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A NEW PALEOCENE UINTATHERE AND MOLAR EVOLUTION IN THE AMBLYPODA

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In several earlier papers there has been mentioned the existence in the Clark Fork Formation of a uintathere earlier and more primitive than any previously known from America.[1] It is the purpose of the present paper to name and describe this form and to discuss briefly its bearing on conceptions of amblypod phylogeny and, particularly, molar evolution. The drawings are by John Germann.

PROBATHYOPSIS, new genus

DIAGNOSIS.—Upper teeth as in *Prodinoceras* so far as known, except that on P^2 the external and posterior borders are more nearly at right angles, the protocone less separate and united to the middle of the ectoloph by a single inconspicuous crest,

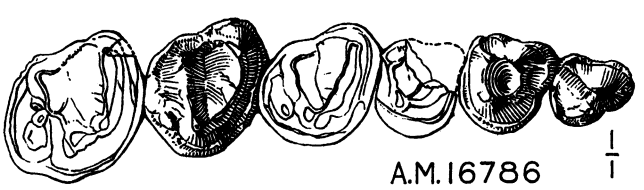

Fig. 1. *Probathyopsis præcursor*, new genus and species. Right upper cheek teeth, crown view. Shaded teeth from type, Amer. Mus. No. 16786, P^3 reversed from left side. Teeth in outline, from a topotype, Amer. Mus. No. 16984. Natural size.

unbasined, the metacone less distinct; that the cingula pass completely around the protocones on all the upper teeth; and that the hypocones are posterior and slightly external, rather than internal, to the protocones. The paraconid shelves of the lower molars more distinct than in *Bathyopsis*, and these teeth relatively longer, narrower, and higher. The posterior talonid crest less continuous than in *Bathyopsis*, but otherwise similar. The talonid of M_3 differing markedly in this respect from that of *Prodinoceras*. A small flange on the lower jaw, but this much less developed than in *Bathyopsis*.

[1] Wood, H. E. 1923. 'The Problem of the *Uintatherium* Molars.' Bull. Amer. Mus. Nat. Hist., XLVIII, pp. 599–604 (see p. 601).
Matthew, W. D. 1928. 'The evolution of the mammals in the Eocene.' Proc. Zool. Soc. London, 1927, pp. 947–985 (see pp. 956, 969–970).
Matthew, W. D., Granger, W., and Simpson, G. G. 1929. 'Additions to the Fauna of the Gashato Formation of Mongolia.' Amer. Mus. Novitates, No. 376, pp. 1–12 (see p. 10).

Probathyopsis præcursor, new species

TYPE.—Amer. Mus. No. 16786, lower jaws with imperfect dentition, and associated upper teeth. Collected in 1913 by W. Stein.

HORIZON AND LOCALITY.—Clark Fork Formation, Clark Fork Basin, Wyoming. The type is from the head of Big Sand Coulee. Other specimens, collected in 1911, 1912, and 1916 by American Museum expeditions under Walter Granger, include

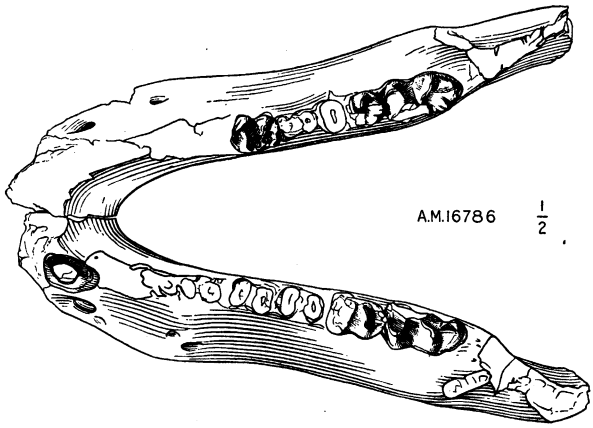

Fig. 2. *Probathyopsis præcursor*, new genus and species. Lower jaws, crown view. Type, Amer. Mus. No. 16786. One half natural size.

Fig. 3. *Probathyopsis præcursor*, new genus and species. Left lower jaw, external view. P_4 reversed from right side. Type, Amer. Mus. No. 16786. One half natural size.

material from this locality and also from opposite the mouth of Little Rock y Creek, from the base of a bluff five miles northeast of Ralston, and from three miles eas t of the mouth of Pat O'Hara Creek. Some of this material may be from the Sand Coulee horizon.

DIAGNOSIS.—With the characters of the genus. Length of M_3, 21.7 mm.

The dentitions of the three earliest known uintatheres, *Probathyopsis*, *Prodinoceras*, and *Bathyopsis*, are all incompletely known, so that further discoveries will expand the distinctions given in the above generic diag-

nosis. *Probathyopsis* and *Prodinoceras*,[1] the latter from the Gashato Formation of Mongolia, are distinct but very closely related genera. Although a more complete basis for comparison may somewhat modify this view, the known distinctive characters of *Probathyopsis* tend toward a somewhat closer resemblance to the later American genera. The stage of evolution is almost the same in the two Paleocene forms, but *Prodinoceras* may prove to be very slightly more advanced. They may be tentatively considered as showing incipient divergence from an immediate common ancestry, *Probathyopsis* leading to some or all of the later American uintatheres, *Prodinoceras* possibly to an otherwise unknown Asiatic phylum.

The known characters distinguishing *Probathyopsis* from *Bathyopsis* all indicate the more primitive nature of the former, and nothing is known which would exclude the possibility of a directly ancestral relationship.

Both Matthew and Wood considered the present genus, which they mentioned but did not describe, as increasing the probability that the Coryphodontidæ and Uintatheriidæ are parallel phyla, quite distinct from each other. The question of the relationship between these two groups is too complex for full discussion here, but the bearing of *Probathyopsis* and *Prodinoceras* on this problem must be mentioned.

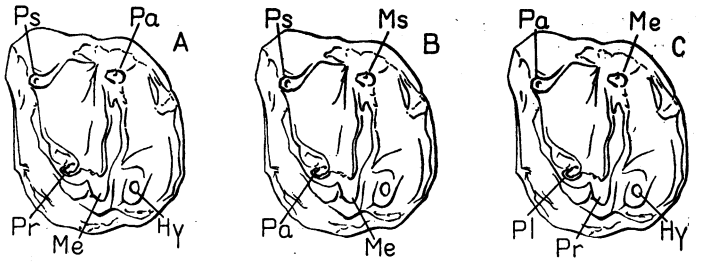

Fig. 4. Theories of cusp homologies in *Uintatherium* upper molar. A, Osborn. B, Matthew, rejected alternative. C, Wood, Matthew, Simpson.

Osborn[2] in 1898 elaborated the conception of the Pantolambdidæ, Coryphodontidæ, and Uintatheriidæ as successive families forming a structurally ancestral series. According to his view, the *Coryphodon* upper molar arose from one like *Pantolambda* by the rotation of the ectoloph and reduction of the paracone, and from this the *Uintatherium* molar

[1]See Matthew, Granger, and Simpson, *op. cit.*, 1929.
[2]Osborn, H. F. 1898. 'Evolution of the Amblypoda. Part I. Taligrada and Pantodonta.' Bull. Amer. Mus. Nat. Hist., X, pp. 169–218.

was derived by further rotation of the ectoloph, so that the metacone became approximated to the protocone. The premolars of *Pantolambda* and *Coryphodon* are closely similar and have homologous parts. Those of *Uintatherium*, according to Osborn's theory of 1898, must have arisen by the complete suppression of the internal heel, and hence have had a very different history from the molars, which they closely resemble.

Wood (*op. cit.*, 1923) has raised serious objections to this view. He holds that the *Coryphodon* and *Uintatherium* upper molar patterns are not formed by homologous elements, but that in the latter Osborn's "metacone" is the protocone, his "protocone" the protoconule, his "paracone" the metacone, and his "parastyle" the paracone; that is, that the *Uintatherium* molar has a normal trigon modified by an unusual type of lophiodonty.

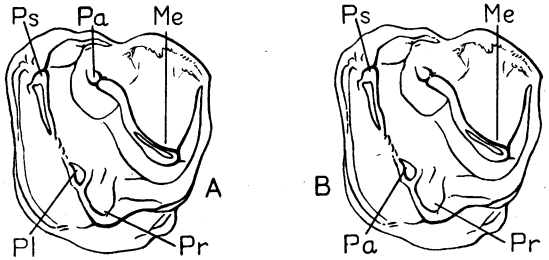

Fig. 5. Theories of cusp homologies in *Coryphodon* upper molar. A, Osborn, Simpson. B, Matthew.

Matthew (*op. cit.*, 1928) advanced, only to reject it, the alternative hypothesis that in *Uintatherium* Osborn's "protocone" and "metacone" are the paracone and metacone, respectively, his "parastyle" and "paracone" the parastyle and metastyle, and that the protocone is lacking, but he concluded that the evidence of *Prodinoceras* (including the genus now named *Probathyopsis*) confirmed Wood's view. For *Coryphodon*, however, he advanced a new theory, namely, that the upper molars of this genus "apparently . . . are derived from something of the *Pantolambda* type, by uniting the anterior limbs of the paracone and protocone crescents into a single crest, and loss of their posterior limbs, the metacone crescent remaining little changed or losing its anterior[1] limb."

Prodinoceras and *Probathyopsis* seem to offer definitive evidence regarding the origin of the uintathere molar and to establish Wood's view beyond much question, as recognized by Matthew. The external ends

[1] A *lapsus calami* for "posterior"?

of the two lophs are clearly the paracone and metacone, and the chief internal cusp is clearly the protocone. The so-called "protoloph" connects the paracone and protoconule, the "metaloph" ("ectoloph" of Osborn in 1898) unites the metacone and protocone. They are not homologous with any of the three perissodactyl lophs. There is an ectoloph in the Paleocene genera, particularly in the premolars, but in the later genera the deepening of the notch between the paracone and metacone causes the disappearance of the ectoloph as such.

This view has the added recommendation that it considers the posterior premolars and anterior molars, almost identical in form, save for the presence of a hypocone in the latter, as composed of homologous parts instead of assigning to them widely different histories.

Careful restudy of the *Pantolambda* and *Coryphodon* molars seems to confirm Osborn's views as to cusp homologies in the latter, although not his mechanical interpretation of their origin. In *Pantolambda* the paracone and metacone are equal, strongly crescentic, their apices median. The last deciduous molar of *Coryphodon* gives a valuable clue to the origin of the pattern of its true molars. Its parts are clearly

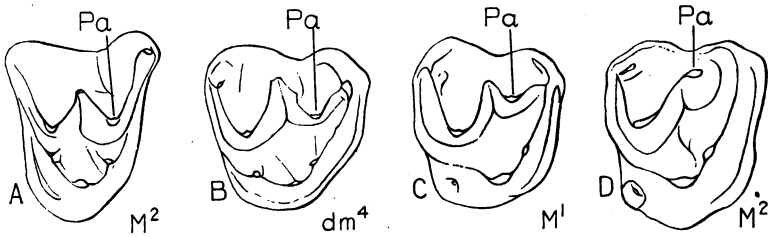

Fig. 6. Structural evolution of coryphodont upper molar. A, *Pantolambda*, M^2. B, *Coryphodon*, dm^4. C, *Coryphodon*, M^1. D, *Coryphodon*, M^2. Not to scale.

homologous with those of *Pantolambda*, but the paracone is reduced in size, less crescentic, its apex relatively more external, and anterointernal to it, below its own anterior crest, the anterior crest of the protocone has unusual strength and distinction. M^1 of the less advanced coryphodonts is intermediate between this and the more aberrant M^{2-3}. The paracone apex is relatively still more external, but this cusp retains traces of its former crescentic nature; the anterior wing of the protocone crescent is still stronger and tends to sever connection with the paracone, and the posterior wing of the metacone is somewhat weaker. In its next stage, the paracone is styloid.

The posterior crest of the *Coryphodon* molar cannot be called the ectoloph, for it represents only the anterior wing of the metacone crescent, and it cannot be said to have rotated, for its relations are exactly as in *Pantolambda*. Nor is the anterior loph a typical protoloph, for it is only the anterior wing of the protocone crescent and in its final development has no connection with the paracone.

The triangular upper premolars of the coryphodonts and those of the uintatheres are superficially similar, but the late Paleocene forms seem to show that the main triangles are not composed of homologous parts in the two groups. In *Coryphodon*, aside from the internal heel,

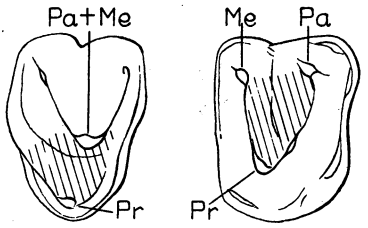

Fig. 7. Homologies of *Coryphodon* (left) and *Uintatherium* (right) upper premolars. Homologous trigons shaded. Not to scale.

the triangle is composed of the paracone-metacone internally and stylar cusps externally—it is an ectotrigon, homologous with the outer part of the molars. In *Uintatherium* the triangle is composed of the protocone internally and of the paracone and metacone externally—it is an endotrigon, homologous with the inner part of the molars. Here, as in the molars, the resemblance of *Coryphodon*, such as it is, is rather with the most specialized uintatheres than with the primitive *Probathyopsis* or *Prodinoceras*.

The lower molars, while less strikingly different, also have separate histories in the coryphodont and uintathere phyla. In both, the anterior loph is a true metalophid, formed by the protoconid and metaconid, but this is a tendency so nearly universal in ungulates as to be no indication of affinity.[1] The heel is distinctive. In *Coryphodon* the talonid loph runs anteroexternal-posterointernally and is a true hypolophid, joining the hypoconid and entoconid. In *Uintatherium*, on the contrary, the main heel loph runs posteroexternal-anterointernally, and, as shown in *Probathyopsis* where it is incompletely formed, unites the hypoconulid

[1]It is, in fact, a fundamental character of the Theria, which has been lost where it does not occur, and emphasized in the present, and many other, groups.

and entoconid. There is also a secondary crest, nearly parallel to this, which runs from the hypoconid toward the metastylid. The latter cusp, absent in *Coryphodon*, is already well developed in *Probathyopsis*.

Both coryphodonts and uintatheres thus represent early attempts at the formation of lophiodont molars, but each has formed these in its own way, converging toward a common adaptive type. The lophiodont perissodactyls represent a third and more successful acquisition of the lophiodont habitus, and they, again, form the lophs in a way peculiar to themselves. The lophs of these three groups are neither homologous nor homoplastic.

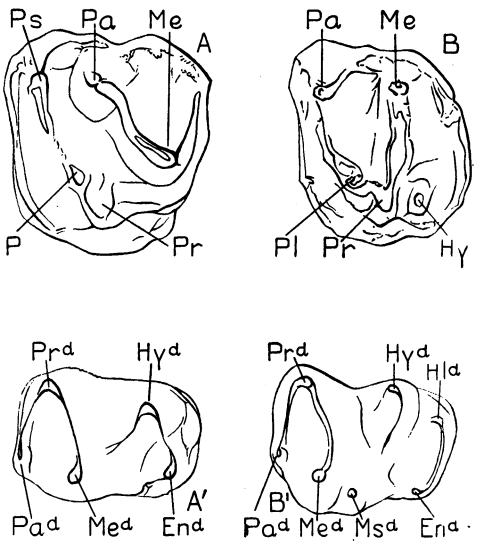

Fig. 8. Independent loph formation in coryphodonts and uintatheres. A, *Coryphodon* upper molar. A', *Coryphodon* lower molar. B, *Uintatherium* upper molar. B', *Uintatherium* lower molar. Not to scale.

The coryphodonts, uintatheres, and perissodactyls seem to me to afford a striking example of the view that when different phyla acquire similar habiti some time after their separation from a common ancestry, there is no inherent tendency for these modifications to arise in the same way in the independent lines. The homologous parts are those alone which were already present in the common ancestry—in ungulate upper molars generally, only the three primary cusps and possibly the conules. There may be a tendency (to call it inherent would involve a personal

definition of the word) to form lophs, for instance, but there appears to be no fixed tendency for these to form in the same way or from the same parts in independent groups, except when these phyla had identical or closely similar molars at or after the inception of lophiodonty. Animals which fulfil this last condition are usually closely related, and an apparent inherent tendency to form lophs in the same way in related phyla is consequently often seen, but I conceive the conditioning factor to be not the metaphysical one of germinal predestination but the physical one of mechanical resemblance.

If the above conclusions regarding molar evolution in the coryphodonts and uintatheres are correct, it is necessary to suppose that when true lophiodonty was first appearing in the two groups the upper molars of their ancestors, although tritubercular in both groups, were of different mechanical types. For the coryphodonts one would infer an ancestry

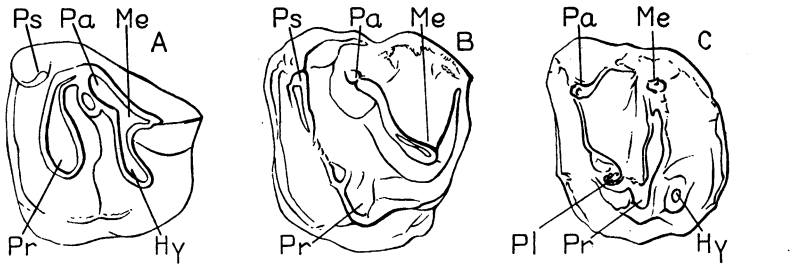

Fig. 9. Independent loph formation in three distantly related ungulate phyla. A, Perissodactyla, *Hyrachyus*. B, Pantodonta, *Coryphodon*. C, Dinocerata, *Uintatherium*. Not to scale.

with strongly selenodont molars, the paracone and metacone apices median. For the uintatheres, projecting backward the *Eobasileus-Probathyopsis* line, one would infer an ancestry with the paracone and metacone non-crescentic, their bases connate, their apices external, the protocone subcrescentic but its crests running to the bases of the paracone and metacone, not anterior and posterior to them.

So far as the dentition is concerned, *Pantolambda* is an almost ideal ancestral type for *Coryphodon*, and it has long been recognized that they are related. Direct ancestry is impossible, for while it would form a suitable basis for the coryphodont dental specialization, *Pantolambda* does not show any actual beginning of this advance, and, judging from the rate of evolution of other phyla, the time between the Torrejon and Clark Fork was much too short to accomplish this degree of evolution.

Probathyopsis is almost as primitive with respect to the upper Eocene uintatheres as is *Pantolambda* with respect to *Coryphodon*, and the relationship is more directly ancestral than in the latter case. *Pantolambda* cannot have been ancestral, either directly or structurally, to *Probathyopsis*. Pantolambdid relationship to the uintatheres requires reëxamination, but the evidence of the dentition of the Paleocene uintatheres suggests that any relationship must be collateral and rather distant.

The uintatheres and coryphodonts are not successive but contemporaneous. Both appear in America in the Clark Fork. Coryphodonts here died out by the Middle Eocene, but they apparently survived in Mongolia into the later part of the period. The known distribution of the principal genera involved in this discussion is as follows:

	Paleocene			Eocene		
	Lower	Middle	Upper	Lower	Middle	Upper
Pantolambdidæ						
Pantolambda		N.A.				
Titanoides			N.A.			
Coryphodontidæ						
Coryphodon			N.A.	N.A.		
Eudinoceras						Asia
Uintatheriidæ						
Prodinoceras			Asia			
Probathyopsis			N.A.			
Bathyopsis				N.A.		
Uintatherium					N.A.	
Eobasileus						N.A.