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Article XVIII.—THE PROBLEM OF THE UINTATHERIUM MOLARS

By Horace Elmer Wood, 2d

The question of the homologies and derivation of the uintathere upper molars presents a difficult problem. My attention was directed to it by Doctor W. K. Gregory, who has also given me in generous measure the benefit of his criticism and suggestions. The drawings are the work of Miss Marcelle Roigneau.

Osborn (1898, 1907) tentatively accepted the view first advanced by Cope (1884) that the upper uintathere molars developed from the *Coryphodon* type as follows (see Figs. 1, 2, 3): "The ectolph swung around so as to form with the protoloph a V opening outwards. Just internal to the apex of the V the hypocone is often developed." He says further (1907): "The lower molars of *Uintatherium* are closely linked with those of *Coryphodon* and *Pantolambda* through the genus *Bathyopsis*, which is strictly intermediate in its mandible and inferior molars and thus supports the view that the upper molars also of *Uintatherium* have passed through stages represented in a general way by *Pantolambda* and *Coryphodon*. The steps in this evolution are the most complicated and difficult to understand, especially the rotation of the ectoloph, a feature which is less positively demonstrated than the other features of this exceptional evolution." Finally, he says (1913): "The specimen (i.e., *Bathyopsis*) thus throws no light upon the still unsettled question of the derivation of the uintathere molar from the primitive amblypod type. . . As a whole the skull and dentition are so closely related to the *females* of the primitive species of *Uintatherium* as to fall almost within the same generic definition. The skull, however, is that of a robust *male*, with well-developed canine tusks, and is consequently to be regarded as in a typical ancestral stage."

Gregory (1910) accepted the "ectoloph rotation hypothesis," "*fide* Osborn." This has become the traditional view, although Scott (1913) enters a slight demurrer when he refers to the Pantodonta as "not ancestral to them (Dinocerata), but collaterally related and descended from a common ancestry." The context and page 285 show that Scott regards *Pantolambda* as probably the common ancestor of the coryphodons and uintatheres.

Although the anterior half of the upper molars of the uintatheres resembles that of *Coryphodon* strikingly, the posterior half is utterly different. On the other hand, there is a striking uniformity throughout the uintathere premolars and molars, both upper and lower, and the rotation of the ectoloph, as Osborn admitted, is so difficult to understand that it seems worth while to review the whole question of the homologies of the upper cheek teeth of the Uintatheriidæ.

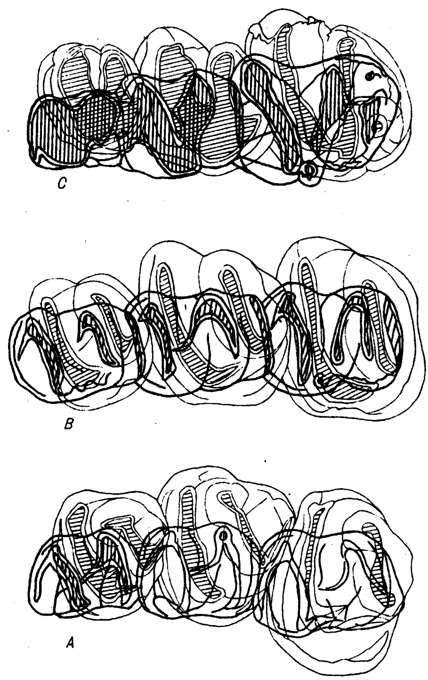

Fig. 1. Occlusal relations of the molars in: *a, Coryphodon testis; b*, hypothetical intermediate form (after W. K. Gregory); *c, Uintatherium stenops.* $\times \frac{1}{2}$.

There are a number of objections to the "ectoloph rotation hypothesis." Osborn, with more complete material, apparently withdrew his earlier suggestion that *Bathyopsis* was intermediate between *Coryphodon* and *Uintatherium* (see above). In any case, the lower molars are far more like *Uintatherium* than *Coryphodon*. They are merely a fraction of a stage nearer than *Uintatherium* to the primitive ungulate type represented by *Coryphodon* or *Homogalax* (*Systemodon*).

I feel that too high a value has been placed upon the resemblance between the lower molars of *Coryphodon* and *Uintatherium* (see Figs. 2, 3). If lower molars alone are considered, *Homogalax* is perhaps as good an ancestor for *Uintatherium* as is *Coryphodon*. In other words, the lower molars of *Coryphodon* and *Homogalax* are equally more primitive than those of *Uintatherium*. An inference of true genetic connection must be founded on stronger evidence than this alone.

The upper molars, always more progressive, must furnish the decisive evidence. The rotation of the ectoloph postulates a surprising fluidity of the ectoloph, associated with virtual immobility of the lower

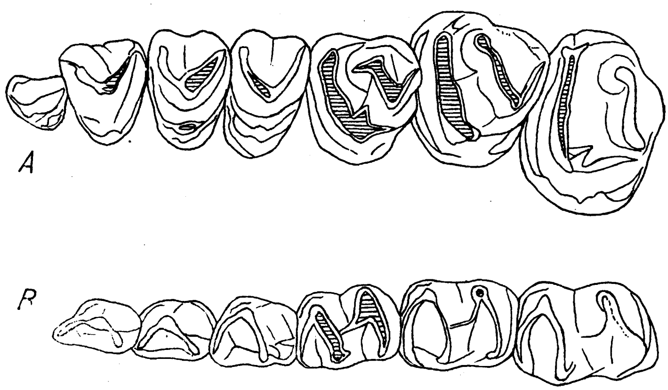

Fig. 2. *Coryphodon testis: a*, left upper and *b*, right lower, cheek teeth. After Osborn. ×½.

molars, of the protoloph and of the hypocene (see above). The cusp which Osborn calls the hypocone (see Fig. 4) can, however, hardly be the hypocone on his theory, unless it split off from the cingulum after the upper uintathere molars had been fully developed in all other respects.

Doctor Matthew contributes a note pointing out that Granger has found an as yet undescribed *Bathyopsis*-like uintathere in the summit of the Paleocene and the base of the Eocene in the Clark Fork Basin of Wyoming.[1] Both molars and premolars, upper and lower, have the uintathere pattern most unmistakably. As *Coryphodon* is not known from the Paleocene, the likelihood that the Uintatheriidæ and Coryphodontidæ are parallel phyla is increased. *Pantolambda* itself is virtually a contemporary of this earliest uintathere.

The possibility of the "ectoloph rotation hypothesis" as far as the occlusal relations go, must be admitted. (See Fig. 1.) Hypertrophy of the hypoconulid in *Coryphodon*, associated with partial atrophy of the

[1]American Museum No. 16984, Clark Fork Formation; No. 16786, ? Clark Fork Formation; Nos. 15860, 16063, 16064, Ralston Formation.

posterior V in the lower molars, might change the upper molars from the *Coryphodon* to the *Uintatherium* type. There are, however, no intermediate stages and such a revolution should not be accepted without strong evidence. The resemblance in the body structure of *Coryphodon* and *Uintatherium* is granted (although numerous differences are also

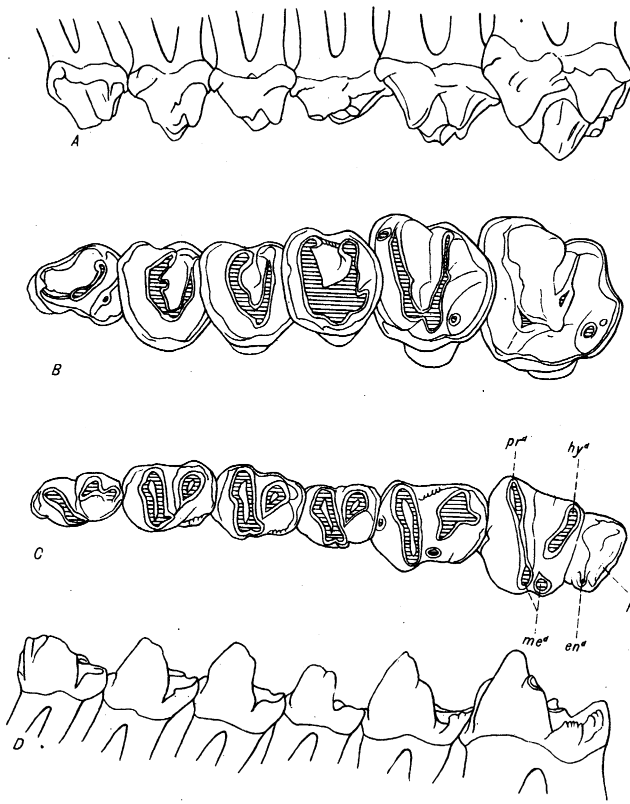

Fig. 3. *A*, outer, and *b*, crown views, of the left upper cheek teeth of *Uintatherium lucare*. *C*, crown, and *d*, inner, views of right lower cheek teeth of *Uintatherium pugnax*. After Marsh. ×½.

present), but it is no greater than might well occur in two parallel phyla which descended from a common pre-pantolambdid ancestor and acquired giantism independently.

The uintathere lower molars and premolars are strikingly similar to each other in pattern (see Fig. 3). There is, fortunately, entire agreement that the corresponding cusps are truly homologous throughout the lower cheek teeth. Since, however, the lower premolars have become molariform independently of the molars, it suggests the likelihood that the upper premolars, bound up occlusally with the lower premolars and becoming molariform *pari passu*, are now homologous, as well as analogous, with the upper molars. There seems little reason to doubt that the upper premolars are of normal tritubercular pattern, being composed of the "protocone," deuterocone and tritocone of Scott's nomenclature. Reversing the reaction P^{2-4}—M^{1-3}, we reach the tentative conclusion that the V in the upper uintathere molars is (as it seems at first glance), a normal trigon instead of a spurious substitute. The postero-internal cusp of the upper molars fits into this theory as the hypocone, or as a pseudo-hypocone split off from the protocone, and analogous to the tetartocone of premolars. In either case its occlusal relations are absolutely normal.

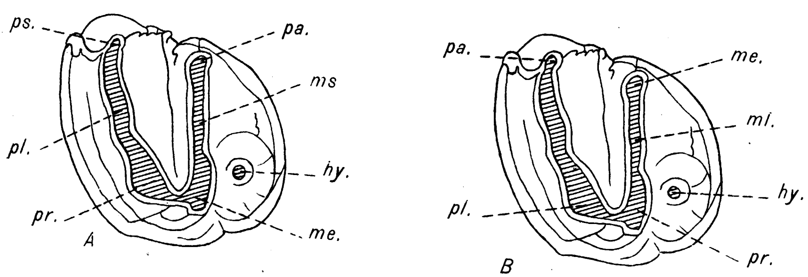

Fig. 4. Third left upper molar of *Uintatherium stenops*. *A*, Cusps labelled according to Osborn; *b*, cusps as identified in this paper. ×⅔.

Although recognizing the deceptiveness of convergence, I feel very strongly the essential unity in ground-plan of the upper cheek teeth. From P^2 to M^3 there are three main cusps, which I believe to be the paracone, metacone and protocone of molars. These cusps form a V of strikingly similar pattern throughout the series. (See Fig. 3.) The parastyle may be traced in all, flattened against the anterior edge of the paracone. The basal cingulum is identical throughout. The lowest point in each V, from P^3 to M^3, is on the anterior crest of the V, just external to the protocone.

It seems probable therefore that in the Uintatheriidæ the trigons and cusps in the molars are homologous with those of the premolars, representing the "secondary trigon" of Gregory (1922). Uintathere molars have a very different pattern from those of *Coryphodon*, formed, according to the theory here advanced, from different cusp elements. (See Figs. 1, 4.) This agrees with Scott's view that the Uintatheriidæ and Coryphodontidæ are parallel but independent phyla. In fact, it separates them somewhat more widely since, if this theory is correct, *Pantolambda*, although an ideal ancestor for *Coryphodon*, is already too highly specialized to give rise to the uintatheres. *Pantolambda* is to the Uintatheriidæ as *Palæotherium* is to the Equidæ.

The ancestry of the uintatheres is still uncertain.

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