is similarly observed in *Uintatherium*, as shown by Marsh. ('Dinocerata,' p. 107.)

None of the generic characters assigned by Cope to *Bathmodon*, *Ectacodon*, *Metalophodon* and *Manteodon* appear to the writer to be valid, as they rest either upon errors in field collection or upon individual variations.

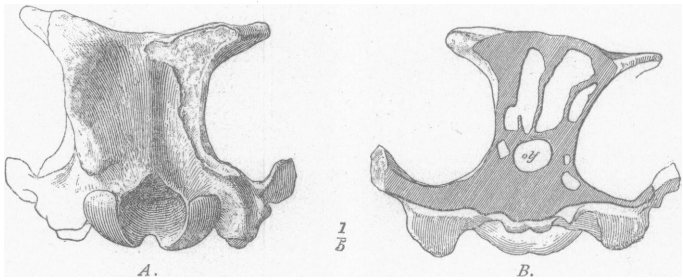


Fig. 10. *Coryphodon elephantopus*, showing flat-topped skull. *A*, view of occiput; *B*, transverse section of cranium through region of olfactory lobes, showing air cells. Coll. U. S. Nat. Mus., No. 111.

Series II.—LARGE CORYPHODONS WITH BROAD, FLAT-TOPPED SKULLS, RUDIMENTARY PARIETAL HORNS, TRIANGULAR CANINES.

12. *C. elephantopus* Cope.

Type, U. S. Nat. Mus. Coll. Superior molar 3; inferior molar 3. Loc., New Mexico. This type has been temporarily displaced.

Cotype, No. 111, U. S. Nat. Mus. Coll. Skull with upper dentition complete; inferior dentition and fragmentary jaw.

Definition.—Superior molars=158 ♂. Skull characters as in *C. testis*, excepting m^3 more quadrate (cotype) with slightly convex mesostyle; m^3 (type) with hypolophid and entoconid 2; incisors equal sized.

Synonyms.

C. obliquus Cope. Type, U. S. Nat. Mus. Coll. A single fragmentary inferior molar. Hypolophid oblique. Entoconid 2 reduced.

This is a smaller animal than *C. testis*, but is found upon a higher level.

Cope's association of type and cotype is open to some question. The type has been temporarily lost, and unfortunately the

TABLE SHOWING THE PROPOSED SPECIES WITH ORIGINAL NAMES, NATURE OF TYPE, ETC.

Spec. No.	NAME.	DATE.	TYPE.	FIGURE.
1	<i>Coryphodon eocœnus Owen</i>	Hist. Brit. Foss. Mamm., 1846, p. 299....	Inf. m. 2 and m. 3...	Figs. 103, 104.
2	" <i>anthracoides Blainville</i> ..	Ann. d. Sc. Nat., VI, 1856, p. 87.....	Skull and teeth.	
3	" <i>oweni Hbvert.</i>	Proc. Am. Phil. Soc., Feb. 16, 1872, p. 418,	Sup. m. 2 and 3 with skeleton	Tert. Ver., pls. 45-57.
4	<i>Bathmodon radians Cope</i>	" " " " p. 420,	Teeth.	Tert. Ver., pl. 49.
5	" <i>semicinctus Cope</i>	" " " " 1872, p. 542.....	Superior molars.....	" " " " 48.
6	<i>Metaphodon armatus Cope</i>	" " " " 1873, p. 70.....	Skeleton	Pal. of N. M., pl. 55.
7	<i>Bathmodon latipes Cope</i>	Proc. Acad. Nat. Sci. Phila., 1873, p. 103,	Inferior molars.....	" " " " pls. 50-57.
8	" <i>brevises</i>	Rep. Vert. Fos. N. M. Wheeler, 1874, p. 120,	Sup. and inf. molars,	" " " " pl. 54.
9	" <i>sinus Cope</i>	" " " " " p. 121a, Sup. and inf. molars,	Inferior molars, 3....	" " " " pls. 50-54.
10	" <i>molestus Cope</i>	" " " " " p. 121b, Inferior molars, 3....	Last sup. and inf. m. 3,	" " " " 48-50.
11	" <i>lomas Cope</i>	" " " " " p. 121c, Last sup. and inf. m. 3,	jaw with teeth.....	" " " " pl. 46.
12	" <i>elephantopus Cope</i>	Syst. Cat. Vert. N. M., 1875, p. 29.....	Inferior molars 3....	Mon. of Dinocerata,
13	" <i>latidens Cope</i>	" " " " " p. 30.....	Sup. and inf. molars,	P. 52.
14	" <i>cuspidatus Cope</i>	Am. Jour. Sci. and Arts, 1876, p. 426....	" " " "	Vert. Pal. N. M., pl. 47.
15	<i>Coryphodon hamatus Marsh</i>	Pal. of New Mexico, Wheeler, 1877, p. 207,	" " " "	" " " " 46.
16	" <i>obliquus Cope</i>	" " " " " p. 209,	" " " "	
17	" <i>lobatus Cope</i>	Proc. Amer. Phil. Soc., Dec. 16, 1881, p. 166,	Last sup. m. with incisors.....	Tert. Ver., pl. 44a.
18	<i>Manteodon subquadratus Cope</i>	" " " " " p. 167,	Superior molars.....	" " " " pls. 44a-c.
19	<i>Ectacodon cinctus Cope</i>	" " " " " 1881, p. 168.....	Sup. and inf. molars,	" " " " pl. 44c.
20	<i>Coryphodon anax Cope</i>	" " " " " p. 171.....	Inferior m. 2 and 3	" " " " 44c.
21	" <i>repandus Cope</i>	" " " " " p. 172.....	Sup. m. 2 and mand.	" " " " 44c.
22	" <i>curvicastris Cope</i>	" " " " " p. 174.....	with teeth.....	" " " " 44c.
23	" <i>marginatus Cope</i>	" " " " " p. 175.....	Superior molars 3....	" " " " 44a.
24	<i>Metaphodon testis Cope</i>	Proc. Acad. Nat. Sci. Phila., 1882, p. 294,	Skeleton	" " " " pls. 44d-g.
25	<i>Bathmodon pachypus Cope</i>	Bull. Amer. Mus. Nat. Hist., X, 1898, p. 210,	Jaw and teeth.....	Op. cit., fig. 16.
26	<i>Coryphodon ventianus Osborn</i>	" " " " " p. 212, Skull.	" " " "	" " " " 27.
27	" <i>wortmani Osborn</i>	" " " " " p. 214, Tarsus.	" " " "	" " " " 28.
28	" <i>singularis Osborn</i>			

¹ Name only.

TABLE OF COMPARATIVE MEASUREMENTS.

[illegible]

characteristic last lower molar, m^3 in the cotype, is wanting. The species must therefore rest upon the characters of the cotype. No lower teeth were found with the fine palate (No. 275, Am.

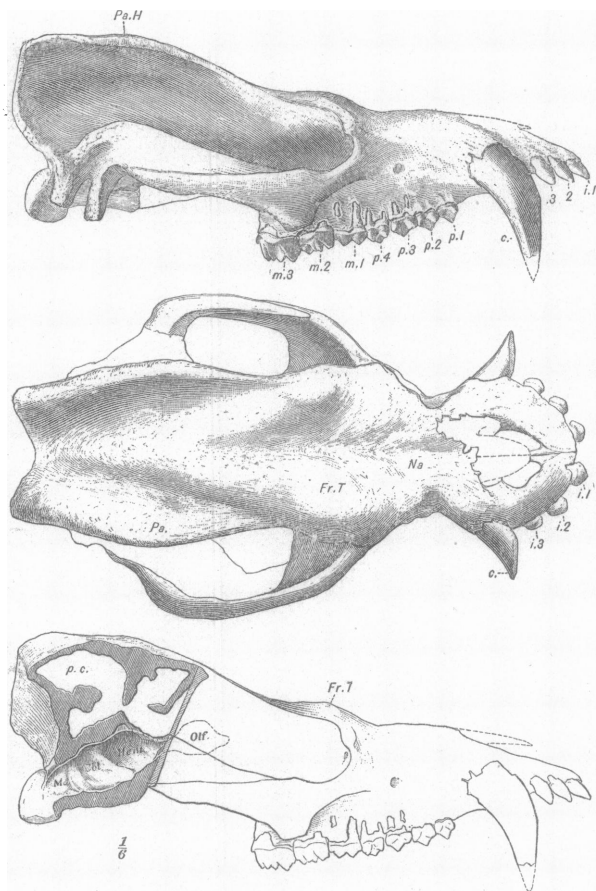


Fig. 20. *Coryphodon elephantopus*. Cotype. Lateral, superior and sectional views of cranium. No. 111, U. S. Nat. Mus. Coll.

Mus.) rightly associated with the cotype by Earle. The cranial and dental characters of the cotype (Fig. 20) are those of *C. testis* and *C. lobatus* upon a smaller scale; m^3 has a well-marked postero-external elbow (Fig. 15), and the paracone is sharply dis-

tinct from the metacone; the ectoloph thus does not form a continuous crest as in the supposed type. The parietal protuberances or rudimentary horns *Pu.H*, are less pronounced but equally rugose; the premaxillary symphyseal borders are extensive although without contact; the incisors are equal in size, *i*₁ and *i*₃ being fully as large as *i*₂ in both jaws. This is therefore a smaller and perhaps more primitive type than either *C. lobatus* or *C. testis*, although skull No. 275 is definitely recorded by Wortman from the Buffalo Basin, the highest true Wasatch level.

Unfortunately the characteristic last lower molar is missing in the cotype; the series *pm* 1-*m* 2 measure 122 mm. The lower jaws of *C. elephantopus* are also represented either by Cope's *C. obliquus* or by his *C. latidens* (see below). The former is more probably the case for the following reason. According to the ratio of upper and lower teeth established in the *C. testis* jaws (see Table, p. 199, No. 3829), the lower grinders in *C. elephantopus* should measure 167 mm. The type lower molar of *C. obliquus* approximately agrees with this size (see Table, p. 199) and character. The last lower molar of *C. obliquus* agrees closely with that of the supposed type of *C. elephantopus*. We may therefore consider the greater or less development of the entoconid 2, which these molars present, as variations similar to those which we have observed in the other species of this series, namely, *C. testis* and *C. lobatus*.

No complete jaw is nearer this size than No. 4321 (Am. Mus., Cope Coll.), in which the lower grinders measure 172 mm.; this specimen is also significant because the last inferior molar on the right side agrees in form with *C. cuspidatus* (*i.e.*, entoconid 2, distinct), while the same tooth on the left side agrees with *C. obliquus* (*i.e.*, entoconid 2, obsolete). Another proof of the variability of these cusps. This jaw, however, may belong to a small female of *C. testis*.

INCERTÆ SEDIS.

21. *Coryphodon repandus* Cope.

Type, No. 4309, Am. Mus., Cope Coll. Superior and inferior molars *m*¹, *m*³, *m*₃, *m*₃. Symphysis of lower jaws. Size=*C. testis*, male. Loc., Big Horn, Wyoming.

This is an indeterminate type. It is distinguished by angulation of ectoloph in m^3 (as in *C. elephantopus*, cotype); perhaps also by the more transverse direction of hypolophid in m^3 ; second incisors only slightly larger than first and third (as in *C. elephantopus*, cotype). The nearest resemblance is therefore to *C. elephantopus*, from which it is distinguished by larger size. Superior molars No. 4366, from New Mexico, furnish a transition in the angular form of the ectoloph of m^3 to the *C. testis* type. Altogether *C. repandus* is of very doubtful validity.

19. *C. cinctus* Cope.

C. (Ectacodon) cinctus. Type: No. 4341, Am. Mus., Cope Coll. Superior molars complete. A strong cusp appearing at postero-external angle of m^3 . Loc., Big Horn, Wyoming.

The distinctive feature of this type, viz., the quadrate form and postero-external basal cusp of m^3 (Fig. 15), and to a less extent on m^2 , are either individual variations or valid specific characters. They are certainly not generic.

Lower teeth which may possibly be correlated (Nos. 4329, 4334, 266) have a triangular heel upon the last lower molar (Fig. 16), with entoconid very distinct and extremely short and oblique hypolophid.

24. *C. testis* Cope.

24. *C. (Metalophodon) testis* Cope. Type: No. 4317, Am. Mus., Cope Coll. Superior molar series. Originally distinguished by reduction of posterior crescent spur in m^2 .

Definition.—Sup. molars=169 ♀ to 182 ♂. Inf. molars=172 ♀ to 192 ♂. Third superior molar typically oval, with oblique posterior crest with primitive paracone, mesostyle and meta-crescent more or less distinct. Third inferior molar with oblique hypolophid, entoconid 2 reduced or vestigial. Second incisor the largest.

This includes the most completely known *Coryphodon*. It has been heretofore described by Earle and the writer as *C. radians*, but is now found to be distinct. The identification with Cope's type of *C. testis* is made by means of a careful comparison with the superior molars in the female skull No. 2963. The form and measurements are identical. As this skull undoubtedly belongs

to the same species as the male skull (Fig. 21) and skeleton, all the characters of this fine type are now available.

This is the largest *Coryphodon* but one, and is very abundant in the Middle Wasatch levels, being represented by a magnificent series of skulls and skeletons in our collection. From these the sexual characters are clearly made out. The large male skull is used in the complete mounted skeleton, Fig. 18 *A*. The smaller

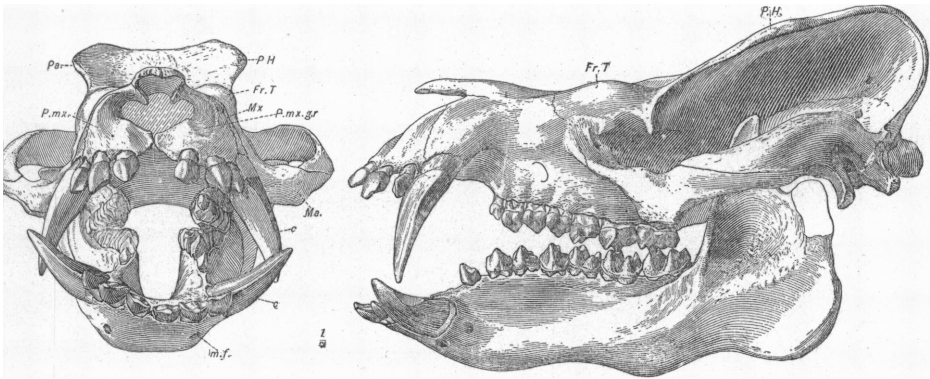


Fig. 21. *Coryphodon testis*. Large male, showing rudimentary parietal horns. Upper canines partly restored. Skull No. 2867, lower jaw, No. 2872. Am. Mus. Coll.

female type of this species is represented in the skull No. 2963, and jaws (Nos. 2868, 259) in contrast with the powerful male skulls (Nos. 2829, 2867) and jaws (4322).

Variations in the last lower molar are considerable, from an oblique to a bilobed (No. 259) or less oblique condition of the posterior crest, with all the stages in reduction of the entoconid 2. Exactly similar variations are found in the lower molars of the larger and smaller members of Series II. The development of entoconid 2 also varies in the posterior molars upon opposite sides of the same jaws of several specimens of *C. lobatus*.

The osteological characters have been fully described and figured by the writer (this Bulletin, 1898, pp. 81-91). Full characters of the vertebral column are shown in Fig. 23.

Certain specimens (skull, No. 2866) of the still larger *C. lobatus* have been found below it, and the much smaller *C. elephantopus*

occurs in the higher levels of Buffalo Basin, Wyoming. Our scanty evidence therefore appears to indicate a retrogression in size in this series, but this is an inference by no means certainly established.

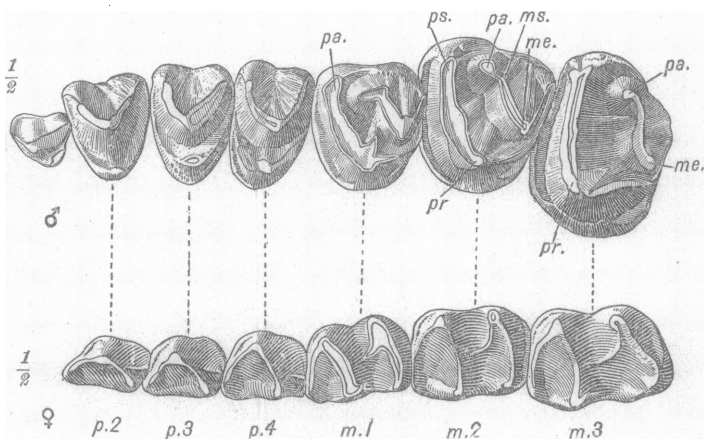


Fig. 22. *Coryphodon testis*. Superior molar series, male (Am. Mus. Coll. No. 274); inferior molar series, female (Am. Mus. Coll. No. 2868).

17. *C. lobatus* Cope.

Type, Nat. Mus. Coll. Sup. molar 3; inf. molar 3; part of sup. and inf. canine, indeterminate.

Definition.—Sup. molars=193 ♂. Inf. molars=196 ♂. Dental characters as in *C. testis*, excepting elongation of protoloph and degeneration of posterior metacone crescent in m². Astragalus usually lacking astragalar foramen. Cranium massive, with widened parietal horn rudiments.

Synonyms.

20. *Coryphodon anax*. Type: No. 4327, Am. Mus., Cope Coll. Superior molar 3; inferior molars, premolars and incisors. Loc., Big Horn, Wyoming.

25. *C. (Bathmodon) pachypus* Cope. Type: No. 4335, Am. Mus., Cope Coll. Astragalus, calcaneum, pelvis, femur, &c. Indeterminate type. Loc., Big Horn, Wyoming.

This is the largest *Coryphodon* known; it surpasses *C. testis* in size, the ratio being 50:45, as indicated by the femora.

Unfortunately the name *C. lobatus* is prior to the more appropriate *C. anax*, and must supersede it. The lower molars defined

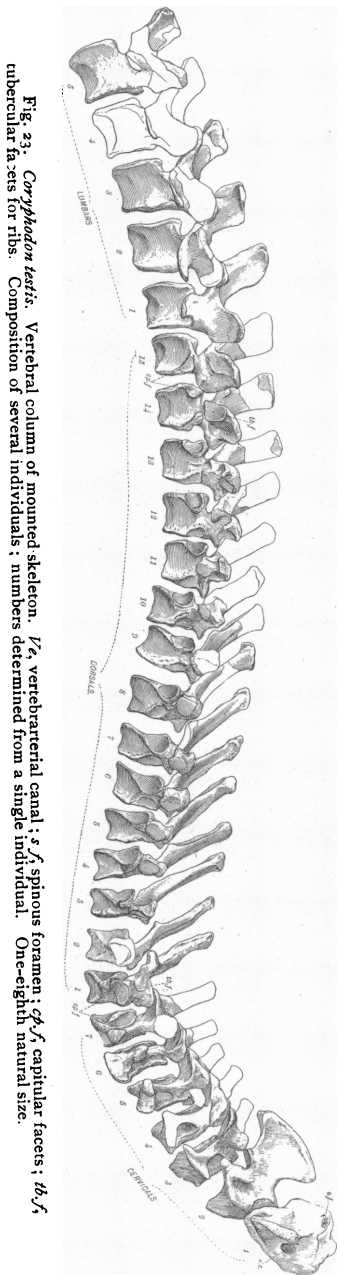


Fig. 23. *Coryphodon testis*. Vertebral column of mounted skeleton. *1-24*, vertebral canal; *s. s.*, spinous foramen; *cp. s.*, capicular facets; *th. s.*, tubercular facets for ribs. Composition of several individuals; numbers determined from a single individual. One-eighth natural size.

as *C. lobatus* Cope, which may be considered as indeterminate types, present exactly the *C. anax* measurements (see Table, p. 198), and exhibit an oblique hypolophid and depressed entoconid 2 upon m_3 , as shown in Fig. 16. This may be considered the typical *C. lobatus* or *C. anax* third lower molar. It is well shown in the large jaw, No. 4333, and in the fragment, No. 4305.

A variation, No. 266, in molars of the *C. lobatus* size is paralleled by a variation, No. 4239, in molars of the *C. cinctus* size, as represented in Fig. 16, in which the three cusps form a posterior triangle, as also in *C. cuspidatus* (No. 4324). If these are not variations they represent three distinct species, which is possible but not probable.

Synonym.—The skeleton defined as *C. pachypus* by Cope (No. 4335) undoubtedly belongs here. The astragalus of *C. pachypus* and of another specimen (No. 2870) exhibit no astragalar foramina, and show a wider interval on the front face of the astragalus between the tibial and navicular facets than we find in *C. testis*.

The massive male skull in our collection (No. 2866) is most interesting in its progressive development of the parietal horn thickenings, parallel with those of *Uintatherium*. Its geological level, however, according to Wortman, is below that of *C. testis*, an observation very difficult to reconcile with the more advanced evolution of its skull and molar teeth.

14. *C. cuspidatus* Cope.

Type, Nat. Mus. Coll. Fragmentary inferior molars 2 and 3, and a portion of the jaw. Originally distinguished by prominent entoconid 2.

Cotype, No. 276, Am. Mus. Coll. Complete lower dentition; upper pm²-m³. This specimen was referred to *C. obliquus* by Earle (1892, p. 162).

Definition.—Inferior m.p.m.=154. Superior m.p.m.=150. Last superior molar oval, antero-posteriorly compressed. Last inferior molar with oblique hypolophid and more or less prominent entoconid 2. Metaconid with rudimentary metastylid. Inferior incisors unequal in size.

This is a diminutive *Coryphodon*, of the size and very similar in molar type both to *C. eocænus* Owen, from the London Clay, and to *C. owenii* Hébert, from the Suessonian of France. The characters of Cope's type are very indefinite; the complete upper

and lower series of teeth, No. 276, therefore serve as a cotype to define this species, the most diminutive of the series. The last lower molar of the right side agrees in form and measurement with Cope's type, although the entoconid 2 is less prominent and isolated; on the left side the entoconid 2 is nearly obsolete, again demonstrating the variability of this cusp. The very small lower canines indicate that the animal is a female.

The enlarged second incisors and

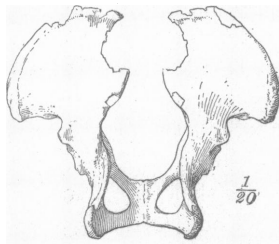


Fig. 24. Back view of pelvis of *Coryphodon lobatus*. Am. Mus., Cope Coll., No. 4335.

general form of m₃ confirm its reference to Series II. A unique feature is the reduplication of the metaconid in m₂ and m₃ into a rudimentary metastylid, parallel with the large metastylid of *Uintatherium*. Another example of this species is No. 4324.

13. *C. latidens* Cope.

Type, Nat. Mus. Coll. ♂. Lower jaws and teeth, left premaxillary and incisors, superior canine. Loc., New Mexico.

Definition.—Inferior m. and pm.=156. Inferior molars short and broad with crests nearly or directly transverse (angle= $\approx 85^\circ$); entoconid 2 vestigial or wanting. Inferior incisors equal sized. Superior canines nearly straight, antero-posteriorly compressed, subtriangular, with an external ridge.

This imperfectly-known animal appears to represent a rather small and specialized form in Series II.

It is distinguished from the type of *C. elephantopus* by the straighter and more compressed superior canine observed in the type, by the transverse position of the crests of the inferior molars, and by the absence of entoconid 2. As shown in the Table, p. 199, the measurements of Cope's *C. latidens* type are identically the same as those of *C. simus*, although Cope speaks of the latter as being much smaller than the former.

Cope has suggested the possible association of *C. latidens* with the cotype skull of *C. elephantopus*. It appears to be distinguished, however, by the form and compressed section of the superior canine. It is, however, certainly related to Series II by the sub-triangular form of the canine and the characteristic swelling of the jaw below m_3 . Unfortunately the types have been temporarily misplaced, and no determination of this question by direct comparison can be made at present. If these jaws should prove to belong to *C. elephantopus*, the species *C. obliquus* will have to be revived.

It will be noted that both types come from New Mexico. In New Mexico, also true Wasatch, we found in 1897 a lower jaw (No. 2563, Fig. 16) of extremely small size, associated with *Meniscotherium*, *Ambloctonus* and *Didymictis*, which may represent a female of this species. Unfortunately the canines are not preserved. The total lower grinding series does not exceed 125 mm., so that this is the smallest Coryphodon jaw known; the last lower molar measures only 30×19 mm.; the posterior crest forms an angle of 85° with the long angle of the jaw; a minute vestige of the entoconid 2 can however be observed.

22. *Coryphodon curvicristis* Cope.

Type, No. 4326, Am. Mus., Cope Coll. Lower jaw fragments containing $pm.4$ to m_3 ; canine.

Definition.—Molar crests transverse. Posterior crest of m_3 directly transverse, crenulate, depressed. Superior incisors with sharply angulate anterior faces. Canines as in *C. testis*.

The systematic position of this species (Fig. 16) is indeterminate. It resembles *C. latidens* in the transverse crest angulation

and in the rather broad proportions of the molars, but exceeds this species in size. The complete superior canine determines the position of the animal in Series II. The canine is powerful, curved and antero-posteriorly compressed, partly as the result of pressure. The inferior premolars are exceptionally short.

A fourth member of this series, *C. ventanus*, is found in the Wind River Beds. It appears to resemble *C. latidens* in the form of the superior canines.

Series III.—SMALLER CORYPHODONS. SPECIALIZED. RELATIVELY NARROW, FLAT-TOPPED SKULLS, (?) WITHOUT PARIETAL HORN RUDIMENTS. CANINES COMPRESSED Laterally AND GROOVED ANTERIORLY. LOWER MOLARS ELONGATE, CRESTS NEARLY OR QUITE TRANSVERSE; M_3 BILOBATE, NO ENTOCONID 2.

In 1872 Cope defined certain teeth as *Metalophodon armatus*, mistaking the posterior superior molars, m^2 , of two individuals for m^2 and m^3 of one individual, as can be proved by a comparison with his type of *C. molestus*. The latter type moreover gives us the cranial characters and constitutes a valuable cotype.

6. *C. (Metalophodon) armatus*.

Type, No. 4315, Am. Mus., Cope Coll. Superior m^2 , m^3 , premolars, superior canine and incisors; two individuals, probably mingled, fully adult.

Cotype, No. 4316, Am. Mus., Cope Coll. Superior m^2 and m^3 , m_3 , premolars, etc., juvenile.

Definition.—Upper and lower canines greatly compressed, with a deep antero-internal groove upon the upper canine. M^2 with powerful anterior crest, m_3 without entoconid 2. Lower molars elongate, crests lunate, nearly transverse. (Angle with long axis of jaw, 81° .)

Synonyms.

9. *C. simus* Cope. Type, U. S. Nat. Mus. Coll. Inferior m and pm=154. Fragmentary skull, probably female. Superior canine. Mandibular rami and teeth. Loc., New Mexico.

10. *C. molestus* Cope. Type, U. S. Nat. Mus. Coll. Skull, dentition and parts of skeleton. Loc., New Mexico.

11. *C. lomas* Cope. Type, U. S. Nat. Mus. Coll. Posterior inferior molar. Loc., New Mexico.

The slender crests and the elongate form of the posterior lower molars in this species at once distinguish it as a type from members of the foregoing series, since they form an angle of 81° , or nearly a right angle, with the long axis of the jaw, and m_3 is entirely devoid of the entoconid (Fig. 16).

Specimen No. 4315, Fig. 17, gives the most distinctive character, shown again in Cope's type of *C. mblestus* (Cope, 1877, Pl. LVI, fig. 4), which agrees with *C. armatus*, namely, the flattened form of the canines. Cope himself referred *C. lomas* to *C. molestus* (1877, p. 237). The type of *C. simus* has lower teeth of the same character, rather long and narrow. The upper canines are, however, described by Cope as triangular and grooved; this raises a doubt as to the reference of this type to *C. armatus*.

The juvenile type specimen of *C. molestus* demonstrates the flat-topped character of the skull (Coll. U. S. Nat. Mus., No. 1119, Cope, *op. cit.*, Pl. LVI); the skull is far less expanded laterally, when seen from above, than any of the skulls in Series II; but this may be in part due to its juvenile and undeveloped condition.

"The inferior canine," observes Cope, "has a flat interior and convex exterior face, which are separated by anteriorly and posteriorly directed cutting edges." The most distinctive feature of the canines therefore is that the antero-posterior diameter greatly exceeds the transverse, as in *Uintatherium*. An aberrant feature is the antero-external groove. The median incisors are as large or larger than the others.

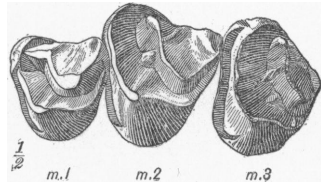


Fig. 25. *Coryphodon armatus* superior molars, left side (type of *C. molestus* Cope).

INSERTÆ SEDIS.

23. *C. marginatus* Cope.

Type, No. 4374, Am. Mus., Cope Coll. Superior molar 3, canine and pm. Loc., Big Horn, Wyoming.

This indeterminate type resembles *C. armatus* in the form of m^3 , but differs from it in the form of the canine, which is less compressed and may possibly represent a milk tooth. The canine corresponds with Cope's description of that of *C. simus*.

WIND RIVER TYPES.

Cope's Wind River material of *Coryphodon*, all of which is now in the American Museum (Nos. 4811, fragments of skull and teeth; 4812, lower molar, incisors and fragments; 4813, lower jaw and fragments; 4814-4817, fragmentary teeth; 4818), merely sufficed to determine the existence of this genus in these beds.

Our Wind River collection and the determination of manus No. 4351 (Am. Mus., Cope Coll.) as belonging to the Wind River Beds, is therefore of very great importance. It demonstrates that *Coryphodonts of considerable diversity and size persisted into the Wind River period*.

Owing to the general scarcity of fossil remains in these beds, the relative abundance of these animals cannot be estimated. Of intermediate size is the jaw of No. 2976, described below as *C. ventanus*; of smaller size there is a well-preserved skull (No. 2977), type of the new species *C. wortmani*. They represent respectively the persistence of at least two series, namely of Series I, and of Series III now discovered for the first time.

SUCCESSORS OF SERIES II.

26. *Coryphodon ventanus*, sp. nov.

Type, No. 2976, Am. Mus. Coll. Jaws and lower teeth. Superior incisors and canine. L. metacarpal IV.

Definition.—Size of *C. testis* ♂. Inferior m and pm series = $e 172$. Superior canines posteriorly compressed, with antero-internal depression and long

sharp external ridge. Lower canines with short external ridge near apex. Second incisors enlarged; lateral incisors much reduced. Posterior inferior molars with crests more transverse than in *C. testis* (angle = 74°) a persistent entoconid 2. (? Cuneiform articulating with Mtc. V.)

This species is clearly distinguished from *C. testis* by the form of the canines, which in this animal are comparatively straight and lance-shaped (Fig. 17), the long axis transverse (unlike *Uintatherium*), with an antero-internal groove which is

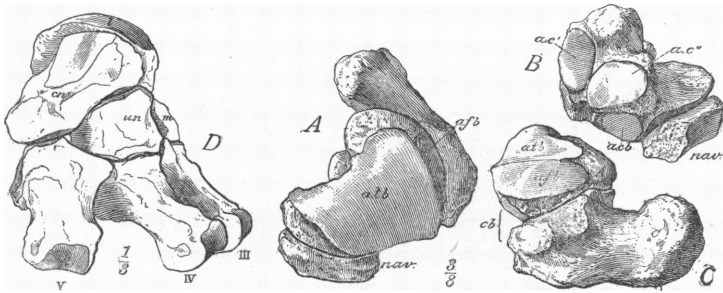


Fig. 26. Foot structure of *Coryphodon*. D, external view of manus of *C. ventanus* (No. 4351, Coll. Am. Mus.); A, superior view of astragalus and calcaneum found near *C. simus*, no tibial facet (Bathmodon type); B, lower surface of astragalus, showing calcaneal and cuboidal facets; C, external view of calcaneum and astragalus, showing reduction of tibio-calcaneal facet. (Coll. U. S. Nat. Mus.)

worn away by the lower canine. They resemble those of *C. latidens* Cope (except in the groove), but are much less compressed than those of *C. armatus* Cope, besides having the long axis in a different plane. The posterior crest of m_3 (Fig. 16) differs from those of *C. armatus* and *C. simus* in form and in the retention of an entoconid 2, and from that of *C. testis* in being slightly less oblique. Another character is the very rapid increase in size of the molar series as we pass backward: $m_1=28$, $m_3=42$.

To this species belong Nos. 2982, 4813, 4812, 277B, and 2978 of our collection. The latter contains the complete lower teeth which exhibit the marked disproportion between the second and the first and third incisors embodied in the definition of this species. The incisor proportions are indicated by the length of roots, $i_1=36$, $i_2=59$, $i_3=28$.

The metacarpal IV agrees in length (54 mm.), and lends some probability to an association with that of the complete carpus No. 4351 from the Wind River.¹ This associated complete carpus (Fig. 26) agrees with some specimens of *Uintatherium* in the very exceptional character *that the cuneiform articulates with Metacarpal V.*

Series I.—PRIMITIVE, NARROW-CRESTED SKULLS. CANINES ROUNDED. INCISORS SUBEQUAL IN SIZE.

The lower teeth are unknown, and the ancestral members of this series have not thus far been determined in the underlying Wasatch formation.

27. *Coryphodon wortmani*, sp. nov.

Type, No. 2977, Am. Mus. Coll. Loc., Wind River, Wyo.

Definition.—Superior m and pm=154. Superior canines rounded. Occiput very high and narrow. Supratemporal ridges converging posteriorly to form a comparatively narrow sagittal crest.

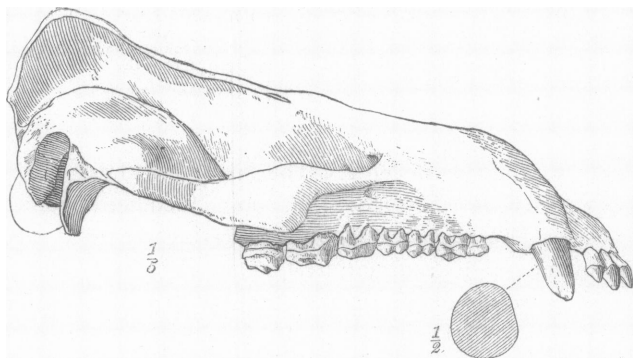


Fig. 27. *Coryphodon wortmani*, type. Lateral view of skull and section of superior canine.²

The discovery of this type (Figs. 18 and 27) in the high level of the Wind River Beds is most surprising. It is far more primitive both in its narrow cranium and rounded canines than any of the

¹ This carpus was mistakenly described by Cope as coming from the Wasatch. Dr. Wortman identifies it as found by himself in the Wind River.

² Dedicated to my colleague Dr. J. L. Wortman.

C. testis series found in the Middle Wasatch. It appears like a direct successor of *Pantolambda cavirictus*.

The median incisors are equal to the others, the lateral incisors being slightly the smallest. The canines have a rounded crown somewhat flattened in front by wear. The superior grinding series present a rudimentary posterior crescent on m^2 and an oval m^3 with short oblique ectoloph. The most unique features are the form of the occiput and the cranium as defined above, which is intermediate between that of *Pantolambda* and *Coryphodon armatus*.

The metatarsal V is short and robust (= 42 mm.), with the characteristic peroneus tuberosity of the true *Coryphodon*. Both femora are finely preserved (length, = 340 mm.), being of the smallest size known.

INSERTÆ SEDIS.

The position of the following types with reference to the Series I-III, which we have been considering, is uncertain.

4. *Coryphodon radians* Cope.

Type, No. 4300, Am. Mus., Cope Coll. Superior molars 1, 2 and 3. Probably associated lower jaw, No. ? 4300. Portions of skeleton. Loc., Evanston, Wyoming.

Definition.—Third superior molar with a spur (metacrescent) upon the posterior crescent of the ectoloph. Third inferior molar without entoconid 2, hypolophid nearly transverse. Lower canines somewhat incisiform.

This classic species, which rests upon somewhat uncertainly associated upper and lower teeth, jaws and skeleton, was the first described in America. The structure of the last upper molar is shown in Fig. 15. The last lower molar has crests nearly as transverse and simple as in *C. latidens*. The most distinctive structure is the lower canine which, although badly broken, exhibits a distinct flare at the base of the inner face, as in the incisors, and is apparently becoming incisiform, an interesting approach to *Uintatherium*.

15. *Coryphodon hamatus* Marsh.

Type, Yale Museum No. 1330. Skull and dentition much worn.

Cotype, Yale Museum No. 1334. Female skull with perfect superior and inferior dentition. Loc., Evanston, Wyoming.

Synonym.

18. *Coryphodon (Manteodon) subquadratus* Cope. Type, No. 4340, Am. Mus., Cope Coll. Superior molar 2, incisors and fragmentary premolar. Loc., Big Horn, Wyoming.

Definition.—Size large. Superior molars with quadrate crowns and well developed hypocones upon m 1 and m 2. Inferior molars with nearly transverse crests; m₃ without entoconid 2.

This species was mistakenly associated with *C. elephantopus* by Earle. In size it equals *C. testis*, but it is well distinguished by the quadrate form of the superior molar teeth in which, according to the figures of Marsh (*Dinocerata*, Fig. 55, p. 52), a representative of the hypocone is present. This is developed from the ridge extending backwards from the protocone. In the inferior molar teeth the crests are nearly transverse, and there is no trace of the entoconid 2.

The unique quadrate tooth with a prominent hypocone, type of *Manteodon subquadratus* (Fig. 15), was without reason considered by Cope as a third superior molar. It proves, upon comparison with Marsh's cotype made by Dr. Matthew, to resemble a second superior molar of *C. hamatus*. It differs, however, from *C. hamatus* in the more distinct development of the posterior spur of the metacone crescent, a character which may subsequently prove to give it distinct specific rank.

The type skull of *C. hamatus* is somewhat fractured. The top of the skull of the cotype, a female, is considerably narrower than that of *C. testis*, female, presenting a condition intermediate between that of *C. testis* and *C. armatus*. The canines in this animal, as in other females, are small.

28. *Coryphodon singularis*, sp. nov.

Type, A hind limb, tibia, fibula and pes No. 2980. Loc., Wind River, Wyo.

A small and unique hind foot and limb from the Wind River Beds, found upon the level of *C. wortmani*, is of excep-

tional interest (Fig. 28). Associated lower tooth fragments, put together by Dr. Matthew, resemble those of a small *Coryphodon*, and clearly separate this animal from *Bathyopsis*. The differences from the pes of *Coryphodon* are very significant, as follows :

1. Navicular laterally reduced, excluded from cuboid by ectocuneiform, a unique condition.
2. Ectocuneiform enlarged, articulating with astragalus (unique).
3. Second or middle phalanges greatly abbreviated upon all digits, I-V, as in *Uintatherium* manus.
4. Front surface of astragalus widened, separating tibial and navicular facets as in *Uintatherium*.
5. Tibia long and slender, unlike *Coryphodon*.

The measurements of the metatarsals are as follows :

Mts. I=22. Mts. II=42. Mts. III=48. Mts. IV=42. Mts. V=34.
Other measurements in Table on page 199.



Fig. 28. *Coryphodon singularis*. Superior and lateral views of pes. Am. Mus. Coll. No. 2980

This animal thus shows one progressive character (4), two entirely unique and distinctive characters (1, 2); the latter, together with (5), sharply separate it from *Coryphodon*; two characters, 3, 4, parallel or approach *Uintatherium*. The other Wind River species, *C. wortmani* and *C. ventanus*, are distinguished from this by their typical metapodials, one of which is known in each type.

The associated femur (No. 2970) is proportioned like the tibia, long and slender.

Prophetic of this type, perhaps, is the pes of *Pantolambda cavirictus* (Fig. 12), in which the navicular is reduced upon the outer side and the ectocuneiform is elongated so as to nearly come in contact with the astragalus.

FOOT STRUCTURE.

Cope (1884, 1, p. 1120) proposed the theoretical groups, *Platyarthra* (with flat astragalus) and *Amblypoda hyodonta* (astragalus without a neck) from which to derive the Amblypoda. Both groups are superfluous now that it is clear that the ancestral Amblypoda can be derived directly from the Creodonta, all of which possess an astragalar neck.

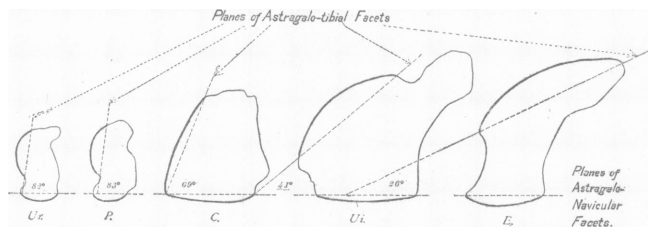


Fig. 29. Angles formed by tibio-astragalar, astragalo-navicular facets, to exhibit widening of front face of astragalus. *Ur*, *Ursus*; *P*, *Pantolambda*; *C*, *Coryphodon testis*; *Ui*, *Uintatherium*; *E*, *Elephas*.

The transition is simple. By *shortening of the neck of the astragalus* (Fig. 29 *P.* and *C.* and *Ui.*) the tibio-astragalar facet is gradually brought almost into confluence anteriorly with the astragalo-navicular facet, as in *C. radians*. In *C. lobatus* and *C. singularis* this space widens as in *Uintatherium*.

1. The variables in these feet are the *astragalar foramen* and the *tibiale facet*. From our present knowledge both these structures (inherited in *Coryphodon* from *Pantolambda*) are *useless or vestigial, inconstantly developed and therefore not constant specific characters*.

In Fig. 26 (identical with *Coryphodon* III, Cope, 1877, Pl. 60), a small astragalus and calcaneum is shown which lacks both astragalar foramen and tibiale facet. In *C. lobatus* (No. 4335, type of *C. pachypus*) there is a large tibiale facet, while the astragalar

foramen is not even grooved. In No. 2870 the tibiale facet is irregular, and a groove represents the astragalar foramen. In *C. testis*, No. 258, the tibiale facet is irregular, the astragalar foramen is wanting; in No. 2869 it is completely bridged over; in No. 4300 (Cope's cotype) it is partly bridged over.

2. In the relative constancy of the tibiale facet and of the astragalar foramen or groove, the pes of *Uintatherium mirabile* is therefore more primitive than that of *Coryphodon*.

CONCLUSION OF PART I.

The phylogenetic conclusions drawn from this analysis of the Taligrada and Pantodonta will be more fully discussed at the close of Part II of this paper, which will treat of the Dinocerata.

The two main results thus far brought out are these: First, the demonstration of a number of separate phyletic lines of Coryphodons; these lines probably represent the local differentiations of the Coryphodon type in adaptation to different feeding ranges, that is, swamp, plain, and upland. The second result is, that certain Coryphodons approach the Dinocerata in some structures as closely as they depart widely from them in others; for example, *C. armatus* resembles *Uintatherium* in canine type, but differs from it in skull type; *C. testis* approaches *Uintatherium* in the upper posterior portion of the skull, but differs from it widely in the anterior portion of the skull, and in the structure of the canine teeth; *C. radians* shows the assumption of the incisiform shape by the lower canines, so distinctive of *Uintatherium*. But no Coryphodon is fully known which fills all the conditions of an ancestor of *Uintatherium*. Until the skull of *Bathyopsis* is known the transition between the above types will remain obscure.

BIBLIOGRAPHY—PRINCIPAL REFERENCES.

- COPE, E. D. 1877.—Report upon the Extinct Vertebrata obtained in New Mexico by parties of the Expedition of 1874. U. S. Geol. Surv. west of 100th Mer. Palæontology, Vol. IV, Part ii.
- “ 1884.—The Vertebrata of the Tertiary Formations of the West. U. S. Geol. Surv., Vol. III, Part i, 1884.
- “ 1884 (1).—The Amblypoda. American Naturalist, Nov. & Dec., 1884, pp. 1110-1121 and pp. 1192-1202. Jan., 1885, pp. 40-55.

- EARLE, CHAS. 1892.—Revision of the Species of *Coryphodon*. Bull. Am. Mus. Nat. Hist., Vol. IV, 1892, pp. 149-166.
- MARSH, O. C. 1876.—On some of the Characters of the genus *Coryphodon*, Owen. Am. Jour. Sci. (3), Vol. XI, pp. 425-428, 1 pl.
- “ 1877 (1).—Brain of *Coryphodon*. American Naturalist, Vol. XI, p. 375.
- “ (2).—Principal Characters of the Coryphodontidæ. Amer. Jour. Sci. (3), Vol. XIV, pp. 81-85, pl. iv.
- “ (6).—Introduction and Succession of Vertebrate Life in America. (Vice-President's Address before the American Association for the Advancement of Science, Nashville (Tenn.) meeting, Aug. 30, 1877.) Proc. Assoc., Vol. XXVI, pp. 211-258, 1 pl. 1878.
- “ 1884 (9).—Dinocerata: A Monograph of an Extinct Order of Gigantic Mammals. With 56 plates and 200 woodcuts. Washington, 4to, XVIII, pp. 237. Author's edition.
- “ 1893 (7).—Restoration of *Coryphodon*. Amer. Jour. Sci. (3), Vol. XLVI, pp. 321-326, plates v and vi. New Haven, Oct., 1893.
- OSBORN, H. F. 1893 (4).—Rise of the Mammalia in North America. (Vice-Pres. Add. Amer. Assoc. Adv. Sci., Sec. Zool., Aug. 16, 1893.) Amer. Jour. Sci., Nov. and Dec., 1893.
- “ (5).—Fossil Mammals of the Upper Cretaceous. Bull. Am. Mus. Nat. Hist., Vol. V, p. 15, Dec. 20, 1893.
- “ 1895 (1).—Fossil Mammals of the Puerco Beds. Collection of 1892. Bull. Am. Mus. Nat. Hist., Vol. VII, Art. 1, pp. 1-70, Mch. 8, 1895. (With Charles Earle.)
- “ 1898.—A complete Skeleton of *Coryphodon radians*. Notes upon the locomotion of the animal. Bull. Am. Mus. Nat. Hist., Vol. X, April 4, 1898, pp. 81-91.