

Article XVII. — FOSSIL MAMMALS OF THE UPPER CRETACEOUS BEDS.

By HENRY FAIRFIELD OSBORN.

It is interesting to return to the study of the Cretaceous mammals, aided by a valuable collection of small isolated teeth and jaws, which the American Museum owes to the skill of Dr. Wortman and Mr. O. A. Peterson of the Expedition of 1892. This collection of about 400 specimens was made primarily with the object of completing the series of types of American fossil mammals, which has been undertaken for the Museum. It represents the great majority, but not all, of the types already described from the Laramie; it apparently adds a few new forms, and enables the writer to offer a further review of the Upper Cretaceous mammals thus far made known through the works of Cope, Marsh and Osborn.

The object of this paper is to show, as nearly as can be done at present, what these Cretaceous mammals were, by bringing the scattered teeth together and reconstructing the upper and lower dentition; and secondly, to consider how they are related in general structure, and in the stages of evolution which they represent, to the older Jurassic and more recent Puerco mammals from the basal Eocene. The main conclusions reached in these studies support and extend the opinions expressed by the writer in earlier papers, namely, that :

1. This Laramie fauna is widely separated from the Upper Jurassic, and is more nearly contemporaneous with the basal Eocene forms of the Puerco, and the Cernaysian of France.

2. It is not highly varied, but on the other hand rather limited in the number of distinct types represented, including only two, or possibly three, of the well-known types of Multituberculata (Allotheria) and several types of Trituberculates which can now be distinguished.

3. The Plagiaulacidæ are represented by species of the genus *Ptilodus* of Cope, which is very characteristic of the Puerco, and

of the genus *Meniscoëssus* of Cope, which is now found to be affiliated with *Polymastodon*, the great Plagiaulacid of the Puerco. The Bolodontidæ are also possibly represented by forms related to *Chirox* of the Puerco. In other words, the Multituberculates, which are distinctively a Mesozoic group, here exhibit their early Tertiary stage of development.

4. The Trituberculates prove to be considerably more varied, yet they exhibit an essentially Tertiary dental type. They apparently have the heterodont Eutherian dental formula ($p=4$, $m=3$), which is very exceptional in the Jurassic. They all present the *tritubercular* stage of tooth development in the upper molars, and the *tuberculo-sectorial* in the lower molars, stages which are also characteristic of the Puerco mammals. Among them also are forms resembling the smaller Creodonta and Condylarthra of the Puerco.

5. The association of the upper and lower, anterior and posterior, teeth has naturally resulted in a great reduction of the number of systematic terms proposed by Marsh with a corresponding gain in our knowledge of the structure of each form.

These conclusions are directly the reverse of those expressed by Marsh in his three papers upon this fauna. They are accordingly sustained in the somewhat detailed studies of the structure and systematic position of these forms which follow, and will be more fully discussed in the conclusion of this paper.

The systematic determination of these forms is attended with great difficulties. The teeth generally come in from the field entirely isolated, since they are found in the sand and among the ant hills completely washed out of the matrix. Rarely the teeth remain in the jaws. Fortunately the characters of the Multituberculate dentition are now well known to the writer through the study of all the collections in this country and abroad. These teeth have been brought together in the composition drawings of Plate VII with some degree of certainty. The association of the upper and lower, anterior and posterior, molars and premolars of the Trituberculates is a still more difficult matter, and has been attempted only in one or two cases. The apparently well-established name *Meniscoëssus* may be superseded

by *Paronychodon lacustris*, a term founded by Cope in 1876¹ upon the tooth of a supposed reptile which appears to be identical with the large lower incisors of *Meniscoëssus*.

I.—THE MULTITUBERCULATES.

The two genera of Multituberculates which can now be fully distinguished and defined in their tooth structure are *Ptilodus* and *Meniscoëssus*. The former genus fits in its place as one of the long succession of Plagiaulacidæ, which began with the Rhætic *Microlestes*, and terminated with *Neoplagiaulax* of the Cernaysian. These species are fully as advanced in structure as those of the Puerco. *Meniscoëssus* also proves to belong to the same family, although it is somewhat exceptional in the sharply crescentic tubercles upon its upper and lower teeth. It is found to have a large cutting premolar (*p4*), and a rudiment of the third premolar (*p3*). A third genus is related either to *Bolodon* or to *Chirox*, presenting low-crowned teeth, surrounded by small conical cusps grooved upon their sides. These have been described under the name of *Allacodon* Marsh.

PLAGIAULACIDÆ Gill.

SYN.—*Cimolomida* Marsh, *Cimolodontida* Marsh, *Dipriodontida* Marsh, *Triprionodontida* Marsh.

The distinctive feature of this family is the cutting fourth lower premolar, opposed to a more or less trenchant upper fourth premolar. It is now well established that the lower molars have two rows of tubercles; the upper molars have three.

In the Laramie representatives of this family there are two types which may be readily distinguished. All the small forms appear to belong to the genus *Ptilodus* (Fig. 1), and are readily distinguishable by conical tubercles upon the molar teeth, by premolars completely covered with very numerous (10 to 14) grooves and ridges on their sides, by smooth lower incisors in which the enamel is wanting upon the posterior and inner faces. All the larger forms belong to the genus *Meniscoëssus*, and are

¹ Proc. Acad. Nat. Sc. Phila., 1876, p. 256.

characterized by molars with crescentic tubercles, the direction of the crescents being reversed in the two jaws; the premolars have deeper but less numerous grooves, and the lower incisors are grooved upon the sides and completely surrounded by enamel.

Ptilodus.

Lower incisors smooth, enamel wanting and dentine exposed posteriorly.

Third premolars small and conical.

Fourth premolars with numerous (12 to 14) fine grooves. Molars with conical or slightly crescentic tubercles.

Meniscoëssus.

Lower incisors striated upon inner and outer surfaces, with complete investment of enamel.

Third lower premolars small and conical. Fourth relatively smaller than in *Ptilodus*, with a few ridges (6 to 8).

Superior molars with strongly crescentic tubercles opening forwards. Inferior molars with crescentic tubercles opening backwards.

Genus **Ptilodus** Cope.

PLATE VII, FIGS. 1-6.

SYN.—*Cimolomys* Marsh, *Cimolodon* Marsh, *Nanomys* Marsh, *Halodon* Marsh, *Allacodon* Marsh (? in part).

This genus is represented by very numerous small isolated teeth of both the upper and lower jaws. As a rule the teeth are completely detached, but sometimes, as in the case of one or two of the molars and the fourth premolar, are found in place. The third lower premolar is so small as to have escaped the scrutiny of the collectors, but it is clearly represented by a distinct alveolus in the three lower jaws of this collection. The lower teeth correspond so closely in their general characters to those of *Ptilodus* that it is quite easy to place them in their proper position. We cannot be equally certain in regard to the upper teeth. The median pair of upper incisors and the minute second incisor are, nevertheless, found corresponding in proportion to these two teeth, as seen in a recently discovered specimen of *Polymastodon*. The fourth upper premolar is readily recognized by its substantial agreement in size with the fourth lower premolar. It is well distinguished, however, by a lower crown surmounted by a serrate or notched cutting edge, and an accessory row of tubercles.

We recall the fact that in the upper jaw of *Ctenacodon* Marsh, in front of the fourth cutting premolar, there are several low

tubercular premolars, as figured by Marsh; similar teeth are found in these deposits and figured by Marsh under the name of *Allacodon*; it is possible either that they represent the anterior upper premolars of *Ptilodus* or *Meniscoëssus*, or that they belong to a distinct form similar to *Chirox*.

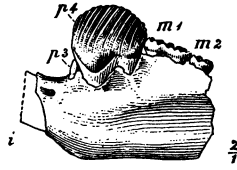


Fig. 1. Type of *Ptilodus trovesartianus* Cope, after original in Cope collection. Twice natural size.

There is considerable variation in the structure and number of tubercles in the upper and lower rows of the molars. These variations probably indicate different species, but it is almost impossible at the present time to use specific terms with any degree of certainty, for we have absolutely no means of placing any two of these teeth together. We will therefore describe the general characters of the upper and lower teeth.

Incisors.—The curved lower incisors have an oval section, flattened upon the inner side where they came in contact. The inner and part of the posterior surfaces are entirely devoid of enamel, which nevertheless covers the front and outer surfaces. They vary in size from extremely minute teeth to teeth three times as large. This variation probably represents the range of size among the species of *Ptilodus*, as we observe a similar wide variation in the fourth premolars (Fig. 2, *a-f*). The median upper incisors are short crowned and slightly notched at the back; they are closely applied with oblique posterior faces, in which the dentine is exposed, and which are therefore kept sharply worn by the lower teeth, as in the Rodents. There was undoubtedly a second upper incisor, but this has not yet been found.



Premolars.—The third lower premolars are minute simply conical or slightly compressed teeth (Pl. VII, Figs. 5-6). The fourth lower premolars (Fig. 2, *a-f*) have a large anterior and small posterior root (see figures of *Halodon serratus* Marsh, *H. formosus* Marsh). They are

Fig. 2. Fourth inferior premolars of the Laramie *Ptilodus*, species indeterminate. Twice natural size.

well distinguished by obliquely arching ridges and grooves, which completely cover the outer and inner surfaces, so that in the unworn teeth the upper border is serrate. The number of ridges varies in the smaller and larger forms from eleven to fourteen. The upper premolars (Pl. VII, Fig. 4) have less elevated crowns, with from six to seven notches upon the main internal crest, and from three to four basal tubercles upon the postero-external ridge. The inner side of these teeth is that which is most worn, indicating that the lower premolars wore against the slightly concave inner sides of the upper premolars. These upper premolars are found in sizes varying in proportion to the variations already observed in the incisors and lower premolars. There are indications of at least two species.

Molars.—The first and second lower molars (Pl. VII, Fig. 1) are sharply distinguished from each other by their length, the first molar being nearly twice as long as the second. The inner and outer sides are also readily recognized by the fact, as observed in *Ptilodus*, that the greater number of tubercles is upon the outer side, and the lesser number upon the inner side.

The first lower molar (type of *Cimolodon nitidus* Marsh) is very abundantly represented; eight or ten are found in this collection. The tubercles in the outer row vary from eight to six, and in the inner row from six to four; the first lower molar has an average of six tubercles in the outer row, and five in the inner row. The second lower molar (see also type of *Nanomys minutus* Marsh) is invariably characterized by two large tubercles in the inner row, and from six to seven very small tubercles in the outer row, which diminish as they extend around the posterior edge of the base of the crown. The form of this tooth is remarkably persistent, for it is substantially similar to the same tooth in the Jurassic *Plagiaulax*.

The first upper molar (Pl. VII, Figs. 3-4) has an elongate crown covered with three rows of conical tubercles (see also types of *Cimolomys gracilis* Marsh, *C. bellus* Marsh, *C. digona* Marsh). The formula of these tubercles is 8 in the middle row, and 8 and 6 respectively in the outer and inner rows; in some teeth there is the formula, 7, 7, 6, and in others it is 10, 10, 9. There are two types of these molars, one with the three

rows of tubercles equally complete (type of *Cimolomys gracilis* Marsh), and a second type with one of the outer rows incomplete (type of *C. digona* Marsh); it is probable that these two types represent different species. The second upper molar has a formula of 5, 4, 3 in its three rows.

It is somewhat uncertain whether the upper molars follow the same laws as the lower; it is probable that in both upper and lower molars the greater number of tubercles is upon the outer side, as in *Polymastodon* and in *Chirox* of the Puerco.

It is very difficult to define the species, because they are all founded upon single teeth which we cannot at present associate. We may describe the larger type, *Ptilodus* (*Cimolomys*) *gracilis*, as characterized by three complete rows of tubercles in the first upper molar, formula 7, 8, 9; and the somewhat smaller types may be placed under *Ptilodus* (*Cimolomys*) *digona* with the inner row of tubercles extending only half the length of the crown; it should be said, however, that this molar is very similar to the second upper molar of *Chirox* Cope; and it is possible, therefore, that it should be associated not with *Ptilodus* but with *Allacodon* Marsh.

Genus **Meniscoëssus** Cope.

PLATE VII.

SYN.—*Dipriodon* Marsh, *Tripriodon* Marsh, *Selenacodon* Marsh, *Halodon* Marsh (in part), ? *Oracodon* Marsh.

This form is fully as abundant as *Ptilodus*, being represented in this collection by numerous teeth from both the upper and lower jaws. As in *Ptilodus* the third lower premolar is so small as to have escaped the scrutiny of the collectors, but it is represented by a distinct alveolus in the jaw. There is also considerable uncertainty as to the upper premolars; they are probably represented by such teeth as the types of *Oracodon* Marsh. The lower incisors are readily distinguished by their plano-convex surfaces, complete enamel, and the striations upon the sides. The upper and lower molars are readily distinguished by their large size and the very marked crescentic form of the tubercles. There can be no uncertainty in placing these teeth together,

as done in Pl. VII, Figs. 7 and 8. The composition of upper and lower teeth represented in Fig. 9 is more or less conjectural.

Incisors.—(See *Halodon sculptus*, *Tripriodon caperatus*, *Halodon serratus* Marsh.) The lower incisors are striated both upon the inner and outer sides, and so flat upon the inner surfaces that it is apparent they were placed very closely together. The larger form and the smaller form indicates that there was great range of size variation in *Meniscoëssus*, the smallest forms being nearly of the same size as the largest forms of *Ptilodus*.

The medium upper incisors (Pl. VII, Fig. 9) are apparently smooth, or very slightly striated; they are notched at the extremity and have a very decided cusp on the posterior face, which apparently serves as a check for the lower teeth, and is so characteristic of all the Multituberculata. These upper incisors may be distinguished from those of *Ptilodus* by their complete investment of enamel, and by the much greater length of the enamel crowns; the *Ptilodus* upper incisors having short, obtuse crowns. The third lower premolar is represented in our collection by its alveolus in the jaw. The fourth lower premolar is readily distinguished from that of *Ptilodus* by the very decided character of its ridges and grooves, which are only from seven to eight in number. They terminate upon the anterior portion of the crown in a decided basal ridge, which is wanting in *Ptilodus*. Another feature is, that the ridges are less distinctly arched than in *Ptilodus*.

The first lower molar (type of *Dipriodon lunatus* Marsh) is a long, narrow tooth, which is very constant in the number of its tubercles; there are five tubercles in the outer and four in the inner row—this is sometimes reduced to four and three. The second lower molar (type of *Dipriodon robustus* Marsh) is equally constant, with four tubercles in the outer and two in the inner row; there sometimes being but three in the outer row. The two tubercles in the inner row indicate the relationship of this form to the true *Plagiaulacidæ*.

In the upper molars the first and second bear the same proportions as in *Ptilodus*. The formula of tubercles in the first upper molars (type of *Selenacodon fragilis* Marsh) varies from 6, 7, 5 to 8, 6, 6; while in the second upper molar it varies from

4, 3, 2 to 4, 4, 3. This comparison proves that the type of *Meniscoëssus conquistus* Cope was also a second molar (type of *Tripriodon cœlatus* Marsh), in which the formula is 4, 4, 4-2.

One of the most interesting features about these molars, and one which enables us to recognize them readily, is, that in the upper molars the crescents open forwards, while in the lower molars they open backwards. The crescents are thus reversed in the two jaws, forming a very effective grinding apparatus. This recalls the fact that the crescents are similarly reversed in the upper and lower jaws of the Ruminant Artiodactyla, although in this case they open respectively outwards and inwards, instead of forwards and backwards. In the type of *Stereognathus* Charlesworth, a form which still remains *incertæ sedis*, there are three rows of crescents opening forwards in what Owen described as a *lower jaw*. Marsh has suggested that this type may be an *upper jaw*; if this were the case it would conform with the cusp arrangement of *Meniscoëssus*.

No teeth are found which can with certainty be considered the upper promolars of *Meniscoëssus*; we naturally look for something similar to the upper premolars of *Ptilodus*, and we find it represented most nearly in the types of *Oracodon anceps* and *O. conulus* Marsh. Several similar teeth are represented in this collection, and they are distinguished from those of *Ptilodus* by tubercles upon both the inner and outer bases of the main ridge; these irregularly tubercular teeth very possibly represent the third and fourth upper premolars of *Meniscoëssus*; none have been found, however, in which the main shear is quite equal in size to the shear of the fourth lower premolar.

In earlier reviews of the dentition of *Meniscoëssus*, the writer was led to confuse the upper and lower molars by Prof. Marsh's description of *Meniscoëssus (Dipriodon) robustus* as a tooth with tubercles in two rows, which has a supposed zygomatic portion of the superior maxillary bone attached. This, together with the supposed lower jaw of *Stereognathus*, which has crescentic tubercles in three rows, led the writer to suppose that *Meniscoëssus* and *Stereognathus* together represented a family, *Stereognathidæ*, characterized by crescentic tubercles placed in three rows in the lower jaw and in two rows in the upper jaw. This proves to be an

error. A comparison of Marsh's type of *Meniscoëssus* (*Dipriodon robustus*) with the lower jaws of *Polymastodon*, proves that the supposed bit of the maxillary bone is in reality the base of the powerful coronoid process of the jaw, which extends downwards upon the outer side of the lower molar. Marsh has also subsequently figured a lower jaw of *Meniscoëssus* containing a molar with two rows of tubercles, proving conclusively that the molars in this genus had two rows below, and three rows above, as in all the other Plagiaulacidæ.

Another point of interest is, that some years ago Cope described a tooth striated on the sides and plano-convex in section, agreeing in every respect with those which we have referred to as the probable lower incisors of *Meniscoëssus*, and made it the type of a small reptile—*Paronychodon lacustris*. This description is prior, and may prove to supersede that of *Meniscoëssus*.

II.—THE TRITUBERCULATES.

PLATE VIII.

It is much more difficult to analyze the Trituberculates satisfactorily. They include a variety of forms just emerging from the primitive tritubercular stage, lending overwhelming proof, if any more were needed, of the unity of origin of the molar types of the higher Mammalia, from a tritubercular stem instead of from a multitubercular, as Forsyth Major has suggested. The Trituberculates are represented in the collection by a series of isolated upper and lower molars; also by a number of fragmentary jaws, some of them containing teeth, and it is obvious that the determination of genera and species from such material is a very hazardous matter. If we compare the first and fourth upper and lower molars of the living *Didelphys*, and observe how widely they differ, or still more, compare the high sectorial first lower molar with the low bunodont last lower molar of the modern dogs and cats, or make the same comparison in an ancient Creodont such as *Didymictis*, we realize that it is impossible to reach satisfactory determinations from the isolated molar and premolar teeth of primitive Trituberculates. This problem has

frequently come up before in Palæontology, and it would be a good rule to follow to use either the upper or lower molars only as types. But as both the upper and lower molars have been used by Marsh, we must advance as best we can by describing the chief types as a basis of comparison with earlier and later forms.

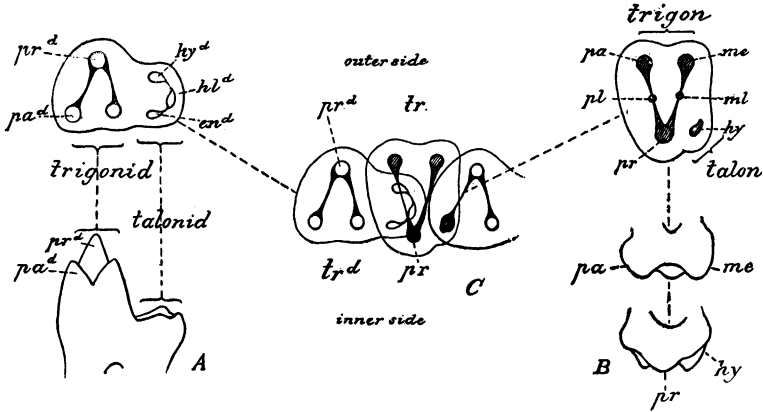


Fig. 3. Relations of typical Tritubercular molars, showing the homologous and functionally analogous parts.

I.—STAGE OF DENTAL EVOLUTION.

The first step is to indicate the general character of the dentition in these mammals. The upper molars are of the simple and generally low-crowned tritubercular type, while the lower molars are sextitubercular, generally with an elevated "trigonid." They thus range themselves with the predominant types of the basal Eocene or Puerco mammals.

Trituberculy in the upper molars is the main type (see Pl. VIII), and takes the form of a low-crowned more or less bunodont tooth, with an elevated internal cusp (protocone), and the intermediate tubercles or conules small or wanting. In none of the molars hitherto described, or of those found in this collection, is there any trace of the hypocone or postero-internal tubercle. About ten distinct types of molars have been found altogether, all much more recent in type than the Jurassic upper molars, which are invariably high crowned or secodont, and at the same time some-

what older in type than the Puerco because they lack all traces of quadrituberculy.

Sexituberculy in the lower molars is the main type (see Pl. VIII, Figs. *A-HI*), but there are some in which the antero-internal cusp (paraconid) is wanting, and others in which the talonid bears only one cusp instead of three. These lower teeth are of two types: first, the 'secodont' or tuberculo-sectorial, with an elevated anterior triangle (trigonid), and a low heel (talonid); second, the 'bunodont,' very similar to that of the small Eocene Primates; in this type the trigonid and talonid are on the same level. The heel usually consists of a broad basin with three well-developed cusps (hypoconid, hypoconulid and entoconid); this strong development of the talonid and depression of the anterior portions of the crown to the same level with the posterior portion affiliates these teeth with those of the Puerco in their general evolution.

Summary of Molar Characters.

Upper Molars.—*a.* Cusps of medium height, trigon not elevated as in the known Jarassic mammals.

b. Protocone, or main internal cusp, on or above the level of the external cusps (paracone and metacone), except in one type.

c. Intermediate tubercles wanting or feebly developed on the spurs of the protocone.

d. External cingulum usually well developed, with one or more supplementary cusps.

e. Internal cingulum entirely wanting, except in one type.

f. No trace of hypocone or postero-internal cusp.

Lower Molars.—*a.* Trigonid usually elevated; sometimes depressed to level of talonid.

b. Talonid, a broad basin usually bearing three distinct cusps (hypoconid, hypoconulid, entoconid).

c. Protocone, or antero-external cusp, invariably the most elevated.

d. Paraconid usually strong; depressed and degenerate in one type. Metaconid strong.

2.—ANALYSIS OF MARSH'S TYPES.

The second step is to examine the types figured by Marsh of the six genera of Trituberculates which he has proposed. For the sake of clearness his figures are here reproduced. The type

of *Didelphops* (*Didelphodon*) *vorax* (Fig. 4, 2) is a low-crowned symmetrically tritubercular upper molar, with all three cusps on nearly the same level, and two small intermediate tubercles externally placed; there is a strong external cingulum notched in the median line. The type of *Cimolestes incisus* (Fig. 4, 14-15) is a lower tuberculo-sectorial molar, quite similar to a third lower molar of *Didelphys*. The type of *Pediomys elegans* (Fig. 4, 23-24)

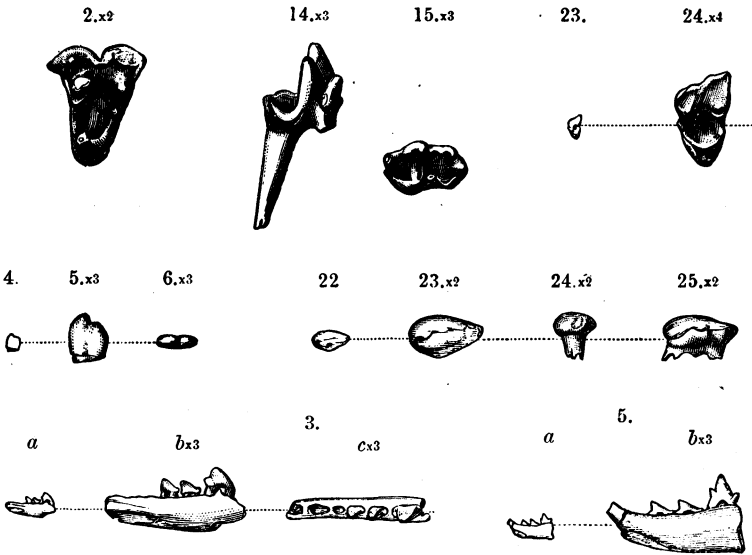


Fig. 4. Type specimens of genera proposed by Marsh. 2, *Didelphops vorax*. 14, 15, *Cimolestes incisus*. 23, 24, *Pediomys elegans*. 4, 5, 6, *Platacodon nanus*. 22-25, *Stagodon nitor*. 3, *Telacodon laevis*. 5, *Batodon tenuis*. Sizes as indicated.

is an asymmetrical upper molar distinguished by a strong anterior spur on the external border; the intermediate tubercles are very small and internally placed. The type of *Stagodon nitor* (Fig. 4, 22-25) is characterized by Marsh by the resemblance of the crown to a drop of viscous fluid; the mammalian nature of the fossil is doubtful. The type of *Platacodon nanus* (Fig. 4, 4-6) is also of doubtful mammalian affinity. The type of *Telacodon laevis* (Fig. 4, 3) is a right lower jaw containing three premolars and three alveoli, which are believed by Marsh to have contained

two more premolars and a canine. The type of *Batodon tenuis* (Fig. 4, 25) is also the anterior portion of a lower jaw containing three premolars and the alveolus of a fourth. It is evident that at present no characters can be assigned to separate the types of *Cimolestes* and of *Didelphops*, or to separate the types of *Batodon* and of *Telacodon* from that of *Pedionmys*. A careful study of these generic types, together with the isolated upper and lower molars associated with them under a number of different specific names by Marsh, shows that *many teeth have been placed together which evidently do not belong together*, as in types of the various species of *Stagodon*, and that it is premature to attempt to associate many of the upper and lower teeth. *The dentition and taxonomy of these mammals cannot be definitely determined until we procure upper and lower jaws with the teeth in situ.* A step in this direction has recently been made by the discovery of Cope of a lower jaw, the type of *Thlaodon*, from another exposure of the Laramie.

The best course to pursue in order to advance our knowledge of the Cretaceous Trituberculates is to lay principal emphasis upon the *forms* of the upper and lower teeth, and avoid the proposal of new generic and specific terms which cannot be defined. The accompanying comparative figures (Pl. VIII) have been prepared in order to bring out the chief types of upper and lower molars.

3.—SUPERIOR AND INFERIOR DENTITION.

PLATE VIII.

We may pass from the most primitive to the most specialized types, taking the upper molars as a standard. *Primitive features* of the upper molars are: Symmetrical form of the trigon or main triangle of cones; large size of the internal cusp or protocone; symmetry of external cusps or paracone and metacone; feeble or non-development of conules; absence of cingulum; absence of external cingular cusps or styles (parastyle and meta-style). *Primitive features* of lower molars are: Elevation of the three main cusps or trigonid; narrowness of the heel or talonid; development of but a single cusp on the talonid.

Superior Molars.

A.—Crown triangular; flattened external border with an anterior cingulum bearing small cusps; main cones, *pr*, *pa*, *me*, subequal; conules, *pl*, small, close to protocone.

Genus *Pedionmys* Marsh.

B.—Smaller; trigon similar to type *A*; external border with strong anterior cingular spur; conules intermediate in position, *pl*, *ml*.

C.—Trigon greatly compressed transversely; no external cingulum; cones, *pr*, *pa*, *me*, subequal. Apparently associated with the lower molar *Cl*.

D.—Trigon extended transversely; external border symmetrical, with fairly developed cingulum; internal cone, *pr*, and external cone, *pa* and *me*, separate; protocone prominent; conules small, externally placed.

Genus *Didelphops* Marsh.

E.—Trigon greatly extended transversely; external border symmetrical, with strong cingulum, and deep median notch; well-developed parastyle, *ps*; conules small, externally placed. This specimen is the type of *D. vorax* (after Marsh).

F.—Crown extended transversely; trigon proper compressed by approximation of external cones, *pa* and *me*, to protocone; external border broad, bilobate, with strong parastyle and metastyle, *ps* and *mts*, and small mesostyle.

Teeth of this type are mistakenly referred by Marsh to *Didelphops*, species *D. comptus*.

They are similar in type to the upper molars of *Ectoconus*, a member of the Puerco Periptychidæ.

G.—Trigon extended transversely; three external cusps in line; protocone depressed; ? paracone elevated; partial internal cingulum.

Upper molars of this type are doubtfully referred to *Batodon tenuis* by Marsh.

They are somewhat similar in type to *Dissacus*, a member of the Puerco Mesonychidæ.

Inferior Molars.

Al.—Trigon is less elevated; paraconid as lofty as protocone; talonid somewhat depressed with large hypoconid and entoconid and small hypoconulid.

These teeth agree in size with Type *A*, superior molar. They are more nearly of the bunodont type than any other teeth known from the Laramie.

Hl.—Protoconid and metaconid depressed; paraconid elevated; talonid rather narrow, with a single cusp.

Cl.—Trigonid and talonid greatly compressed transversely; sexicuspidate.

This transversely compressed crown is somewhat similar in type to *Haploconus xiphodon* Cope, also to *Zetodon*, another aberrant member of the Puerco Periptychidæ.

Genus *Cimolestes* Marsh.

Il.—Protoconid and metaconid elevated; paraconid extremely depressed; talonid supporting three cusps broader than trigonid.

The type of *Cimolestes incisus* Marsh, although larger than this tooth, has similar characters.

El.—Trigonid elevated; protocone elevated above paraconid and metaconid; talonid broad.

The tooth corresponds in size with the type of *Didelphops vorax*; its association is uncertain.

It thus appears that there are six or seven quite distinct types of superior molars (*A-G*), and a similar number of inferior molar types. The upper and lower molars referred by Marsh to various species of *Pediomys*, *Didelphops*, *Cimolestes*, *Batodon* and *Telacodon* conform more or less closely to one or the other of these types; some of the lower molars figured by Marsh are even more strikingly bunodont than our type *Al*.

The premolars determined by Marsh as *Stagodon validus*, *tumidus* and *nitor* are as his terms indicate of a stout character, which we should expect to find associated with our Type *F*, superior molar. They are also somewhat similar to the premolars of some of the Periptychidæ, such as certain species of *Haploconus*, *Ectoconus* and *Periptychus*.

III.—FAUNAL RELATIONS OF THE LARAMIE MAMMALS.

The first question is one of age. These mammals are found in the Laramie, or uppermost of the six great divisions of the Cretaceous. Their exact stratigraphical position is in the middle or lower half of the Laramie Beds. Thus far they are only known to occur in the Wyoming exposures associated with remains of the large *Dinosaurians* such as *Agathaumus* (*Triceratops*), *Diclonius*, *Lalaps*. In New Mexico, as observed by Wortman, some of these Dinosaurs continue to the very top strata of the Laramie, which in turn are conformably overlaid by the basal Eocene or Puerco.

Therefore the Puerco mammals, although they are separated by a considerable interval (of Upper Laramie) in which no mammals have been found, are still much nearer to these Laramie mammals than the latter are to the Middle Jurassic mammals of the Atlantosauros Beds.

The second question is one of faunal relations. In his latest paper upon the Cretaceous Mammalia (March, 1892), Prof. Marsh draws two general conclusions as to the structure and relations of these mammals. First, as to their geological relations and age, he says:

“They are mainly Mesozoic in type, and more nearly related to the Jurassic forms below than to those in the Tertiary above.

.... Bearing in mind all that is known to-day of the development and succession of vertebrate life in America, from the early Silurian on to the present time, it is safe to say that the faunal break as now known between the Laramie and Lower Wahsatch, is far more profound than would be the case if the entire Jurassic and the Cretaceous below the Laramie were wanting."

Second, as to the faunal relations of these mammals, he says :

"The geological lesson now taught by these mammalian relics and their associated vertebrate fossils is no less important, but hardly what was expected. These remains are not transitional between Mesozoic and Tertiary forms, but their affinities are with the former without a doubt; thus indicating a great faunal break between the time in the Cretaceous when they lived, and the earliest known Tertiary, or between the Ceratops horizon and the Coryphodon Beds of the Eocene Wahsatch. The lower division of the Coryphodon Beds or Lower Wahsatch (Puerco) is clearly Tertiary, and the great break is between this horizon and the Ceratops Beds of the Laramie. Each of these faunas is now known by many species of vertebrate fossils represented by hundreds of specimens, and the more the two are compared the stronger becomes the contrast between them. Instead of placing them close together, as some geologists seem inclined to do, it will be more profitable in future to search for the great series of intervening strata containing the forms that lead from one to the other."

Both of these conclusions appear to the writer to be directly the reverse of the lesson taught by a comparison of the Laramie fauna with the Jurassic and the Puerco or basal division of the Eocene. The fact is, these Laramie mammals are surprisingly near those of the Puerco, and in some cases almost identical with them; in other cases they are of a somewhat older type. Therefore, *the greatest gap to be filled by future discovery is between this Laramie fauna and the Jurassic.* For this Laramie fauna is separated from the Puerco about as widely as the Puerco is from the Wahsatch, but no more widely; whereas it is separated by a profound gap from the Jurassic fauna, as proved, first, by a comparison of the general stages of evolution seen in mammals which belong to both periods; second, by the advanced special

evolution of the molar pattern, which is of a modern type in the Laramie, while it is wholly of antique type in the Jurassic, and finally by the difference between the typical modern or Eutherian dental formula seen in the Cretaceous, and the primitive formula found in the Jurassic.

A valuable key to the relative age of the Jurassic and Laramie faunas is seen in the stages of dental evolution of the Plagiaulacidæ. The Laramie stage is very close to that observed in the Puerco of America, and the Cernaysian of France. As long ago pointed out by the writer, these little mammals serve admirably to mark the progress of geological time by the absolute regularity of their evolution, indicated in the steady loss of the anterior premolars, by the regular addition of ridges to the fourth lower premolar, and of tubercles to the upper and lower molars.

COMPARATIVE TABLE OF THE PLAGIAULACIDÆ.

	JURASSIC.	CRETACEOUS.	LOWER EOCENE.	
	Purbeck.	Laramie.	Puerco.	Cernaysian.
Number of lower premolars.....	4-3	2	2-1	1
“ grooves on pm. 4.....	7-9	11-14	12-15	14
“ tubercles on first lower molar, outer, inner...	4-2	6-4	6-4	9-6

There can remain no doubt from this comparison that the Laramie Plagiaulacids stand much nearer the Puerco and Cernaysian types than they do to their Jurassic ancestors. In fact it is nearly impossible to distinguish the larger members of the Cretaceous *Ptilodus* from the Puerco *Ptilodus*; they are in substantially the same stage of dental evolution, and so nearly alike that the writer was for a long time tempted to believe that the Laramie and Puerco faunæ were contemporaneous. This must still be regarded as a possibility, although the Puerco in its exposure in north-western New Mexico is plainly seen to overlie the Cretaceous.

We find entirely analogous proof of the gap between the Laramie and the Jurassic, and of the affinity of the Laramie with the Puerco among the Trituberculates, using this term to cover animals possibly belonging to the Marsupials, Insectivores, Creodonts, and the like.

COMPARATIVE TABLE OF JURASSIC AND UPPER CRETACEOUS
TRITUBERCULATES.

	JURASSIC.	CRETACEOUS.	LOWER EOCENE.
	Purbeck.	Laramie.	Puerco.
Typical dental formula	4. 1. 4. 8.	? 1. 4-5. 3.	3. 1. 4. 3.
Molar types.....	Triconodont and tritubercular, second only.	Tritubercular second and bunodont.	The same.
Upper Molars.....	High crowned. No intermediate cusps.	Low crowned. Small intermediate cusps. No hypocone.	The same. The same. A hypocone, variable.
Lower Molars.....	Narrow spur-like talon cusp.	Broad heel-like talon, bearing 1-3 cusps.	The same.

In this table the transition from the Jurassic to the Laramie is seen to be very wide. In the Laramie the modern placental or marsupial dental formulæ are established—the teeth behind the canine are usually seven, and do not usually exceed eight. Marsh observes in one jaw what he considers five premolar alveoli. Second, out of the high crowned upper molars of the Jurassic, such as those of *Amblotherium* and *Spalacotherium*, a relatively low-crowned or bunodont tritubercular molar has been evolved; as this is a possible parent form of the ungulate and primate upper molars, it is an essentially Tertiary type. Third, the lower molars have evolved a broad talonid or heel, which in many cases present three cusps, whereas in Jurassic types the talonid is a spur or a narrow simple basin. Fourth, the trigonid, which is always very elevated in the Jurassic types, sinks in some cases to the level of the talonid—another modernization looking towards ungulate and primate ancestry.

Two features make the Laramie fauna appear more ancient than the Puerco: first, the non-development of an internal cingulum, which is common in the Puerco; second, the entire absence of the hypocone, which is quite strong in some Puerco mammals. On the other hand the upper and lower molars of Types *F*, *G*, *I*, *Cl*, respectively, are analogous to *Ectoconus*, *Dissacus*, *Diacodon* and *Haploconus* of the Puerco.

The zoölogical affinities of this fauna are at present hard to determine. *Ptilodus* and *Meniscoëssus* are still provisionally referred with the Multituberculates to the Monotremes. *Thlaodon* exhibits a jaw without an angle, and with a surprising resemblance to that of *Polymastodon*; the jaw is certainly neither of the typical placental nor of the marsupial type; this animal may therefore be provisionally considered a trituberculate Monotreme.

The placentals and marsupials, and the question whether one or both of these orders is represented in this fauna, is still unsettled. Not a single jaw has been found or reported sufficiently complete in the delicate region of the angle to determine positively its placental or marsupial structure. Portions of the jaws which are preserved indicate the presence of the marsupial type of inflection, while others point to distinct placental angulation.

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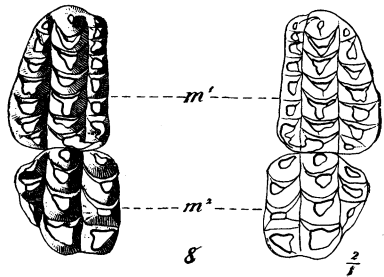
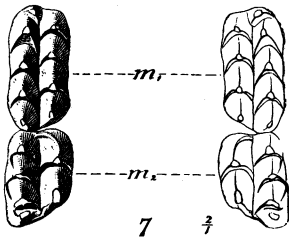
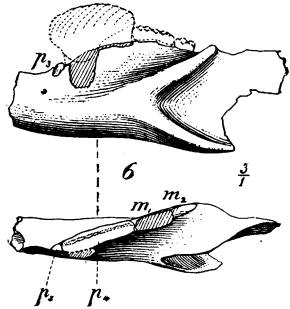
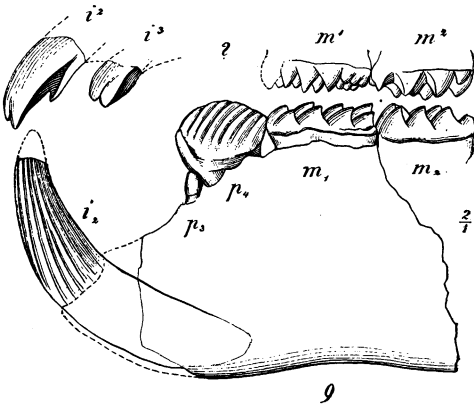
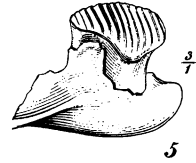
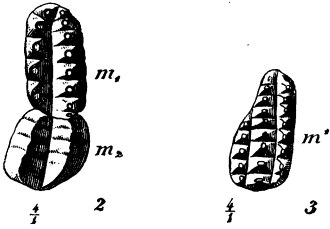
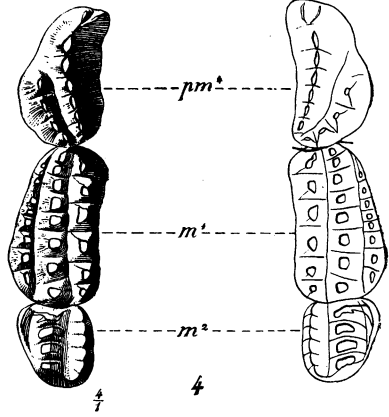
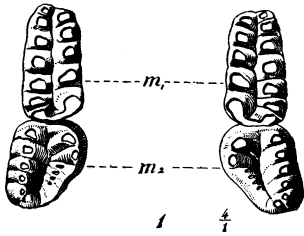
EXPLANATION OF PLATE.

PLATE VII.

Laramie Multituberculates.

[Sizes as indicated.]

1. *Ptilodus*.—First and second inferior molars ; on left side *in situ*, on right side reversed. These teeth belong to two individuals.
2. *Ptilodus*.—First and second inferior molars, worn considerably. These teeth belong to two individuals.
3. *Ptilodus*.—First superior molar of the left side
4. *Ptilodus*.—Fourth superior premolar, first and second molars placed together and reversed in outline to show probable relations. The three shaded teeth on the left side of drawing belong to three individuals
- 5, 6. *Ptilodus*.—External and superior views of two lower jaws, showing proportions of the teeth.
7. *Meniscoëssus*.—First and second inferior molars of two individuals placed together and reversed to exhibit the natural position.
8. *Meniscoëssus ? conquistus*.—First and second superior molars of two individuals placed together and reversed to show the natural position.
9. *Meniscoëssus*.—Composition side view of upper and lower dentition as far as known. Teeth and jaws combined from eight individuals. The superior premolars are not yet known with certainty.





EXPLANATION OF PLATE.

PLATE VIII.

Laramie Trituberculates.

[All figures three times natural size.]

ABBREVIATIONS.—*pr*, protocone; *pa*, paracone; *me*, metacone; *pl*, protoconule; *ml*, metaconule; *ps*, parastyle; *mts*, metastyle; *end*, entoconid; *hld*, hypoconulid.

A.—Crown and side views of three superior molars, probably of the left side. Genus not determined.

B.—Crown views of four superior molars of the right and left sides. Genus *Pedionys* Marsh.

C.—A superior molar, and an inferior molar of the right side. Genus not determined.

D.—Crown and side views of two superior molars of the right side. Genus not determined.

E.—Crown view of a left superior molar. *Didelphops vorax* Marsh, after Marsh.

F.—Crown views of two superior molars, probably of the left side. Genus not determined.

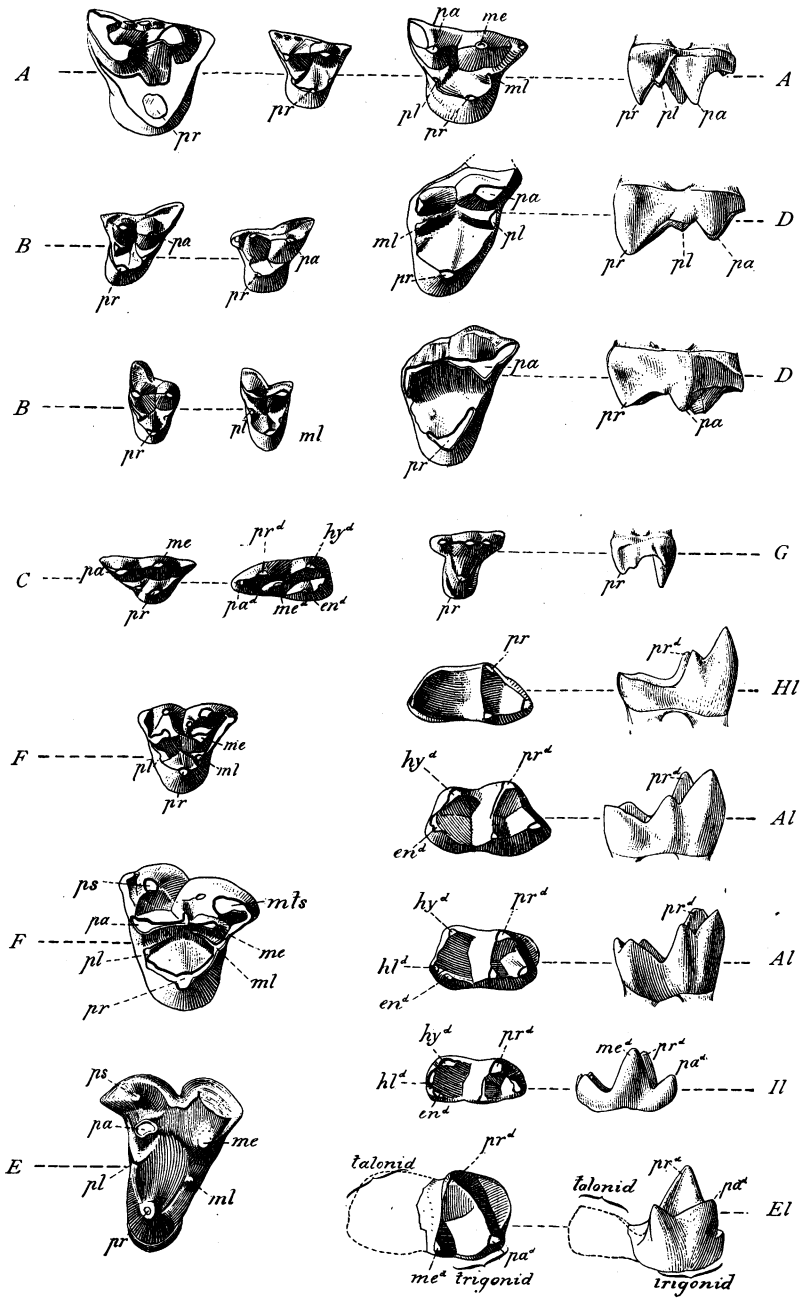
G.—Crown and side views of a superior molar. Genus not determined.

El.—An inferior molar of the left side. ? *Didelphodon*. Crown and inside views.

Al.—Two inferior molars of the left side. Genus undetermined. Crown and inside views.

Hl.—Crown and inside views of a lower molar from the left side. Genus not determined.

Il.—Crown and inside views of a lower molar from the left side. Genus not determined.



UPPER CRETACEOUS MAMMALS.

