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### NEW PANTODONTA AND DINOCERATA FROM THE UPPER PALEOCENE OF WESTERN COLORADO

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ASSISTANT CURATOR OF PALEONTOLOGY

The upper Paleocene Plateau Valley beds have been famous hitherto chiefly for having yielded skeletons of the large pantodont *Barylambda faberi*. The 1932 and 1933 expeditions of Field Museum collected excellent material of this species, together with some fragmentary remains of smaller mammals which suggested that the horizon was equivalent in age to the Tiffany of southwestern Colorado (Patterson, 1936, pp. 397-398). In addition, a few teeth and bone fragments were obtained that were sufficient to indicate the presence of other large mammals in the formation, but too incomplete to provide any positive information about them. In 1935 Mr. Edwin B. Faber of Grand Junction, Colorado, to whose interest and initiative is due the discovery of the Plateau Valley horizon, collected the right  $M_2$  of a large and specialized uintathere belonging to an unknown genus. This specimen has been mentioned briefly by me (1936, p. 397) and by Scott (1937, p. 475). In the early spring of 1937 Mr. Alfred A. Look, also of Grand Junction, and his son found a partial skull of an entirely new type of pantodont. The skull was on the surface and near-by a number of bones were exposed. Upper cheek teeth of this new form were among the problematical specimens found in 1933.

In the summer of 1937, thanks to the generosity of Mr. Stanley Field, a third expedition was sent into the Plateau Valley area. The personnel consisted of Mr. James H. Quinn and myself, reinforced for parts of the season by Mr. Elmer S. Riggs, Mr. Clayton A. Quinn, and Mr. Theodore Burdosh. Mr. Look's prospect was investigated and yielded a nearly complete skeleton. Several good specimens of the large uintathere, first discovered by Mr. Faber, were recovered, as well as remains of a smaller form of the same group. Mr. Quinn was so fortunate as to unearth a partial skeleton of a

small pantodont related to *Barylambda*. In addition to the outstanding discoveries of the larger forms, a small collection of medium-sized mammals was made. No true microfauna has yet been found, a lack which is in striking contrast to other upper Paleocene localities.

Detailed description of this new material has been delayed by pressure of other work, particularly by research on parts of the South American collections brought together by the Marshall Field expeditions. In view of this situation and because of the importance of the new pantodont and uinthere material—it is safe to state that it profoundly modifies current concepts of these two groups—it has been decided to bring out this preliminary paper.

Grateful acknowledgments are due to my companions in the field, and to those residents of Mesa County who aided in collecting specimens or who facilitated our work in other ways. In particular, I may mention Mr. Faber and Mr. Look, Mr. J. Elvin Harris and Mr. Douglas Harris and their families, of Mesa, and Mr. Hatton Edgerley of DeBeque. The preparation of the material has been carried out with great skill by Mr. Quinn. The photographs are the work of Mr. C. H. Carpenter, the retouching is by Mr. Carl F. Gronemann, and the drawings are by Mr. Frank Gulizia.

### Order Pantodonta<sup>1</sup> Cope

#### Family Coryphodontidae Marsh 1876

#### *Sparactolambda*<sup>2</sup> gen. nov.

*Type species*.—*S. looki* sp. nov.

*Distribution*.—Upper Paleocene, Plateau Valley beds, Colorado.

*Diagnosis*.—Dentition  $I\frac{2}{3}$   $C\frac{1}{1}$   $P\frac{4}{4}$   $M\frac{3}{3}$ . Upper canine enlarged, tusk-like;  $P^{3-4}$  with antero-posteriorly compressed protocones,

<sup>1</sup> Simpson (1937a, pp. 265–269) has discarded the old name Amblypoda altogether, and has employed Pantodonta for the natural group composed of *Coryphodon*, *Pantolambda*, and their allies. My own preference would have been to restrict the term Amblypoda to this group, and a fairly sound case could have been made for such a procedure. In his original description of Amblypoda (1875, p. 23) Cope stated that he proposed “. . . to regard *Bathmodon* [= *Coryphodon*] as the type of a distinct order of *Mammalia*, which will also include the genera *Loxolophodon* and *Uinthereium* in a distinct subdivision.” This would indicate that he had the coryphodonts primarily in mind when he proposed the order, and is somewhat at variance with Simpson’s statement that Amblypoda was based “. . . about equally on the coryphodonts and the uintheres.” However, as Simpson has pointed out, “Amblypoda” has so long been employed to cover an unnatural association of three distinct groups that continued usage of the term, even in a restricted sense, would probably be confusing, and for this reason it is perhaps desirable to eliminate it entirely.

<sup>2</sup> In allusion to its probable pulling-feeding adaptation (see below), and to its tooth structure and relationship with the other *-lambda* genera.

cingula running internally from bases of paracones and metacones not connected to apices of protocones; upper molars broader antero-posteriorly and narrower transversely than in *Barylambda*, proportions of  $M^1$  to  $M^2$  to  $M^3$  about as in *Pantolambda* and *Coryphodon*, paracones notably more internal than metacones. Lower incisors broader and less conical than in *Barylambda* and *Pantolambda*, approaching those of *Coryphodon*; lower canine very large and long antero-posteriorly, crown consisting of an anterior, pointed, slightly recurved apex and a long, blunt edge or blade sloping downward and backward, root very stout, buttressed antero-internally and tapering posteriorly—altogether a unique tooth;  $P_1$  with paraconid and metaconid well differentiated,  $P_2$  with large centrally situated metaconid; lower molars without metastylids, lower crowned and with trigonids and talonids of  $M_{1-2}$  farther apart than in *Barylambda*.

Head rather smaller in proportion to body size than in *Coryphodon*, larger in proportion than in *Barylambda* and *Pantolambda*. Skull with anterior narial opening terminal; muzzle flaring; premaxillaries very short, ascending rami confined to narial opening and not appearing on side of face; nasals narrow, as in *Coryphodon*, not greatly expanded posteriorly, in contact with maxillaries for nearly all their lengths; zygomatic arches slighter than in *Coryphodon*, but flared outward as in that form; sagittal crest high, long; occiput decidedly triangular, condyles not extending posteriorly beyond it. Mandible with horizontal ramus increasing in depth anteriorly; chin deep, abrupt, and strong; condyle nearly on level with cheek teeth; coronoid process comparatively low; angle not extending posteriorly beyond condyle.

Neural arches of cervicals greatly strengthened; centra of dorsals and lumbar considerably longer than in *Barylambda*; sacrum low; anterior caudals flattened dorso-ventrally, tending to unite with sacrum.

Clavicle thick, very deep. Head of humerus wider antero-posteriorly than in *Coryphodon*, with anterior groove as in that genus, articular surface extending on to great trochanter; deltoid crest high, thinner transversely than in *Barylambda*; entepicondylar foramen present, situated high on entepicondyle. Centrale completely united with cuneiform, forming a thick wedge between lunar and trapezoid; magnum not articulating with Mc. II; ungual phalanges deep, short claws.

Pelvis approaching that of *Coryphodon*, ilium not as expanded. Tarsus very *Coryphodon*-like, astragalus without neck; metatarsals

stouter than in *Barylambda*, Mt. V with very large, robust, peg-like lateral process.

***Sparactolambda looki*<sup>1</sup> sp. nov.**

*Holotype*.—F.M. No. P15520, partial skeleton.

*Horizon and locality*.—Plateau Valley beds, about 80 feet above the base, three miles west of DeBeque (one mile west of the Finley Ranch House), Mesa County, Colorado; found by Alfred A. Look.

*Paratype*.—F.M. No. P15523, incomplete skull, sacrum, right os innominatum. Found by Alfred A. Look one-quarter mile west of the holotype.

*Diagnosis*.—As for the genus; for measurements see pages 360–361.

*Discussion*.—This animal is of extraordinary interest from two points of view. In the first place, it shows profound structural modifications in response to the acquisition of an unusual habitus, one hitherto unknown among the Pantodonta. In the second, it is, apart from these modifications, intermediate in many respects between *Pantolambda* and *Coryphodon*, and therefore of great importance in pantodont phylogeny. The habitus adaptation may be briefly discussed first in order to clear the way for consideration of the more important although somewhat less spectacular characters of taxonomic significance.

*Sparactolambda* presents the following combination of unusual features: large, unique lower canine consisting of anterior hook and posterior blade, heavy chin (associated with the canine development), low coronoid and condyle, small angle (in comparison with other pantodonts), greatly strengthened cervicals, strong clavicle, and clawed manus. In addition, the ulnar articulation on the humerus is very extensive, the upper lip of the sigmoid notch is slight, thereby permitting great mobility, and there is a tendency toward the development of grooves and rugosities above the distal articular surfaces of the metacarpals, seen particularly on Mc. II, as in the chalicotheres and certain carnivores. This array may most logically be interpreted as an adaptation to a diet consisting in large part of roots and underground tubers. These presumably were laid bare by the powerful claws and then caught up by the hooks of the lower canines. They were then further uprooted by pulling and jerking the head and neck—the strong dorsal neck muscles imparting great power to these movements<sup>2</sup>—and sliced

<sup>1</sup> Named for Mr. Alfred A. Look, the discoverer of the type specimens.

<sup>2</sup> Bohlin believes, correctly I think, that dorsal thickening of chalicothere cervicals is indicative of similar habits (1936, p. 325).



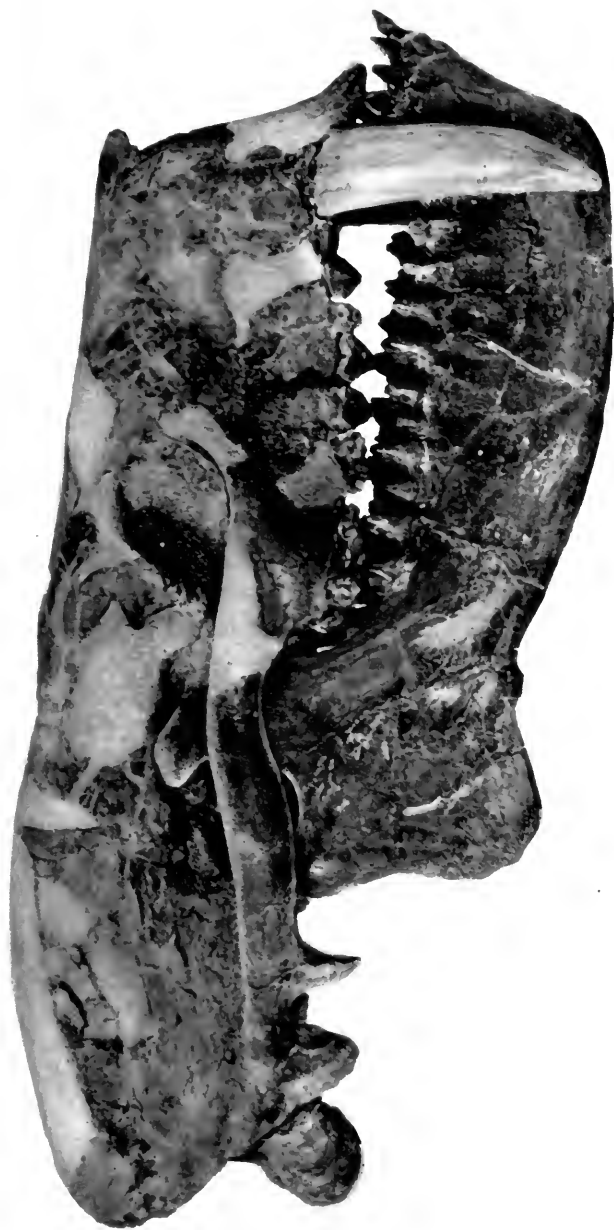


FIG. 100. *Sparactolambda looki* gen. et sp. nov. Skull and jaws, right lateral view. F.M. No. P15520, holotype, and F.M. No. P15523, paratype. Upper canine restored from holotype.  $\times \frac{2}{3}$ .

off by the upper canines acting against the blades of the lower. The reduced coronoids and angles and the low condyle permitted a gape sufficiently wide for the mandible to clear the upper canines.

Certain heritage characters, such as the clavicle and the prominent deltoid crest of the humerus, which did not come into existence *pari passu* with the acquisition of this adaptation, were nevertheless of great use to it and probably underwent additional responsive modification. The upper canine probably comes under this category. If *Sparactolambda*, as I believe, is to be regarded as an offshoot of a stock that was approaching *Coryphodon* from a *Pantolambda*-like ancestry, then an enlarged upper canine was very likely a part of its heritage. Such a structure would have been of advantage in the development of the feeding mechanism suggested above, in all probability playing a large part in conditioning the peculiar shape of the lower canine. Incorporation of the upper canine into this mechanism may in part explain those features—more vertical implantation and more compressed form—in which it differs from that of *Coryphodon*.

Turning now to the taxonomic bearing of this new form, those characters, apart from the adaptive modifications just mentioned, in which it compares or contrasts with *Pantolambda*<sup>1</sup> and *Coryphodon* may be reviewed briefly.

*Dentition.*—In the upper canine and lower incisors *Sparactolambda* approaches closer to *Coryphodon* than does any other early pantodont now known. The premolars, as indicated in the diagnosis, display some distinctive characters of their own; the lower molars have strong paraconids, somewhat more prominent than those of *Pantolambda*. The upper molars resemble those of the two genera under comparison both in intramolar and in length-width proportions, but seem to be aberrant in that the paracone is much more internal in position than the metacone. At first sight this condition might be interpreted as supporting Matthew's view of the homologies of the coryphodont molar (1928, p. 970; see Simpson, 1929, fig. 5B, for graphic representation). The structural series of *Pantolambda* and *Coryphodon* milk and permanent molars presented by Simpson (1929, pp. 5, 6, fig. 6), however, strongly suggests that the paracone migrated outward rather than inward in the coryphodont phylum. For the present at least it seems preferable to regard the internal paracone as a peculiarity of the *Sparactolambda* phylum.

<sup>1</sup> Comparisons made with *P. bathmodon* (Matthew, 1937, pp. 167–180, figs. 38–42, pls. 40–50). I suspect that *P. cavirictus* may represent another genus.

*Skull*.—Apart from the notably shortened premaxillaries, a character probably correlated with the feeding mechanism, the skull is almost ideally transitional between *Pantolambda* and *Coryphodon*, and has on the whole a decidedly *Coryphodon*-like appearance. The muzzle is rather more expanded than that of the former genus and is about as much so as that of the latter. The arches are comparable in slenderness to those of the Torrejon genus but are bowed outward to nearly the same extent as in *Coryphodon*. The sagittal crest does not extend as far forward as in *Pantolambda* and would require but little widening to bring it to the condition seen in *C. wortmani* (Osborn, 1898, fig. 18B, p. 194). The basicranial region is not as compressed antero-posteriorly as that of *Coryphodon*, being about as long as in *Pantolambda*.

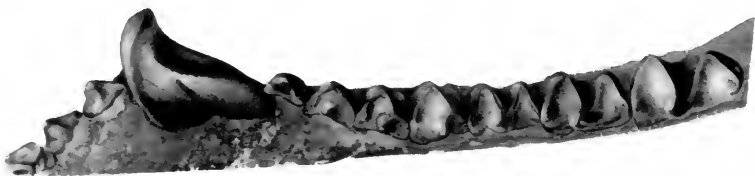


FIG. 101. *Sparactolambda looki* gen. et sp. nov. Right lower dentition, crown view. F.M. No. P15520, holotype.  $\times \frac{1}{2}$ .

*Vertebrae*.—The formula cannot be determined at present. The dorsals and lumbers agree with those of *Pantolambda* and *Coryphodon* in having much longer centra than those of *Barylambda*. The structure of the sacrum and anterior caudals of *Sparactolambda* constitutes one of the most interesting and important resemblances to *Coryphodon* in the entire skeleton. The sacrum in both genera is decidedly flattened, the posterior centrum being very thin dorso-ventrally. One of the notable features of *Coryphodon* is the presence of a long pseudosacrum composed of five or more vertebrae. This was first reported by Osborn (Osborn and Wortman, 1892, p. 120) who found it detached, and suspected that it might have occurred in the distal half of the tail. The true structure has only recently been revealed by specimens in the United States National Museum and in the Museum of Comparative Zoology (Patterson, 1939). The pseudosacrals are exceedingly flat and are united to each other by the neural spines and transverse processes as well as by the centra. Two incomplete pseudosacrals are preserved in the holotype of *Sparactolambda* and these, as far as preserved, are almost identical with those of *Coryphodon*.

*Shoulder girdle and fore limb.*—The scapulae are unfortunately incomplete; the parts preserved indicate, however, that they were somewhat wider than in *Coryphodon* and hence probably closer in proportions to those of *Pantolambda*; the coracoid process is extremely long and robust. On the other hand the humerus resembles that of the lower Eocene rather than that of the Torrejon form, especially, as noted in the diagnosis, in the structure of the head; the anconeal fossa is much shallower than in *Coryphodon*. Since an entepicondylar foramen is now known to occur in certain specimens of *Coryphodon* (Patterson, 1939), the presence of this element in *Sparactolambda*

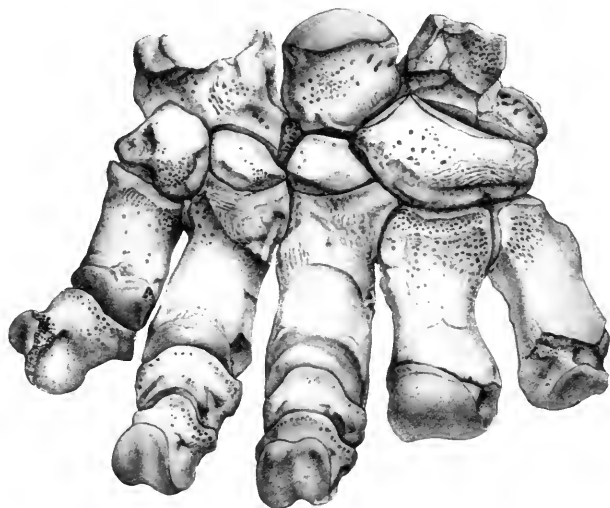


FIG. 102. *Sparactolambda looki* gen. et sp. nov. Left manus. F.M. No. P15520, holotype.  $\times \frac{1}{2}$ .

does not constitute a difference between the two forms. The ulna is close to that of *Coryphodon* in massiveness, in the posterior bowing of the shaft, and in the inclination of the olecranon, but differs in the less produced upper border of the sigmoid notch, as noted above, and in the much less rounded lateral and medial borders of the shaft. The radius is closer to that of *Coryphodon* both in shape and proportions than it is to that of *Pantolambda*.

The manus combines features of both genera in a most instructive manner. The lunar is more nearly as in *Pantolambda* and not as wide as in *Coryphodon*.<sup>1</sup> The scaphoid and centrale are completely

<sup>1</sup> The various species of *Coryphodon* exhibit some variation in the development of these features.

fused, as noted in the diagnosis, the centralar portion being nearly as large as the separate bone in *Pantolambda*. Matthew long ago suspected (1897, p. 321) that the pantodont centrale disappeared by absorption and not by fusion. If the condition in *Sparactolambda* is a reliable criterion, it would seem that fusion preceded absorption, which would account satisfactorily for the small, thin scaphoidal wedge extending between the lunar and trapezoid of *Coryphodon*. In the distal carpal row the trapezium > magnum > trapezoid,<sup>1</sup> as in *Coryphodon* and in contrast to *Pantolambda* (Osborn, 1898, p. 187). On the other hand the unciform does not cover more of the proximal end of Mc. III than does that of *Pantolambda*,<sup>2</sup> and likewise the magnum does not articulate with Mc. II. The metacarpals are relatively a little larger than in *Coryphodon* but are notably broader than in *Pantolambda*. The proximal phalanges are shorter than in *Pantolambda*, but longer than in *Coryphodon*; the intermediate ones are about as long as in the former. They are robust, and have very deep, grooved articular surfaces for the claws.

*Pelvis and hind limb.*—The pelvis has advanced far beyond the condition seen in *Pantolambda*. The ilium has lost the trihedral rod-like shape, and has expanded into a broad flat plate resembling, but not as large as, that of *Coryphodon*. The antero-external angle has begun to be carried backward, resulting in a rounded supra-iliac border. The flange along the medial border described by Matthew in *Pantolambda* is absent. The ischium and pubis are shortened to almost the same extent as in *Coryphodon*. The proportions of the post-acetabular lengths, measured from a point opposite the center of the acetabulum, to the total pelvic lengths in the three genera is as follows: *Pantolambda*<sup>3</sup> 47 per cent, *Sparactolambda* 41 per cent, *Coryphodon*<sup>3</sup> 38–40 per cent. Matthew (1937, p. 177) suspected that the differences between the ilia of *Pantolambda* and *Coryphodon* might be due largely to size, but stated, nevertheless, that the shape of the ilium "... forms a striking difference between taligrades and amblypods as at present known, and emphasizes the relationship between taligrades and condylarths." I believe that the *Sparactolambda* ilium satisfactorily disposes of this argument. The only femur preserved is too crushed for accurate comparison; it may be noted, however, that the third trochanter is considerably higher than in either *Pantolambda* or *Coryphodon*. The cnemial crest of the

<sup>1</sup> I.e. in area of anterior faces, to which Osborn was presumably referring.

<sup>2</sup> See footnote, page 358.

<sup>3</sup> Measured from the published figures of Matthew, Cope, and Osborn.

tibia does not extend as far distally as in the Torrejon genus. In common with the manus, the pes combines features of both genera. The astragalus, the foot bone which has been most heavily emphasized taxonomically, agrees in every essential with that of *Coryphodon*. The calcaneum and navicular are closer to those of *Pantolambda*, the former having a smaller fibular facet and a more slender tuber calcis than the calcaneum of *Coryphodon*. The distal



FIG. 103. *Sparactolambda looki* gen. et sp. nov. Right pes. F.M. No. P15520, holotype.  $\times \frac{1}{2}$ .

tarsals are arranged as in *Pantolambda* and are not displaced on the metatarsals as they are in *Coryphodon*. The metatarsals, on the other hand, are much shorter than in *Pantolambda*.

#### MEASUREMENTS

(In millimeters)

P15520	C	P <sup>1</sup>	P <sup>2</sup>	P <sup>3</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>
A-p diam.*.....	32.4	12.3	11.0	11.8	14.5	17.8	19.5
Tr. diam.†.....	14.0	8.9	23.4	....	22.3	28.5	32.4

P15523					M <sup>1</sup>				M <sup>2</sup>		M <sup>3</sup>	
A-p diam.*	.....	.....	.....	.....	.....	15.0	18.4	.....	.....	.....	.....	.....
Tr. diam.†	.....	.....	.....	.....	.....	23.3	28.2	31.6	.....	.....	.....	.....
P15520	I <sub>1</sub>	I <sub>2</sub>	I <sub>3</sub>	C	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	
A-p diam.*	10.0	13.9	13.8	43.0	12.8	11.0	13.3	14.7	19.0	23.3	29.7	
Tr. diam. trigonid†	6.0	7.8	8.2	22.3	8.0	12.0	13.8	15.0	14.4	16.0	17.9	
Tr. diam. talonid†	.....	.....	.....	.....	.....	.....	.....	.....	13.4	15.2	15.8	

\* Measured from mid-points of anterior and posterior faces.

† Maximum.

#### SKULL (P15523)

Length from posterior border of canine to condyle	325
Depth of facial region at anterior border of orbit	85
Width across zygomatic arches	232
Width of occiput	123
Depth of occiput to ventral rim of foramen magnum	92

#### MANDIBLE (P15520)

Length from anterior border of symphysis to posterior border of condyle	290
Depth of ramus at anterior border of M <sub>1</sub>	59

To sum up, knowledge of *Sparactolambda* enables us to unite *Pantolambda* and *Coryphodon* much more closely than has been possible hitherto. These three genera seem to constitute a natural group distinguished in many ways from *Barylambda* and its newly discovered ally, *Haplolambda* (diagnosed below). In view of this, the old classification that placed *Barylambda* and *Pantolambda* in one family and *Coryphodon* in another no longer seems to be in accord with the facts. As pointed out in greater detail below (pp. 369-373), it now seems necessary to suppress the family Pantolambdidae and to elevate the following group from subfamily to family status.

#### Family Barylambdidae Patterson, 1937 (new usage)

##### Barylambda Patterson.

*Barylambda* Patterson 1937, Field Mus. Nat. Hist., Geol. Ser., 6, pp. 229-231.

A detailed account of this form was nearly ready for publication at the time the 1937 expedition left for the field, but was immediately rendered out of date by the discoveries made in that season. It was then decided to defer full publication until a complete account of all the upper Paleocene Pantodonta could be prepared. To facilitate comparisons with the newly defined genera I give here the emended diagnosis.

I<sup>3-2</sup><sub>3</sub> C<sup>1</sup><sub>1</sub> P<sup>3</sup><sub>4</sub> M<sup>3</sup><sub>3</sub>. First and second upper incisors small, conical, I<sup>1</sup> sometimes absent; I<sup>3</sup> large, caniniform. Canine moderately enlarged. Upper molars fully selenodont, narrower antero-posteriorly and wider transversely than in Coryphodontidae and M<sup>1</sup> relatively larger. Lower incisors conical, increasing in size from I<sub>1</sub> to I<sub>3</sub>. Lower canine medium sized. Lower premolars with paraconid

wings directed well anteriorly, especially on  $P_{\overline{2}-\overline{3}}$ .  $M_{\overline{1}}$  larger,  $M_{\overline{3}}$  smaller relative to  $M_{\overline{2}}$  than in Coryphodontidae; metastylid rudimentary on  $M_{\overline{1}-\overline{2}}$ , developed on  $M_{\overline{3}}$ , metastylid ridges running downward and backward well into the talonid valleys.

Skull with anterior nares terminal; muzzle not expanded; facial region short, wide, deep; nasals very wide, greatly expanded posteriorly; premaxillaries weak, not sutured medianly, ascending rami barely appearing on side of face and not reaching nasals; skull roof extremely wide and somewhat flattened across orbits; temporal ridges strong; zygomatic arches but little bowed outwardly; cranium low; occiput semicircular, condyles extending well beyond it posteriorly. Symphysis of mandible long, sloping; coronoid process high; angle large.

Cervicals with exceedingly weak neural arches; dorsals and lumbar very short in comparison with those of Coryphodontidae; sacrals with high spines, transverse processes and ribs greatly expanded and encroaching upon gluteal face of ilium; tail long, massive, provided with chevrons, deeper than wide anteriorly, spines of anterior caudals high, centra notably longer than those of dorso-lumbar, neural arches complete on anterior half of series.

Clavicle present, well developed. Scapula almost as wide as long; suprascapular border extensive, gently arched; acromion process long, robust. Head of humerus large, very deep antero-posteriorly, without anterior groove, articular surface not extending on to great trochanter; deltoid crest very strong, wide; entepicondylar foramen present. Manus with large separate centrale; magnum articulating with Mc. II; phalanges shortened; unguals broad, flat, those of digits II-IV deeply fissured.

Pelvis exceedingly broad; ilium shorter antero-posteriorly than in *Sparactolambda* or *Coryphodon*, antero-external angle considerably more anterior in position than in the genera just mentioned and bearing a plate-like process,<sup>1</sup> ilium notched medially by gluteal process of sacrum. Femur broad, flattened antero-posteriorly, no pit for ligamentum teres in head. Tibia and fibula much more massive than in Coryphodontidae. Pes with heavy tarsus, relatively slender metatarsus and phalanges; astragalus without neck; calcaneum with very robust tuber calcis, fibular facet small<sup>2</sup> or absent;

<sup>1</sup> By a *lapsus calami* in an earlier paper (Patterson, 1935, p. 154) this process was stated to be on "the antero-internal corner."

<sup>2</sup> Stated to have been entirely wanting (Patterson, 1935, p. 158), but present on a specimen prepared subsequently.





FIG. 104. *Barylanbda faberi* Patterson. Left lateral view of skeleton. F.M. No. P14945. Skull, epiphyses of scapulae and pelvis, left lower leg and pes largely restored from other individuals. Approximately  $\times \frac{1}{14}$ .

distal tarsals not displaced on metatarsals; phalanges shorter than in *Pantolambda*, longer than in *Coryphodon*; unguals small.



FIG. 105. *Barylambda faberi* Patterson. Posterior view of skeleton. F.M. No. P14945. Epiphyses of pelvis, left lower leg and pes largely restored from other individuals. Approximately  $\times \frac{1}{10}$ .

**Barylambda faberi** Patterson.<sup>1</sup>

*Titanoides faberi* Patterson 1933, Amer. Journ. Sci., (5), 25, pp. 415-425; 1934, Proc. Amer. Phil. Soc., 73, pp. 71-101; 1935, *ibid.*, 75, pp. 143-162.

*Barylambda faberi* Patterson 1937, Field Mus. Nat. Hist., Geol. Ser., 6, pp. 229-231.

The largest known pantodont;<sup>2</sup> for preliminary description and discussion see the papers cited.<sup>3</sup> A left lateral view and a posterior view of the mounted skeleton are given here. These supplement a right lateral view given by Scott (1937, fig. 302, p. 480) and an oblique front view published in the Field Museum Annual Report for 1937 (pl. 21).

**Haplolambda**<sup>4</sup> gen. nov.

*Type species*.—*H. quinni* sp. nov.

*Distribution*.—Upper Paleocene, Plateau Valley beds, Colorado.

*Diagnosis*.—Generally similar to *Barylambda* in the known parts, differing as follows: canines very small;  $M_3^a$  reduced, metacone of  $M^a$  vestigial, talonids of  $M_{1-2}$  narrower. Skull with much weaker temporal ridges. Mandibular ramus more slender, symphysis shorter. Shaft of radius more slender, proximal and distal ends notably wider. Trapezium and Mc. I completely fused, the compound bone having a double articulation with Mc. II, the additional articular surface situated below, slightly behind and almost at a right angle to the usual one; Mc. V wider, nearly twice as wide as the other metacarpals, distal articular surface with median constriction.

**Haplolambda quinni**<sup>5</sup> sp. nov.

*Holotype*.—F.M. No. P15542, anterior half of skeleton.

<sup>1</sup> The parentheses surrounding the author's name have been omitted. See W. H. Osgood, "An Outworn Nomenclatural Practice," Science, n.s., 89, pp. 9-11, 1939.

<sup>2</sup> I know of no *Coryphodon*, certainly of no mounted specimen, that exceeds *Barylambda* in size.

<sup>3</sup> I may mention here that the isolated tibia and fibula (F.M. No. P14904) referred to this species in 1934 (pp. 88-91, figs. 10-11) appear, in comparison with material obtained later, to be too small for this species. Among the undetermined specimens collected in 1937 are some jaw fragments of a pantodont similar to *Barylambda* and *Haplolambda*, and intermediate in size between them. It is possible that the bones in question belong to this form.

<sup>4</sup> In allusion to its less spectacular appearance when compared with *Barylambda* and *Sparactolambda*, and to its tooth structure and relationship with the other *-lambda* genera.

<sup>5</sup> Named for Mr. James H. Quinn, the discoverer of the holotype specimen, without whose diligent and successful collecting the Plateau Valley faunal list would be much smaller than it is.



FIG. 106. *Haplolambda quinni* gen. et sp. nov. Skull and jaws, left lateral view. F.M. No. P15542, holotype.  $\times \frac{3}{5}$ .

*Horizon and locality.*—Plateau Valley beds, fifteen feet above the base. One and one-half miles north of Mesa and about 75 yards east of the DeBeque-Mesa road.

*Diagnosis.*—As for the genus; known parts comparable in size to *Pantolambda cavirictus*; for measurements see below.

The entepicondyle of *Haplolambda* appears to be considerably reduced in comparison with that of *Barylambda*, but, since the humeri were in fragments and the entepicondylar contacts not exact, I have refrained from mentioning this probable additional character in the diagnosis. The discovery of this new Paleocene genus, which is more closely related to *Barylambda* than to *Pantolambda* and



FIG. 107. *Haplolambda quinni* gen. et sp. nov. Left upper cheek teeth, crown view. F.M. No. P15542, holotype.  $\times \frac{1}{4}$ .

*Sparactolambda*, is, for pantodont phylogeny, an event second only in importance to the finding of *Sparactolambda* itself. It is greatly to be hoped that future field work will bring to light the posterior half of the skeleton, and reveal how far this medium-sized animal had progressed toward the acquisition of graviportal characters in the pelvis and how close the structure of the sacrals and caudals is to that of *Barylambda*.

#### MEASUREMENTS

(In millimeters)

	(all measurements)										
	P <sup>1</sup>		P <sup>2</sup>	P <sup>3</sup>		P <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>		M <sup>3</sup>	
A-p diam.*.....	...	...	9.7	9.8	11.6	15.9	13.8	11.9	...	...	
Tr. diam.†.....	8.7	21.0	24.0	24.5	27.8	29.4	25.2	...	...	...	
	I <sub>1</sub>	I <sub>2</sub>	I <sub>3</sub>	C	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
A-p diam.*.....	6.5	8.2	10.0	8.7	13.0	16.1	15.9	17.3	18.0	18.9	...
Tr. diam. trigonid†	5.2	5.8	7.4	7.3	8.2	13.1	14.3	....	15.0	12.2	...
Tr. diam. talonid†	...	...	...	...	...	...	...	....	11.6	10.0	...

\* Measured from mid-points of anterior and posterior faces. † Maximum.

#### SKULL

Length premaxillary to condyle.....	282
Width across zygomatic arches.....	152
Depth of face at anterior border of orbit.....	65
Width of occiput.....	101
Depth of occiput from apex to ventral rim of foramen magnum.....	52

#### MANDIBLE

Length anterior border of symphysis to posterior border of condyle.....	222
Depth of ramus beneath anterior border of M <sub>1</sub> .....	30

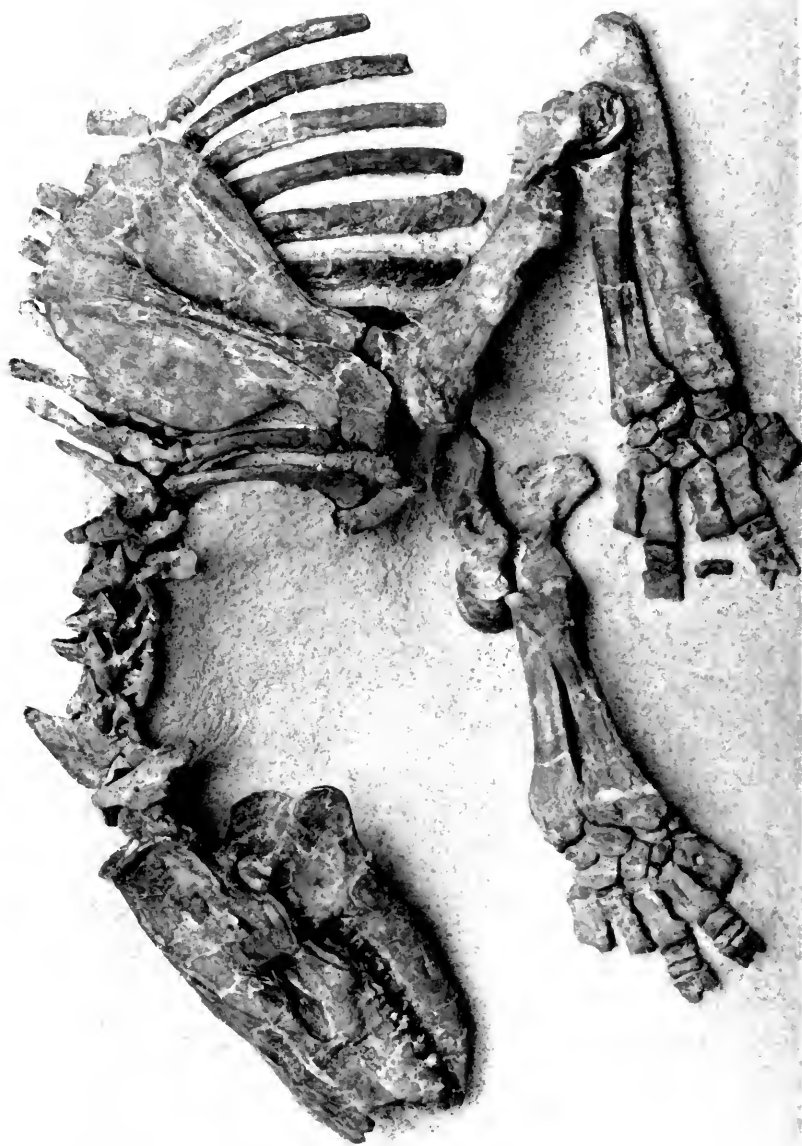


FIG. 108. *Haplolambda quinni* gen. et sp. nov. F.M. No. P15542, holotype, as mounted. Approximately  $\times \frac{1}{5}$ .

## THE TAXONOMY OF THE PANTODONTA

Until very recently it was generally supposed, largely as a result of Osborn's work (1898), that *Coryphodon* was closely related to the uinatheres, and that *Pantolambda*, although showing some resemblances to *Coryphodon*, was a near ally of the periptychids. This view found extreme expression in Matthew's great monograph on the Puerco-Torrejon faunas (1937) in which, following Gregory (1910), *Pantolambda* and *Coryphodon* were separated ordinally. Although Matthew tended in general to favor the "horizontal" method of classification it would appear from his text that he was not entirely satisfied with it in this case. Thus in one place (p. 172) he says of *Pantolambda* that "it is a very primitive type, and its amblypod affinities have been unduly stressed"; in another (p. 163), "*Coryphodon* should be derived from some as yet undiscovered genus of Pantolambdidae . . ."; and again (p. 183), "Nevertheless, it [*P. cavirictus*] may serve to show that a great part of the difference between the two genera [*Pantolambda* and *Coryphodon*] is merely due to the difference in size and does not indicate any wide diversity of origin." The discovery of *Barylambda*, a graviportal form combining resemblances to *Pantolambda* with structural approaches to *Coryphodon*, occurred subsequent to Matthew's death but prior to the appearance of his monograph. The combination of characters exhibited by this animal indicated that Matthew's last quoted suggestion was correct and that *Pantolambda* and *Coryphodon* were members of a natural group—the assemblage now known as the order Pantodonta. Recognition of this fact supported ordinal separation of the uinatheres (a separation that I believe to be firmly established by the new material described below), and at the same time cast doubt on the reality of the supposed *Pantolambda*-periptychid relationships (Patterson, 1934, pp. 95-97). This latter question has been settled recently by Simpson (1937a, pp. 216-224) who, after a thorough re-examination of all evidence, has concluded that the Periptychidae should be replaced in the Condylarthra. With this transfer accomplished the last of the obstructions that interfered with a proper conception of the three orders concerned has been removed and the way cleared toward a better understanding of them. The scheme of classification to be presented below is about as far removed as possible from Matthew's placing of *Pantolambda* and *Coryphodon* in different orders. The evidence herein reported may make it appear that he was unduly conservative but it must be remembered that all the new material bearing on pantodont

phylogeny has only been made available during the past five years. *Pantolambda* is a generalized form so much more primitive than *Coryphodon* that, lacking knowledge of the intermediates, no cautious investigator would have been justified in connecting the two except in the broadest way.

Prior to the discovery of the new genera here described, the American Pantodonta<sup>1</sup> seemed to fall naturally into two divisions—the Coryphodontidae and the Pantolambdidae. Reference of *Barylambda* to the latter family was the only course then possible, although it was recognized that the animal was not a descendant of *Pantolambda*. The selenodont dentition, small size of the head in comparison with that of the skeleton, presence of a centrale, tail size, and various other osteological features of *Barylambda* were regarded as family characters of the Pantolambdidae (Patterson, 1934, 1935).

It has been pointed out above that *Haplolambda* is, in its known parts, essentially a small edition of *Barylambda* and that *Sparactolambda* is structurally intermediate between *Coryphodon* and *Pantolambda*. The characters in which these two groups of genera contrast with each other may now be reviewed:

<i>Coryphodon</i> group	<i>Barylambda</i> group
Dentition	Dentition
Molars increasing in size posteriorly; <sup>2</sup> upper molars wider antero-posteriorly along ectolophs and narrower transversely; lower molars usually without metastylids.	M <sup>2</sup> largest, M <sup>1</sup> large, M <sup>3</sup> comparatively small; M <sub>1</sub> relatively larger, M <sub>3</sub> relatively smaller than in the <i>Coryphodon</i> group; upper molars wide transversely, narrow along ectolophs; metastylids rudimentary on M <sub>1-3</sub> , developed on M <sub>3</sub> .
Skull	Skull
Muzzle and arches flared; nasals comparatively narrow, moderately expanded posteriorly; facial region but little deeper than cranial; occiput extending posteriorly beyond condyles.	Muzzle and arches not flared; nasals very wide, greatly expanded posteriorly; facial region notably deeper than cranial; condyles extending posteriorly beyond occiput.
Vertebrae	Vertebrae
Dorsals and lumbar s comparatively long; sacrum flattened dorso-ventrally, spines low; tail originally long but reduced in later genera, without chevrons, anterior caudals much flattened in later genera and tending to unite with sacrum.	Dorsals and lumbar s much shortened; sacrum with high spines, transverse processes and ribs forming a crescent-shaped mass that encroaches upon gluteal face of ilium; tail very large, provided with chevrons, deeper than wide anteriorly.

<sup>1</sup> The Mongolian Pantolambdodontidae are not discussed here.

<sup>2</sup> A tendency rather than a hard and fast rule. Certain of the *Coryphodon* specimens figured by Cope have M<sup>2</sup> as large as, perhaps slightly larger than M<sup>3</sup>. M<sub>1</sub> tend to be larger in *Pantolambda* (cf. Matthew's figures) than in *Coryphodon*; *Sparactolambda* is closer to the latter in this respect.



## Manus

Centrale small, becoming fused with scaphoid and finally reduced to a vestige.

## Pelvis and hind leg

Ilium developing from a trihedral rod-like form to a broad flat plate on which the antero-external angle is carried well backward.

## Manus

Centrale large (possibly enlarged from the primitive condition).

## Pelvis and hind leg

Ilium very broad, antero-external angle situated somewhat farther forward. Femur with flatter and broader shaft, tibia and fibula shorter and stouter than in the *Coryphodon* group.

I believe that the two generic groups just contrasted may be regarded as natural assemblages. It would seem therefore that the division of the American Pantodonta into Coryphodontidae and Pantolambdidae was a horizontal arrangement, with the latter family containing members of divergent stocks, rather than a natural classification. In this light a re-appraisal of the resemblances between *Pantolambda* and *Barylambda* strongly suggests that the points of similarity are due to common retention of heritage characters (probably ordinal) and do not necessarily indicate close relationship. In fact the differences between the two genera now appear to be more important than the resemblances, and no good reason remains for referring them to the same family. The validity of the Pantolambdidae depends therefore upon whether it can properly be retained for a part of the *Coryphodon* group. *Sparactolambda* seems to me to prevent any such arrangement. Combining as it does the molar structure of *Pantolambda* with many skeletal characters hitherto regarded as typical of *Coryphodon*, it renders family separation of the extremes of the *Coryphodon* group impracticable if not impossible. Attempts to force *Sparactolambda* into narrowly redefined Pantolambdidae or Coryphodontidae result in a manifestly artificial and thoroughly unsatisfactory arrangement. The new evidence seems to require that the Pantolambdidae be suppressed, that the Coryphodontidae be broadly redefined so as to include *Pantolambda* and *Sparactolambda*, and that the *Barylambda* group be given family status.

The families may be defined as follows:

Coryphodontidae:<sup>1</sup> Medium-sized to large animals. Molars tending to increase in size posteriorly; earlier genera with fully selenodont upper molars, later genera with crescents considerably modified; lower molars usually without metastylids; canines becoming tusk-like in certain genera.

<sup>1</sup> The Coryphodontidae are a more inclusive group than the Barylambdidae and it is conceivable that future discoveries may necessitate the erection of subfamilies. *Pantolambda* may eventually be separable as a persistent primitive and *Sparactolambda* as an aberrant adaptive type, but such a course would be decidedly premature at present.

Head increasing in size relative to size of skeleton; muzzle flaring; nasals of moderate width; skull roof broad and flat posteriorly in late forms. Dorsal and lumbar vertebrae comparatively long; sacrum with low spines, becoming flattened; tail originally long but undergoing progressive reduction, without chevrons, anterior caudals flattened in later genera and tending to fuse with sacrum. Centrale small in early forms, becoming fused with scaphoid and largely absorbed in later. Ilium developing from a trihedral rod-like structure to a broad flat plate with the antero-external angle carried well backward in the terminal genera.

*Barylambdidae*: Medium-sized to large animals.  $M_1^1$  larger,  $M_3^3$  smaller relative to size of  $M_2^2$  than in *Coryphodontidae*; upper molars remaining fully selenodont; lower molars developing metastylids; canines small to moderately enlarged. Head remaining small relative to size of skeleton; muzzle not flared; nasals very wide, greatly expanded posteriorly. Dorsal and lumbar vertebrae short; sacrum with high spines, transverse processes and ribs forming a crescent-shaped mass that encroaches upon gluteal face of ilium; tail very large, with chevrons, deeper than wide anteriorly. Centrale large, remaining separate. Ilium very broad, antero-external angle not carried as far backward as in later *coryphodontids*. Tibia and fibula short, stout.

Recognition of these two divisions makes the position of *Titanoides* a little more certain. The lower molars agree with those of the *Coryphodon* group in their progressive increase in size and in the absence of metastylids. On the basis of these characters (the only ones definitely known) the genus falls into the *Coryphodontidae* as here redefined, thus confirming Simpson's (1937b, p. 14) assignment (to the "*Pantolambdinae*") and rejecting my tentative reference to the "*Barylambdinae*" (1937, p. 230). This is in accord with the course followed by Jepsen (1930, pp. 506, 508) who placed *Titanoides* in the *Coryphodontidae*,<sup>1</sup> and stated that it "... seems to be a pre-*Coryphodon* stage of amblypod evolution and may be in the direct ancestral line of *Coryphodon* . . ." It is very possible that this suggestion will prove to be correct. If, as seems conceivable, *Titanoides* resembled *Sparactolambda* in the possession of coryphodont skeletal characters it may well have been near the direct line. The normal lower canine (Gidley, 1917, p. 431) shows at least that the genus did not pursue root-pulling evolutionary bypaths. Scott (1937, p. 479) has recently erected the family *Titanoideidae* for *Barylambda* and *Titanoides*. On present evidence, however, it appears that the former genus cannot be included in such a group, and that the latter alone is not entitled to familial distinction.

<sup>1</sup> The soundness of this reference was inferentially questioned by my earlier mistaken assignment of *Barylambda faberi* to *Titanoides*, an inference that I am glad to be in a position to correct.

From the new discoveries it is becoming apparent that the pantodonts were the dominant large ungulates during part at least of Paleocene time. In common with later dominant groups they seem to have undergone a considerable adaptive radiation, of which we probably know only a small part as yet. Knowledge of the Pantodonta has more than doubled during the present decade and in this increase the Plateau Valley has played a major part. It is therefore a great pleasure to have been able to name the important forms obtained from this horizon in honor of the three men whose discoveries have so notably enlarged our conception of the order.

One further point remains for consideration. Matthew (1937, pp. 301, 303) reported four major types of foot structure among Paleocene mammals, two of which—the creodont-condylarth and the “taligrade”—are affected by the evidence reported here. The former was regarded by Matthew (pp. 106–107, 303) as ancestral to the Carnivora, Artiodactyla, Perissodactyla and Notoungulata, the latter as ancestral to the “Amblypoda,” Arsinoitheria, Pyrotheria, Astrapotheria and Hyracoidea. Transfer of the Peripitychidae to the Condylarthra, however, has destroyed “Taligrada” in the inclusive sense, while *Sparactolambda* appears to have removed all possibility of revival of the group in the original sense. Since the Pantodonta (at least as now known) can hardly be regarded as ancestral to any other order, it follows, broadly accepting Matthew’s view, that the entire ungulate ancestry is to be sought in the creodont-condylarth complex. This does not affect, other than perhaps to render somewhat more compact, Matthew’s tentative conception of an early placental dichotomy into “proto-creodont” and “proto-insectivore” divisions (1937, fig. 57, p. 211; fig. 83, p. 302), an important generalization that seems to be in accord with present evidence.

### Order Dinocerata Marsh, 1872

#### Family Uintatheriidae Flower, 1876

#### *Bathyopsoides* gen. nov.

*Type species.*—*B. harrisorum* sp. nov.

*Distribution.*—Upper Paleocene, Plateau Valley beds, Colorado.

*Diagnosis.*— $I_3^2$   $C_1^1$   $P_3^3$   $M_3^3$ . Metacone on  $P^2$  more distinct than in *Probathyopsis*;  $M^1$  notably smaller than  $P^4$  and  $M^2$ ; cingula less extensive than in *Probathyopsis*, more extensive than in *Prodinoceras*. Lower incisors conical, with long crowns and external

(posterior) heels; lower canine considerably larger than incisors, flattened transversely; molar metastylids long antero-posteriorly;  $M_1$  relatively smaller,  $M_2$  relatively larger than in *Bathyopsis*; posterior talonid crests of  $M_{1-2}$  compressed antero-posteriorly, entoconids subordinated in them;  $M_3$  with small entoconid. Skull without indication of parietal horns; sagittal crest extending forward to plane of glenoid cavities, occiput consequently triangular and cranial table less extensive than in *Bathyopsis*. Diastemata between canines and  $P_2$  about as in *Bathyopsis*, much longer than in *Probatyopsis* or *Prodinoceras*. Mandibular flanges very large, generally similar to those of *Bathyopsis* but differing in that they meet ventrally beneath the symphysis in a wide  $\Omega$  rather than in a narrow  $\Lambda$ .

***Bathyopsoides harrisorum*<sup>1</sup> sp. nov.**

"... a rather large and advanced uintathere..." Patterson 1936, Proc. Geol. Soc. Amer., 1935, p. 397.

*Holotype*.—F.M. No. P15546, lower jaws lacking anterior end of symphysis, coronoid processes, and condyles; dentition nearly complete but cheek teeth poorly preserved; various skeletal fragments. Found by James H. Quinn.

*Paratypes*.—F.M. No. P15552, partial skull, lacking rostrum, left side of cranial table, and left zygomatic arch; cheek teeth poorly preserved. Found by James H. Quinn. F.M. No. P15574, incomplete right mandible with  $P_4$ — $M_2$  and isolated canine, various skeletal fragments. Found by Clayton A. Quinn.

*Horizon and localities*.—Plateau Valley beds, about 150 feet above the base of the horizon. Holotype collected in Plateau Valley, one mile north of the Douglas Harris ranch house. Paratypes collected four miles north of Mesa and about 200 yards east of the DeBeque-Mesa road, P15552 occurring some thirty feet above P15574.

*Diagnosis*.—As for the genus. Comparable in size to *Bathyopsis fissidens*. For measurements see page 378.

*Discussion*.—The upper canine is not preserved in the type material. Incomplete isolated specimens of this tooth which are surely referable to *Bathyopsoides* show that it was fully as large, proportionately, as in the Bridger uintatheres, somewhat flattened transversely, and with a ridge on the lateral face. The only notable

<sup>1</sup> Named for the Harris family of Mesa, Colorado, to whose friendly aid and hospitality we owe much of our success in the field.



FIG. 109. *Bathypopsoides harrisorum* gen. et sp. nov. Skull and jaws, right lateral view. F.M. No. P15546, holotype, and F.M. No. P15552, paratype. Upper canine restored from isolated specimens; ramus and flange of left side complete; lower canine crushed upward.  $\times \frac{3}{4}$ .

feature of the upper cheek teeth is their very close resemblance to those of all other genera of the order. The lower incisors are strikingly different from those of the Bridger forms (cf. Osborn, 1881, pl. 3, figs. 3-4).<sup>1</sup> Nevertheless the presence of well-developed external heels does foreshadow the great enlargement of these elements in the later members of the order. It is unfortunate that these teeth are unknown in *Bathyopsis*, a genus in which they might be structurally intermediate between the two extremes. The lower canine appears to have had the same degree of inclination as the incisors; it agrees with that of *Bathyopsis* in being larger than the incisors.

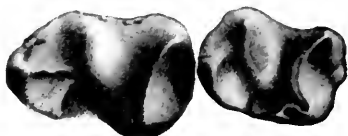


FIG. 110. *Bathypsoides harrisorum* gen. et sp. nov. Left  $M_{2-3}$ , crown view. F.M. No. P15546, holotype.  $\times \frac{1}{4}$ .

The metastylid of  $M_{2-3}$  is almost as large and prominent as the metaconid; that on  $M_{3-4}$  is very small. The compressed posterior talonid crest and the subordinated entoconid of  $M_{1-2}$  are of some interest because in these features *Bathypsoides* differs from *Proathyopsis* and from *Bathyopsis*<sup>2</sup> and approaches, to judge from the figures given by Osborn (1881) and by Marsh (1886),<sup>3</sup> the middle Eocene untatheres.

The structure of the skull, except for those differences mentioned in the diagnosis, is very similar to that of *Bathyopsis* (Osborn, 1913). The preorbital constriction is not quite as prominent as in the lower Eocene genus, and the occiput does not appear to extend posteriorly beyond the condyles. The postglenoid processes of P15552 do not project as far ventrally, but this condition is perhaps accentuated by distortion. In palatal and zygomatic structure and in breadth of condyles the two forms are essentially identical. The

<sup>1</sup> Marsh's figures of the incisors are inaccurate, as has been pointed out by Matthew (1937, p. 170).

<sup>2</sup> Amer. Mus. No. 14803, a very fragmentary specimen identified as *Bathyopsis* includes an  $M_{2-3}$  similar to that of *Bathypsoides* in the posterior talonid crest. Conceivably this species represents another genus.

<sup>3</sup> Matthew (1937, p. 170) states that this monograph bears the date 1884 on the title page. This must have been either a misprint or a *lapse* on Matthew's part because such copies as I have seen bear the date 1886, and Marsh himself relates (p. 237) that the author's edition was printed in February, 1885.

basicranial region of *Bathyopsoides* is so poorly preserved that no structural details can be seen but the proportions are almost exactly those of *Bathyopsis*.

The mandibular flange resembles that of *Bathyopsis* and differs from that of *Uintatherium*<sup>1</sup> in that it slopes evenly instead of abruptly backward and upward into the ramus. The resemblance and difference is reversed, however, in the case of the  $\Omega$ -shaped ventral union of the flanges.

The more important associated skeletal remains include two incomplete vertebrae and the proximal end of an ulna belonging to P15546, the holotype, and an unciform found with P15574. In addition, an isolated femur, P15548, which is almost certainly referable to *Bathyopsoides*, was collected by Mr. Edgerley three miles west of DeBeque.

The vertebrae are an anterior dorsal and a lumbar. The former is, as far as preserved, almost exactly like those of *Uintatherium*; the latter has an equally large neural canal but a somewhat longer neural arch. The olecranon preserved on the ulna fragment has the same degree of inclination as that of *Uintatherium*, but is not expanded transversely; the articular surface is narrower than in the Bridger genus. The unciform is not as deep in the anterior face as that of *Uintatherium*, and the articular area for the lunar and for the medial half of the cuneiform is much higher. In the latter feature *Bathyopsoides* approaches the contemporary pantodonts, differing from them, however, in the lack of any pronounced demarcation between the surfaces for the lunar and cuneiform.

The isolated femur is very similar to that of *Uintatherium* in the structure of the shaft, position of the second trochanter, and absence of the third trochanter, the latter character sharply distinguishing it from any pantodont femur. The head, however, is set more obliquely to the long axis of the bone and is but little higher than the great trochanter. The position of the head in the Bridger uintatheres is an extreme graviportal adaptation comparable to that occurring in the elephants, and it is therefore not surprising to encounter a more primitive position for it in their Paleocene forerunners. In the structure of the distal end *Bathyopsoides* differs from *Uintatherium* in the more upwardly extended patellar trochlea and in the more divergent condyles.

<sup>1</sup> Including *Dinoceras*, *Tinoceras*, etc. The synonymy of the Bridger uintatheres seems to be in an even worse state, if such be possible, than that of the lower Eocene coryphodonts.

## MEASUREMENTS

(In millimeters)

P15552	P <sup>2</sup>	P <sup>3</sup>	P <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>
A-p diam.....	15.0	15.7	17.2	16.4	22.6	22.5
Tr. diam.....	11.5	14.8	18.3	16.2	21.8	24.0
	P15546		P15574		P15106*	
P <sub>4</sub> , a-p diam. ....	....		16.7		....	
P <sub>4</sub> , tr. diam. trigonid ....	....		11.8		....	
P <sub>4</sub> , tr. diam. talonid ....	....		10.9		....	
M <sub>1</sub> , a-p diam. ....	....		16.4		....	
M <sub>1</sub> , tr. diam. trigonid ....	....		11.4		....	
M <sub>1</sub> , tr. diam. talonid ....	....		9.7		....	
M <sub>2</sub> , a-p diam. ....	20.1		21.0		20.4	
M <sub>2</sub> , tr. diam. trigonid ....	14.8		15.0		15.7	
M <sub>2</sub> , tr. diam. talonid ....	13.6		12.8		13.8	
M <sub>3</sub> , a-p diam. ....	25.0		....		....	
M <sub>3</sub> , tr. diam. trigonid ....	16.4		....		....	
M <sub>3</sub> , tr. diam. talonid ....	14.8		....		....	

\* The original specimen discovered by Mr. Faber.

## SKULL (P15552)

Length from posterior border of canine alveolus to posterior border of condyle.....	316
Zygomatic width.....	220
Width across condyles.....	93
Depth from apex of occiput to ventral rim of foramen magnum.....	117

## MANDIBLE (P15546)

Length from posterior border of canine alveolus to posterior border of M <sub>3</sub> ..	152
Width of symphysis behind canines.....	88
Depth of flange.....	91
Width across flanges, ventral.....	147

## FEMUR (P15548)

Length.....	428
Proximal width.....	155
Distal width.....	126

## Probathyopsis Simpson

*Probathyopsis* Simpson 1929, Amer. Mus. Nov., No. 387, p. 1.*Probathyopsis newbilli*<sup>1</sup> sp. nov.*Probathyopsis* sp. Patterson 1936, Proc. Geol. Soc. Amer., 1935, p. 397.

*Holotype*.—F.M. No. P15549, incomplete lower jaws with partial premolar-molar dentition; a young individual with M<sub>3</sub> not yet erupted.

*Horizon and locality*.—Plateau Valley beds, Plateau Valley, Colorado, one mile north of the Douglas Harris ranch house. Found by James H. Quinn some fifty yards away from the holotype of *Bathyopsoides harrisorum*.

*Diagnosis*.—P<sub>4</sub>, M<sub>2</sub>, relatively larger than in *P. praecursor*,<sup>2</sup> M<sub>1</sub> relatively smaller; teeth larger and wider than those of *P. praecursor*. For measurements see page 381.

<sup>1</sup> Named for Mr. Thomas J. Newbill, Jr., my companion on the 1932 expedition.<sup>2</sup> I am greatly indebted to Dr. Barnum Brown for the loan of the holotype of this species.



*Discussion.*—The cheek teeth, although of the usual, almost stereotyped untathere pattern, exhibit several differences from those of *Bathyopsoides*. The paraconid remnant is noticeably

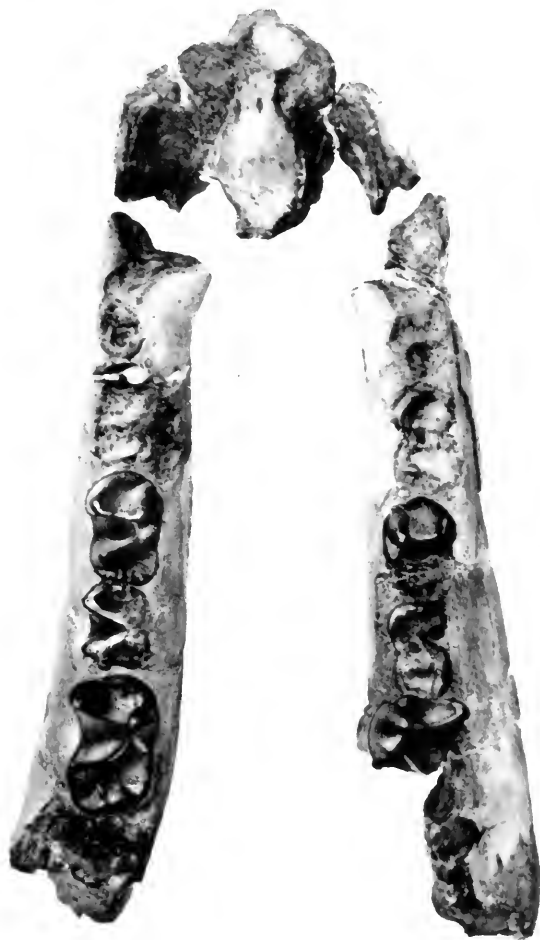


FIG. 111. *Probathyopsis newbilli* sp. nov. Incomplete lower jaws and dentition, crown view. F.M. No. P15549, holotype.  $\times \frac{1}{4}$ .

stronger on  $P_4$ – $M_2$  of *P. newbilli*, the talonid shelf on  $P_4$  is more prominent and farther removed from the hypoconid, and the entoconid of  $M_2$  is very distinct. In addition, the metastylid of  $M_2$  is smaller and that of  $M_3$  larger than in *B. harrisorum*. In contrast to *Bathyopsoides*,  $P_1$  is present and there is little or no diastema

between it and the canine. The symphyseal fragment indicates that a small flange, comparable to that of *P. praecursor*, was present.<sup>1</sup>

In view of the fact that the tooth proportions of *P. newbilli*, its diagnostic characters, are very similar to those of *B. harrisorum*, the possibility that the former might be a female of the latter was considered. However, the structural differences, all shared with *P. praecursor*, can hardly be dismissed as sexual. Six specimens of  $M_{\bar{x}}$ , three each of *B. harrisorum* and *P. newbilli*, show no intergradation in entoconid and metastylid structure. It seems necessary, therefore, to regard the characters of *P. newbilli* as having taxonomic significance.

Four fragmentary specimens may be referred to the species under discussion. These are a right  $M_{\bar{x}}$ , P15584, the trigonid of a right  $M_{\bar{x}}$ , P15577, an incomplete left lower canine, P15578, and a right  $M^1$ , P14939.<sup>2</sup>

The lower canine lacks the apex and part of the external surface. It is considerably larger than the corresponding tooth of *P. praecursor* and has a rather flatter lateral face, but agrees in the presence of a posterior basal tubercle and of a prominent antero-internal cingular ridge. In the last two features both canines differ from those of *B. harrisorum*.

$M^1$  differs from that of *P. praecursor* in slightly smaller size (significant in view of the small  $M_T$  of *P. newbilli*), stronger and higher parastyle, metaloph and protoleph more nearly parallel and slightly closer together, metaloph tending to run postero-internally, and cingulum not encircling the protocone. From *Prodinoceras* it differs in much smaller size, weak external cingulum, and in the more posterior and less internal position of the hypocone. The *Bathyopsoides* material does not contain an  $M^1$  sufficiently well preserved for comparison.

<sup>1</sup> Simpson's figure (1929, fig. 3) shows the flange as being rather more prominent than it actually is; the ventral extremity merges more gradually backward into the ramus than is shown. The total depth is 41 mm.

<sup>2</sup> I referred to this specimen in 1936 (pp. 397-398) in stating that "*Probathyopsis* sp. was found some 200 feet higher in the formation." In the 1932 and 1933 seasons all the material collected, except for this specimen, a fragmentary *Bathyopsoides* upper canine (not then recognized as such), and an incomplete chelonian, came from the lower 50-75 feet of the series. In 1937, however, it was found that the fossils had a vertical distribution of some 300 feet. There is no evidence as yet that more than one faunal unit is represented by the material collected. Of the *P. newbilli* specimens the holotype, P15584, and P14939 were found in the upper third of the fossiliferous zone, P15577 near the base, and P15578 about midway between the two other occurrences.

## MEASUREMENTS

(In millimeters)

*P. newbilli*

	Holotype					<i>P. praecursor</i>
	P14939	P15578	P15549	P15584	P15577	Holotype A.M. 16786
M <sup>1</sup> , a-p diam. ....	13.0	....	....	....	....	....
M <sup>1</sup> , tr. diam. ....	11.7	....	....	....	....	....
Lower C, a-p diam. ....	....	16.7	....	....	....	13.3
Lower C, tr. diam. ....	....	....	....	....	....	8.5
P <sub>4</sub> , a-p diam. ....	....	....	15.4	....	....	13.4
P <sub>4</sub> , tr. diam. trigonid..	....	....	11.1	....	....	9.2
P <sub>4</sub> , tr. diam. talonid..	....	....	9.8	....	....	8.7
M <sub>1</sub> , a-p diam. ....	....	....	13.3	....	....	....
M <sub>1</sub> , tr. diam. trigonid..	....	....	....	....	....	....
M <sub>1</sub> , tr. diam. talonid..	....	....	....	....	....	....
M <sub>2</sub> , a-p diam. ....	....	....	18.5	19.2	....	....
M <sub>2</sub> , tr. diam. trigonid..	....	....	13.5	13.5	11.9	....
M <sub>2</sub> , tr. diam. talonid..	....	....	10.8	10.8	....	9.7
M <sub>3</sub> , a-p diam. ....	....	....	....	....	....	21.0
M <sub>3</sub> , tr. diam. trigonid..	....	....	....	....	....	....
M <sub>3</sub> , tr. diam. talonid..	....	....	....	....	....	12.2

## THE ORDINAL STATUS OF THE DINOCERATA

Since the appearance of Wood's paper (1923) pointing out the fundamental differences between the uintathere and coryphodont molars, the view that the two groups represent distinct orders has been steadily gaining ground (Simpson 1929, 1931; Patterson 1934; Simpson 1937a). Matthew in his Puerco-Torrejon monograph (1937) retained the old classification, but, as has been pointed out above, a good part of the crucial evidence now available was unknown to him. Scott (1937, pp. 477-478) admitted that ordinal separation of uintatheres and pantodonts might be found to be desirable in the future, but stated that "...it must...be recognized that the families now included in the †Amblypoda [Uintatheriidae, Coryphodontidae, Pantolambdidae, etc.] are more nearly related to one another than they, or any of them, are to other groups." The bearing of the Plateau Valley material on this question must be briefly considered.

The Plateau Valley appears to be somewhat older than the Clark Fork, and it follows therefore that in *Bathyopsoides harrisorum* and *Probathyopsis newbilli* we are dealing with the earliest uintatheres thus far found in North America, if not in the world.<sup>1</sup> In the case of *P. newbilli* a phylum of the family already known from the Gray Bull and Clark Fork is carried back a stage further. The new species is fully as advanced as the Clark Fork *P. praecursor*, per-

<sup>1</sup> The Gashato of Mongolia which contains *Prodinoceras* cannot be exactly correlated, but is almost certainly upper Paleocene.

haps slightly more so, and is probably not directly ancestral. This is significant as to the stability of the phylum, but is not particularly startling.

The discovery of *Bathyopsoides*, however, is an event of first-rate importance in the furthering of our knowledge of uinthere evolution. In this animal we have a form which in the upper cheek teeth, in the upper canine, and in the development of diastemata is comparable to the terminal North American members of the group; a form as large as and more specialized in flange structure than *Bathyopsis* from the upper part of the lower Eocene. The known parts of its skeleton are clearly of uinthereid type. So advanced a form strongly suggests a long period of independent development for the group prior to upper Paleocene time. Neither in *Bathyopsoides* nor in *Probathyopsis* can I detect any significant approach either to the pantodonts or to the peripitychid condylarths. The Pantodonta do not seem to be closer to the Dinocerata than to other groups such as the Creodonta and Condylarthra. The essentially static cheek teeth of the known uintheres (upper Paleocene to upper Eocene) probably indicate that their characteristic pattern, so different from that of the pantodonts, was acquired long before the first appearance of the order in the record. For these various reasons I feel compelled to regard the ordinal separation of the Dinocerata as valid and necessary.

The structural succession *Probathyopsis*–*Bathyopsis*–*Elachoceras*–*Uinthereium*–*Eobasileus* admirably illustrates the trend of evolution in the later uintheres. This succession has been regarded as phyletic, but *Bathyopsoides* suggests that such a view may not be entirely correct. *Probathyopsis* may well have been ancestral to *Bathyopsis* but I am by no means certain that the latter is in turn ancestral to the later members of the order. In at least one striking character—flange structure—*Bathyopsoides* is closer to *Uinthereium* than is *Bathyopsis*. Although we have no evidence at present that the Dinocerata had as complex a radiation as the Pantodonta, it is nevertheless likely that future discoveries will reveal that the genera we know now are inadequate in number for a proper understanding of the phylogeny.

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384 FIELD MUSEUM OF NATURAL HISTORY—GEOLOGY, VOL. VI

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