Skull Structure of the Multituberculata

By George Gaylord Simpson

Article VIII.—SKULL STRUCTURE OF THE MULTITUBER-CULATA[1]

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Figures 1 to 9

The Order Multituberculata is of interest and importance as having been a dominant mammalian group throughout the Mesozoic, as covering a larger known span than any other order of mammals, as having a peculiar and puzzling anatomical structure, and as bearing on numerous essential problems of modes and methods of evolution, of mammalian classification, of molar history, and many others. Because of its total extinction, its great antiquity, the small size of its members, and the invariably obscure and fragmentary nature of their remains, knowledge of this group as a whole has been more slowly and hardly won than for almost any other order of mammals and remains very incomplete.

The purpose of the present paper is to summarize previous knowledge of the skulls of Multituberculata and to add to it a detailed description of the skull of *Ptilodus*, based in large part on previously undescribed specimens and revealing many important characters hitherto unknown. Among presumed or actual multituberculates, part of the skull has been known in *Tritylodon* (front half only, Triassic in age), *Ctenacodon* and its allies (only a few parts adjacent to the teeth, Upper Jurassic), *Djadochtatherium* (front half, Upper Cretaceous), *Taeniolabis* (most of skull, but no details in the basicranium, Lower Paleocene), and *Ptilodus* (most of skull, but lacking many details, especially in the basicranium, Middle Paleocene). Fragments around the upper dental alveoli are also known for several other genera, but these are not very characteristic, add nothing of importance to what is known from the genera listed, and need not be discussed. Except for *Ptilodus*, there is nothing to add to data on these genera and they are not redescribed, but each is briefly discussed from the point of view of comparison with *Ptilodus*, which is now well enough known and, as will be shown, is sufficiently typical to serve as a basis of comparison for the whole group. The description of *Ptilodus* itself follows, and then comments on the bearing of new facts on the affinities of the multituberculates.
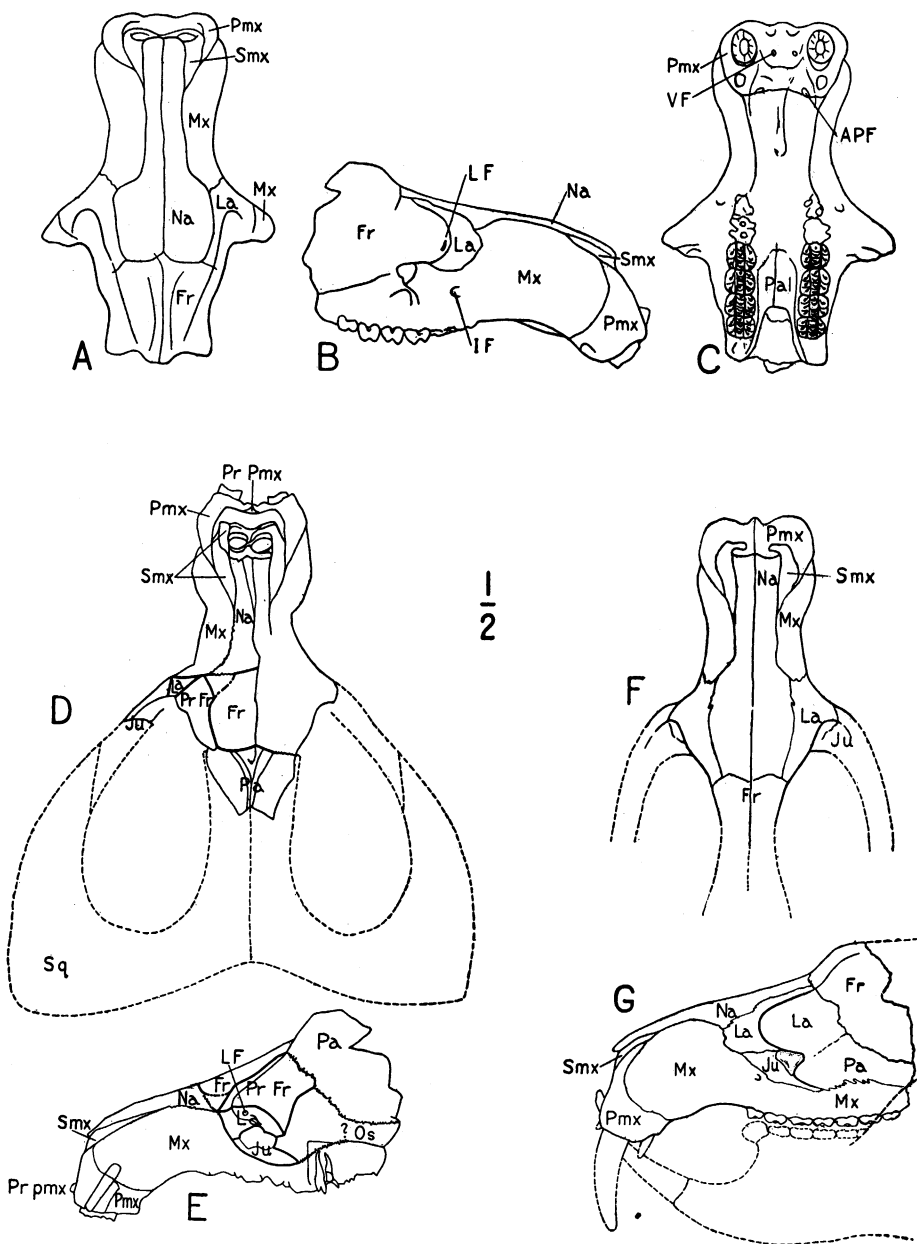

Fig. 1. *Tritylodon longaevus*. Interpretations of structure of type skull by Simpson (A–C), Petronievics (D, E), and Broom (F, G). A, D, F, dorsal views. B, right lateral view. C, palatal view. E, G, left lateral views.

APF, anterior palatal foramen. Fr, frontal. IF, infraorbital foramen. Ju, jugal. La, lacrimal. LF, lacrimal foramen. Mx, maxilla. Na, nasal. Os, orbitosphenoid. Pa, parietal. Pmx, premaxilla. PrFr, prefrontal. PrPmx, median process of premaxillae. Smx, septomaxilla. Sq., squamosal. VF, vascular foramen. All redrawn and relabeled for uniformity, after the authors cited. All one-half natural size.

TRITYLODON

The partial skull of *Tritylodon longaevus* Owen, from the Rhaetic of South Africa, was acquired by the British Museum in 1884, and since that date it has been repeatedly studied and figured. The principal original observations on it are those of Owen (1884), Osborn (1887), Seeley (1895), Broom (1905, 1910, 1914), Petronievics (1917, 1922), and Simpson (1928*a*). The specimen, which consists only of the facial part of the skull, is poorly preserved and the presence of numerous suture-like cracks has led to very diverse views on its structure. The three most recent original interpretations of the skull are here reproduced: Broom, 1910 (his figure of 1914 derives all its facts from this), Petronievics, 1917 (his paper of 1922 does not alter this), and Simpson 1928*a*.

Broom's interpretation and mine are essentially the same, except that he shows the anterior zygomatic root as formed by the jugal. Although all previous students and Petronievics interpreted this point as did Broom, long study persuaded me that it is probably not correct. Petronievics' interpretation differs from both Broom's and mine in considering what we regard as the expanded posterior ends of the nasals to be the frontals, what we regard as the frontals to be the parietals, and what we regard as posterosuperior processes of the lacrimals to be prefrontals. Like Petronievics, both Owen and Seeley had previously considered the anterior and posterior ends of Broom's and my nasals to be suturally separate, Owen calling the most posterior bones preserved parietals, as did Petronievics, and Seeley calling them postfrontals. Petronievics' identification of prefrontals agreed with Seeley's earlier opinion. The specimen permits no certainty as to these moot points, but very careful comparison of the work of both Broom and Petronievics with the actual specimen convinced me that Broom's view is by far the more probable in these respects. Aside from this, it is possible but improbable that the posterosuperior process of the lacrimal, as shown by Broom and me, or Petronievics' prefrontal, belongs to neither of these but perhaps to the nasals or frontals. On other important points the three interpretations agree.

There is a limited habitus resemblance of the face of *Tritylodon* to that of *Ptilodus*, but on the whole the two are very different, the bulbous, rather rectangular snout of *Tritylodon* is unlike the triangular snout of *Ptilodus*. The nasals are narrower, anteriorly, in *Tritylodon*, and on Petronievics' interpretation they end more anteriorly and with less expansion, on Broom's and mine more posteriorly and with greater expansion, in either case not agreeing well with the known nasals of later multi-
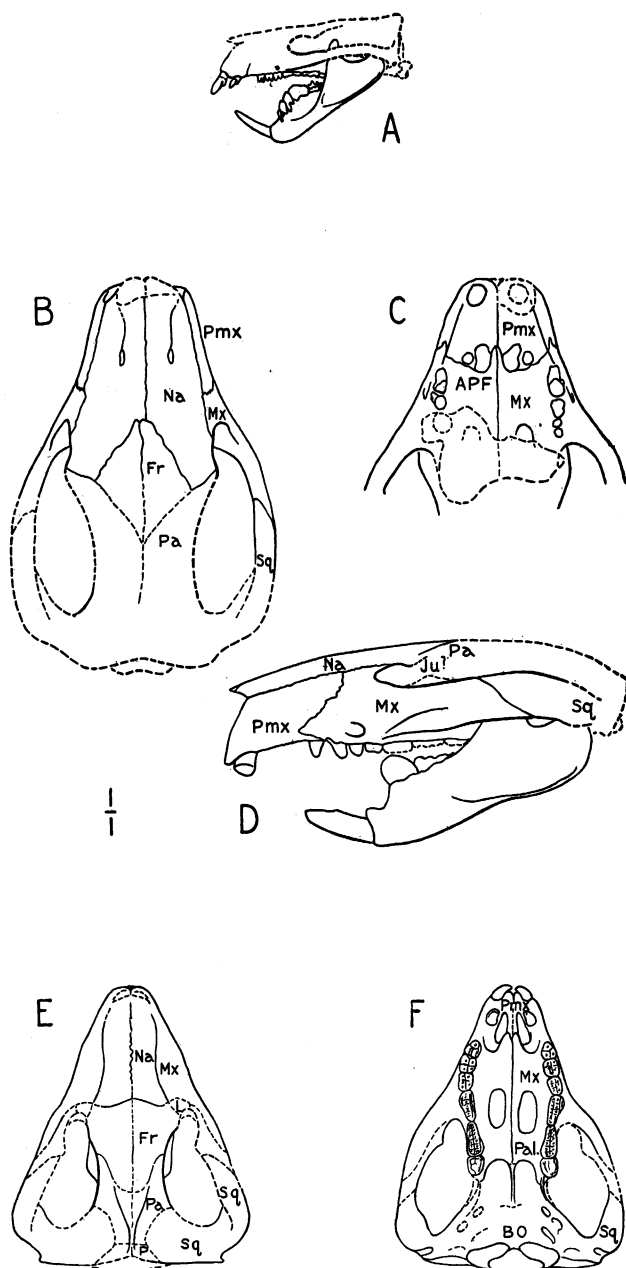
Fig. 2. Skulls of multituberculates. A, *Ctenacodon* sp., composite restoration of skull and jaws, left lateral view. B–D, *Djadochtatherium matthewi*, the type; B, dorsal view, C, palatal view, D, left lateral view. E–F, *Ptilodus montanus* (type of *Ptilodus* "*gracilis*"); E, dorsal view, F, palatal view.

APF, anterior palatal foramen. BO, basioccipital. Fr, frontal, IP, interparietal. Ju, jugal. Mx, maxilla. Na, nasal. Pa, parietal. Pal, palatine. Pmx, premaxilla. Sq, squamosal. Parts in broken lines hypothetical or doubtful. A, new, data from Simpson. B–D, after Simpson. E–F, after Broom. B–F redrawn. All natural size.

tuberculates.   Even in Petronievics' interpretation there is a large facial expansion of the lacrimal in *Tritylodon*, whereas none is known in later forms.   On all interpretations the superoanterior border of the orbit is formed by a different element than in the later known skulls, although if this should prove to be really part of the frontal it would resemble *Ptilodus* and if part of the nasal, *Djadochtatherium*.   In Petronievics' interpretation the frontal is more anterior than in the latter genera and very different in shape and in relationship to the parietal.   In Brooms' and my view it is decidedly more posterior.   In any case the structure of the dorsal part around the orbital region does not agree well either with later multituberculates or with contemporary and earlier mammal-like reptiles.   If other students are correct in seeing a jugal in the specimen, this is radically unlike all known later multituberculates, but if my interpretation is correct the zygomatic root is much the same as in the latter and the jugal might be, but is not proven to be similar.   The large septomaxillaries in *Tritylodon* are unique.

Altogether, the known part of the skull of *Tritylodon* gives no evidence of any relationship to the genera discussed below, nor does it suggest an essentially primitive condition from which they could be derived.

CTENACODON

The skull is very imperfectly known in the Upper Jurassic multituberculates, typified by *Ctenacodon* from the Morrison in Wyoming and the Purbeck in England.   In this genus and the closely allied *Psalodon* and *Bolodon* the whole alveolar border, most of the facial part of the maxilla, the anterior part of the zygoma, part of the palate, most of the premaxilla, and the whole lower jaw are known (Simpson, 1928a, 1929). On the probable assumption that the glenoid surfaces had relations similar to those in *Ptilodus* and *Taeniolabis*, the shape and size of the cranium can be roughly approximated from the lower jaw, and these known parts thus permit a hypothetical reconstruction of the skull the general form of which is probably reasonably near the truth (Fig. 2A; a similar but cruder reconstruction was given in Simpson, 1926).   The known morphological details aside from jaw and dentition, are, however, few.   The premaxilla was relatively somewhat more elongate than in *Taeniolabis* or *Ptilodus*, but only to the degree that would be expected in a more primitive form and quite unlike the aberrant development in *Djadochtatherium*. The infraorbital foramen is unusually small.   Other known details agree rather closely with *Ptilodus*.

As far as this limited knowledge goes, there is nothing in *Ctenacodon*

and its close allies to exclude them from the ancestry of any of the known later genera, and there is more resemblance to *Ptilodus* than to *Taeniolabis*, probably also more than to *Djadochtatherium*.

DJADOCHTATHERIUM

Djadochtatherium, from the upper Cretaceous Djadokhta Formation at Shabarakh Usu in Mongolia, is known from the front part of a skull with much of one zygoma, lower jaws, and some skeletal fragments (Simpson, 1925, 1928b). The form of the muzzle is much as in *Ptilodus*, although somewhat less triangular, and the structure also has many points of agreement. There are, however, some pronounced differences.

The premaxilla is much longer in *Djadochtatherium* than in any of the other genera here discussed, its facial exposure larger than the strictly facial part of the maxilla, and the nasals are also relatively very large, even more, relatively, than in *Taeniolabis*, which they resemble more than they do *Ptilodus*. Posteroexternally they are in contact with the parietals, as in *Taeniolabis* and not *Ptilodus*, and they seem to reach the superior orbital rim, separating the dorsal exposures of the maxillae and parietals, which is more extreme than in *Taeniolabis* but not profoundly different. The frontals, thus excluded from the orbital rim, are small and (together) lozenge-shaped, also more or less as in *Taeniolabis* rather than *Ptilodus*. The zygoma arises more anteriorly than in *Taeniolabis* and *Ptilodus*, is formed to a greater extent by the maxilla, and is even stouter. As in *Taeniolabis* and *Ptilodus*, there is no evidence of a jugal, which was reduced or absent, and the maxilla is widely in contact with the squamosal in the zygoma. The palatal processes of the premaxilla are relatively elongate, as are the facial processes, and the anterior palatal foramina are relatively small and far posterior to I^2. There are palatal vacuities in the maxillae, as in *Ptilodus* and unlike *Taeniolabis*. There is a large foramen in the dorsal surface of each nasal, suggesting those of *Ptilodus*.

The many and peculiar resemblances of *Djadochtatherium* to *Taeniolabis*, *Ptilodus*, or both, stamp it as definitely a member of the same natural group. It cannot, however, be considered as structurally ancestral to either of the two later genera. It is decidedly aberrant in several respects, notably the peculiar development of the premaxillae and of the nasals.

TAENIOLABIS[1]

Taeniolabis is very limited in distribution, being nearly or quite confined to a single level in a limited area of the Puerco Formation, Lower

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[1] Called *Polymastodon* in most publications prior to 1929.

Paleocene, but it is relatively abundant within these limitations.   An attempt to reconstruct the skull from the lower jaw and a few cranial fragments was accurate as far as this scanty material permitted, but inevitably assumed a more orthodox mammalian skull outline than the
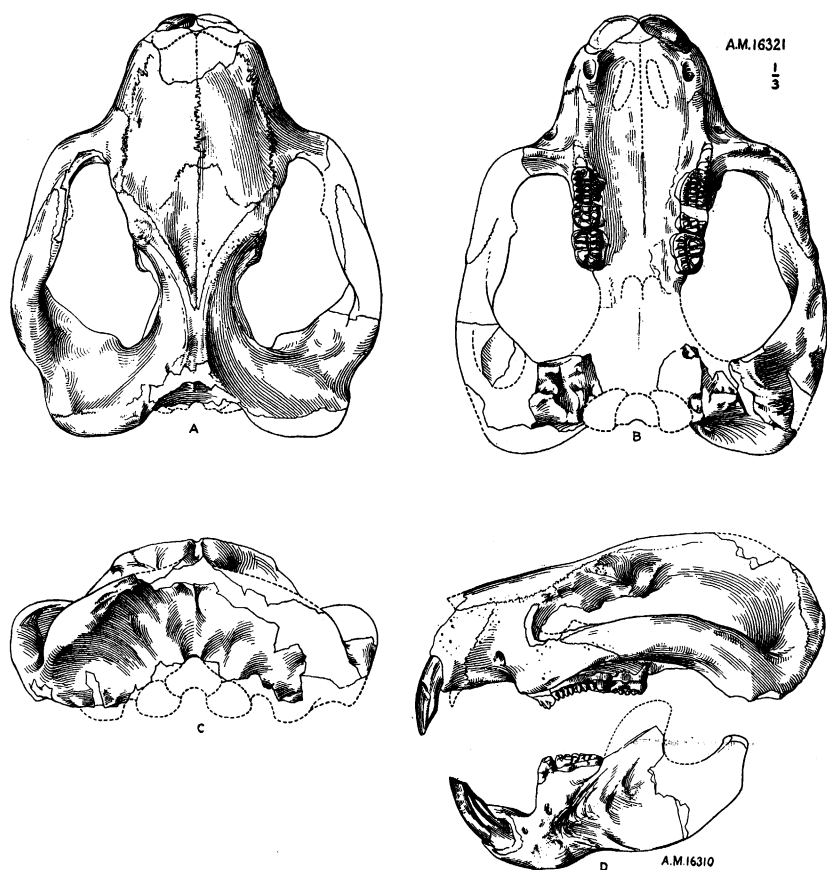

Fig. 3.   *Taeniolabis taoensis*.   Skull (and jaws in D).   A, dorsal view.   B, palatal view.   C, occiput.   D, left lateral view.   After Granger and Simpson.   All one-third natural size.

genus actually had, and so shows the skull much too narrow and the cranium somewhat too shallow (Gregory, 1910; the drawing as is credited, is from a plastic reconstruction made under the direction of W. D. Matthew).   In 1913 W. J. Sinclair found a skull, broken into innumerable

fragments. ~~These were pieced together by Walter Granger and produced~~
a splendid specimen, almost free of distortion and essentially complete,
although none of the basicranial detail can be made out.   This was de-
scribed by Broom (1914) and later in more detail by Granger and Simpson
(1929).   The only essential point in which the two interpretations differ
is that Broom speaks of a small oval vacuity, which we believe to have
been absent, on the basis of specimens clearer in this particular region and
not studied by Broom.   It should be noted that both sets of illustrations
show a dotted postorbital process and Broom's a small but definite jugal,
but that both these points are hypothetical and are not indicated, nor
definitely disproved, by the specimen.

Taeniolabis is the largest known multituberculate, and the skull is
very different in habitus from any other known.   It is relatively very
wide, the width nearly equal to the length, and the short, blunt muzzle
and heavy, squared zygomata give it an aspect more quadrate than tri-
angular.   The musculature and correlated crests and processes are also
strongly developed.   Aside from these plastic modifications, the propor-
tions make a peculiar impression much like *Ptilodus*.   *Taeniolabis* has
the same sort of development of facial, frontal, and palatal regions and
the same extreme shortness and relatively great width of the cranium,
especially the basicranium, which similarly appears almost impossibly
disharmonious with the rest of the skull.

The more pronounced known differences from *Ptilodus* in detail are as
follows.   The markedly shorter snout is accompanied by a relatively
much shorter facial part of the maxilla (correlated with loss of premolars
and reduction of the area where they occurred).   This also has the effect
of placing the orbit decidedly more anteriorly, well anterior to the middle
of the skull.   The nasals are relatively shorter but are tremendously
broad throughout, with less difference between anterior and posterior
widths than in *Ptilodus*, and extend decidedly farther posteriorly, nearly
to the level of the posterior edge of the orbit rather than the anterior, as
in *Ptilodus*.   This expansion has brought them into contact with the parie-
tals, thus eradicating the maxillo-frontal contact seen in *Ptilodus*.   The
maxilla sends a process posteriorly above the orbit, and there comes in
contact with the parietals which extend only slightly more anteriorly
than in *Ptilodus* and are otherwise very similar to those of the latter
genus.   The dorsal exposure of the frontals is relatively smaller than in
Ptilodus, as if limited by the expansion of the nasals, and they are, to-
gether, roughly lozenge-shaped, inserted along the midline between the
posterolateral nasal expansions.   Their posterior outline is closely simi-

lar to *Ptilodus*. The maxilla forms a smaller proportion of the zygoma than in *Ptilodus* and does not send an inferior process back to the glenoid as in that genus. There was probably no palatal vacuity, and even if present it must have been relatively much smaller than in *Ptilodus*.

Despite these differences, the fundamental resemblance of *Taeniolabis* and *Ptilodus* is obvious, and their relationship would be evident from the skull structure even if it were not already established from the dentition and lower jaw. From comparison with earlier multituberculates, with Triassic mammal-like reptiles, and with the most generalized mammalian structure, it is clear that *Taeniolabis* is more specialized than *Ptilodus* in almost every respect in which they are known to differ in the skull (and also the dentition and lower jaw). *Ptilodus* is, indeed, an excellent structural ancestor for *Taeniolabis*.[1]

PTILODUS

PREVIOUS WORK

The first known skull of *Ptilodus* (or of any multituberculate except the equivocal *Tritylodon*) was found in Montana in 1908 by A. C. Silberling and was prepared by J. W. Gidley and described by him in 1909 (see references). The specimen is listed below among the materials for the present study. Gidley gave retouched photographs of the skull as preserved, and presented a brief but important and generally accurate description. The principal points disproved or rendered improbable by later discovery are as follows: the zygoma is not slender (broken in his specimen), the jugal may be absent and almost surely does not reach the glenoid posteriorly or the lacrimal anteriorly, the presence of a facial exposure of the lacrimal is very doubtful, and alisphenoid canal and bulla are probably lacking. Gidley's opposite suggestions on these few points were tentative and derived from the imperfection of his specimen and not at all from inaccurate observation of it.

In 1914 Robert Broom published a new study of the same specimen, including reconstructions of dorsal and palatal views which are here reproduced. He added several important and accurate new observations, as mentioned in the description in this paper below. The only essential structural differences between Broom's reconstructions and

[1] Of course I do not mean to say that it is an actual ancestor—it is younger—but *Taeniolabis* seems almost certainly to have been derived from some Cretaceous genus essentially like *Ptilodus* in skull and dentition. Granger and I (1929, p. 667) have, however, already expressed our conviction that this ancestor was not *Meniscoessus*, as Osborn thought.

those based on better and more numerous materials here presented (aside from the addition of many details not visible at all on Broom's and Gidley's specimen) are all involved in the insertion of several hypothetical elements, stated and shown as such, in his figures.   Thus he shows hypothetical facial lacrimal, interparietal, and jugal, the latter about as Gidley had tentatively supposed.   There is no conclusive evidence in any specimen now known for the existence of any of these three elements. Their possible presence cannot be entirely denied, but in view of the present more extensive material it has become improbable, and in any case remains purely hypothetical and so is omitted from the new reconstructions.

Broom's and Gidley's figures and descriptions have been copied or abstracted more or less correctly in numerous general works but as far as these made no additions or intentional alterations they need not be listed here.   Scott (1913, Fig. 304) gave a life restoration of the head which is probably as good as any that could be made even now, although the proportions (being based directly on a crushed specimen) would require slight modification.   The ears, always a stumbling block in restoration, are particularly so here since there is no bony indication of any part of the external ear in *Ptilodus* and even the position of the meatus is unknown, as well as the size and shape of the auricle, if indeed there was one, which is far from certain.   In fact *Ptilodus* is so very unlike any animal of which the external appearance is known that I question whether we can infer even a rough approximation of what it looked like when alive.[1]   Abel (1911, Fig. 416) attempted a new reconstruction of the side view of skull and jaws, based only on Gidley's figures, but the result was unfortunate.

In a memoir now in press, I have discussed the multituberculates of the Fort Union of Montana, chiefly from a systematic point of view, and have summarized knowledge of Gidley's skull of *Ptilodus*, which forms part of the collection on which that memoir is based.   As far as the structure is shown by that specimen, the description agrees with that here given but is much less detailed and was written before this paper was undertaken or its most important new materials were at hand.   The specimen is not refigured.

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[1] A restoration of *Ornithorhynchus*, for instance, or of most other highly isolated types of mammals, if based only on the bony structure, would be grotesquely unlike the facts.   It is an amusing and sobering experiment to attempt restorations of such recent animals along conservative lines and then to compare them with the known reality.   Such limitations need not, however, inspire a complete distrust in restoration in general, which surely is both valuable and necessary.

MATERIALS AND RECONSTRUCTION

The principal material used for the present study of *Ptilodus* is as follows:

U. S. N. M. No. 6076. Skull and jaws, nearly complete but in many respects poorly preserved or obscure, crushed dorsoventrally, with some associated skeletal parts.—"Gidley's skull."

Amer. Mus. No. 35490. Skull, lacking premaxillae and tips of nasals, fragmented and obliquely crushed but the separate fragments well preserved and for the most part clear in structure, with associated femur, ulna, and some other fragments.— "Our skull."

U. S. N. M. No. 9710. Central portion of a skull, badly crushed and fragmented but revealing a few important characters.

U. S. N. M. No. 9735. Most of right maxilla, with palatal process unusually well preserved.

U. S. N. M. No. 9762. Part of right upper jaw with the more lateral part of palate well shown.

Amer. Mus. No. 35491. Posterior part of cranium (dorsal, occipital, and lateral), little crushed but badly flaked and fragmented, revealing important features of the braincast and some other details.

Amer. Mus. No. 35492. Part of right maxilla and associated lower jaws.

Confirmation and a few minor details have been derived from other specimens (I have studied more than two hundred specimens of this genus), but those listed show practically all that is known.   All are from the Upper Lebo (No. 2 beds) of the Fort Union Group of the Crazy Mountain Field, Montana, the first from the Silberling Quarry and the others all from the Gidley Quarry.   U. S. N. M. No. 6076 is unusually small and was made type of a new species, *Ptilodus gracilis* Gidley (preoccupied = *Ptilodus admirabilis* Hay), but the abundant material now in hand shows it to be a small individual of the highly variable species *Ptilodus montanus* Douglass, to which all the other specimens listed also belong.

No single specimen is entire, and all, particularly those more nearly complete, have been crushed and otherwise seriously damaged, so that any approximately complete view of the skull must be based on a composite reconstruction.   No two specimens are of exactly the same size or agree exactly in structural detail, and the data derived from them have had to be adjusted to each other, so that the result is fictitious to the extent of not being a portrait of any individual but is valid in being within the range of variation and of possibility for this species in every respect, as far as the reconstruction is successful.   It is inevitable that the reconstructions are erroneous in some respects not now observable, first in probably omitting some structures not clearly shown in any specimen

now in hand, and second in probably introducing some errors in the relative proportions and in the relationship of parts derived from different individuals. Despite these inevitable errors, nothing purely hypothetical has been introduced and the figures and description as given are probably reasonably close to the real and complete structure.

The National Museum specimens were prepared by J. W. Gidley, and the American Museum specimens by Albert Thomson, with additional preparation of details (expecially in the basicranium) by me. The reconstructions were drawn in essentials by me and added to (for instance, in drawing in the teeth) and inked by John C. Germann. The National Museum specimens were found by A. C. Silberling and the American Museum specimens by the Third Scarritt Expedition, 1935, of which Silberling was also a member, under my leadership.

THE SKULL AS A WHOLE

The skull is strikingly triangular, although the sides are less straight than in some previous restorations. The rostrum is bluntly pointed. The lateral contour bulges slightly in front of the infraorbital foramina and is moderately constricted at these, then swells out again more rapidly into the arches. The greatest width is across the glenoid processes or across the posterior parts of the zygomata. The extreme shortness of the postzygomatic region is the most striking superficial character of the skull. The postorbital constriction is relatively slight and far back on the skull, nearly half way from the anterior orbital rim to the occiput.

In lateral view the rostrum appears deep and tapers little anteriorly. The nares are completely anterior. The open orbit is almost exactly in the middle of the skull, and the arch is relatively stout and gently curved. The depth of the cranium is a doubtful point, as it is particularly obscured by crushing, but in the figure it has been adjusted to a very incomplete but, in this dimension, little distorted fragment, as well as to the necessary relations of the different bones, and is thus shown to be slightly deeper than the orbital region, its superior contour with a moderate fronto-parietal swelling (surely less than in Abel's restoration).

The ventral view is characterized by the relatively enormous palate and choanae and very small, especially short, basicranium. This disparity is so striking that the figure looks very inconsistent or downright impossible, yet it cannot be much, if any, exaggerated in this respect. The palate is widest at about P^3 and in general is more expanded anteriorly than posteriorly. The basicranium, proper, is about twice as broad as long and gives a strange impression of having been stretched

laterally, or compressed anteroposteriorly, with respect to almost all other mammals.

It is striking that the points in which *Ptilodus* least resembles other mammals in general aspect are, on the whole, resemblances to the advanced mammal-like reptiles, although certain structural details brought out below suggest that this resemblance may be in part superficial.
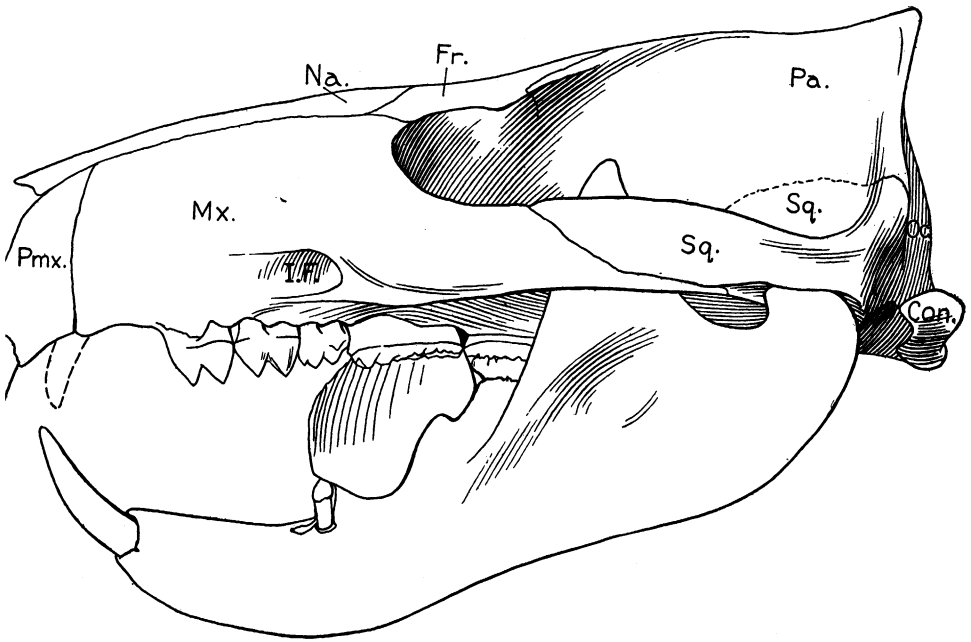

Fig. 4. *Ptilodus montanus*. Composite restoration of skull and jaws, left lateral view.

Con., occipital condyle. Fr., frontal. IF, infraorbital foramen. Mx., maxilla. Na., nasal. Oc., occiput (elements indistinguishable). Pa., parietal. Pmx., premaxilla. Sq., squamosal. About three times the size of an average individual of the species.

ROSTRUM

The nasals are large bones, stout anteriorly and moderately expanded posteriorly. The tips are broken in the known specimens. All the sutures seem to have remained open throughout life. Posteriorly, despite the expansion, there is contact only with frontals and maxillae, and the orbital rim is not reached. There are prominent vascular foramina in

the nasals.   In the restoration they are drawn from American Mus. No. 35490, and in U. S. N. M. No. 6076 they are also well developed but differ slightly in position and there are three in the right nasal.

The premaxilla is a small and rather featureless bone with a short, high facial exposure.   The premaxillo-maxillary suture is nearly vertical and a posterosuperior process is hardly present.

The maxilla is greatly developed and is the largest single bone in the skull, forming most of the side of the rostrum and much of the whole middle part of the skull.   The long facial part is convex vertically, becoming flattened on the zygomatic root, into which it passes without abrupt change.   The infraorbital foramen is single, of average size, at the base of the anterior end of the zygomatic root, above the posterior end of P^3.   The anterior orbital rim is not perfectly preserved in any case and certainty is impossible, but there is no suggestion of facial exposure of a lacrimal and the maxilla probably forms this rim.   There is a short, oblique suture with a frontal above the orbit, but no contact with the parietal.

PALATE

The palatal processes of the premaxillaries are small, mere reflected edges along the anterolateral rims of the anterior palatal foramina.   The exact angle at which these elements are placed is not well shown, since this region is disturbed and repaired with plaster in U. S. N. M. No. 6076, which nevertheless shows it best.   I believe that the specimen and the previous figures based on it have the premaxillaries too projecting, making the snout too pointed and too long, but in any case the difference is not great.   This also influences the shape and to less extent the size of the anterior palatal (or incisive) foramina, but these were certainly relatively very large, especially posteriorly where they notch the maxillae.

Aside from the emargination for this foramen, the palatal process of each maxilla is marked anteriorly by a deep, funnel-shaped pocket running back to a blind, pointed end within the bone.   The peculiar relationships of this pocket are clearer in the figures than they can easily be made in words.   Broom mentioned these and supposed that they might indicate the retention of a large nasal floor cartilage.   This is quite possible, yet the pockets do not look as if they had been filled with cartilage, having smoothly molded sides and also one or two foramina entering from the maxilla, above, and slightly grooving the bone as if beneath epithelium, and it is also difficult to visualize reasonable origin and relationships for

such a cartilage.   As a very tentative suggestion, it is also possible that
this excavation lodged the organ of Jacobson.   It is true that this organ
must, in this case, have been remarkably large and not exactly like that
of any other known animal, but this skull is unique in many respects,
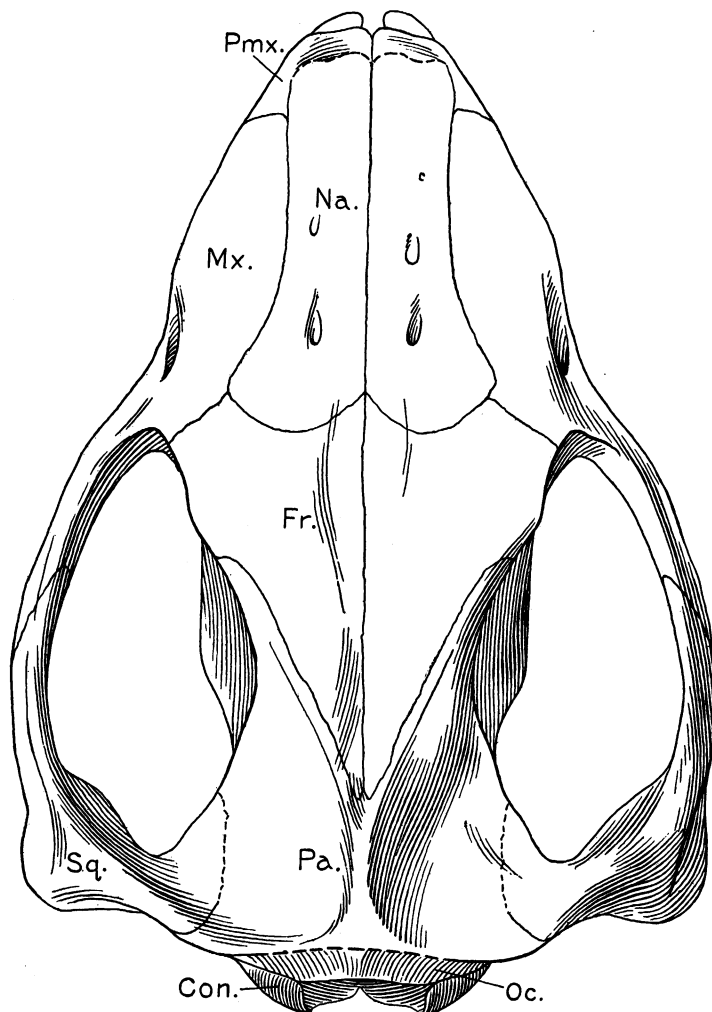

Fig. 5. *Ptilodus montanus.* Composite restoration of skull, dorsal view.
    Con., condyle. Fr., frontal. Mx., maxilla. Na., nasal. Oc., occiput (ele-
ments indistinguishable). Pa., parietal. Pmx., premaxilla. Sq., squamosal.
About three times the size of an average individual.

including these excavations however they are interpreted, and there is
nothing impossible in such a size and position for this organ.   If this is
the correct interpretation, then there is some secondary possibility that
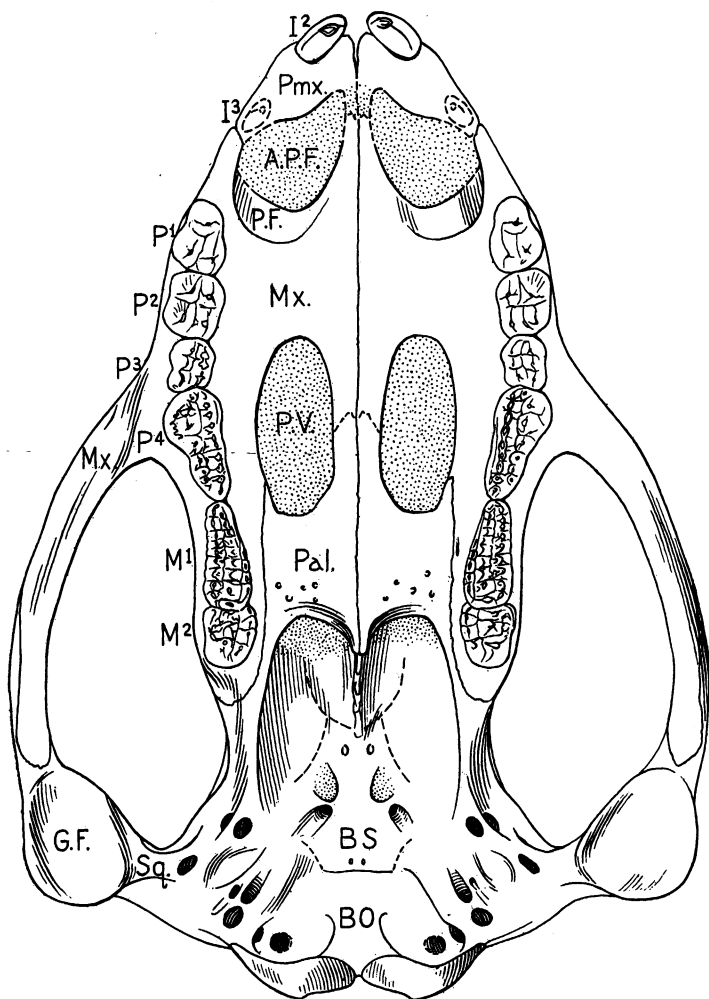

Fig. 6.   *Ptilodus montanus.*   Composite restoration of skull, palatal view.
    APF, anterior palatal foramen.   BO, basioccipital.   BS, basisphenoid.
GF, glenoid fossa.   Mx., maxilla.   Pal., palatine.   PF, palatal fossa.   PV,
palatal vacuity.   Sq., squamosal.   About three times the size of an average indi-
vidual.

part of the bony wall of the pocket, especially the anteromedian part, is really a prevomer, but no suture against the maxilla can be surely identified on the several specimens that show this region.   Further speculation is useless, however, since there is no established probability that the organ of Jacobson was here, and even if it were, it would not follow that a prevomer must be present.

In the middle part of the palate, between P^{3-4} of the two sides, is a pair of large palatal vacuities that appear to be constantly present and little variable in size or shape, their edges smoothly curved.   They are separated by a median bar into which both maxillae and palatines enter, although the exact position of the suture between them has not been determined.   The maxilla forms the whole lateral border of the vacuity, meeting the palatine at the most posteroexternal part of this.   Posterior to this point, the maxilla hardly forms any definite palatal process, but continues as a massive alveolar process carrying M^{1-2}.

The palatines are closely applied against the respective alveolar processes of the maxillae and they form all of the stout transverse palatal bar posterior to the vacuities.   The choanae are nearly as broad as the posterior part of the palate and extend forward between the last molars nearly to the level of the anterior ends of these teeth.   Along this border the palatines are slightly thickened and ridged, and they extend posteriorly into a median point.   There are a few irregular, very minute foramina in the palatines anterior to this thickening, but there appear to be no distinct posterior palatal foramina.   There is, instead, in the lateral part of each palatine a large, horizontal, anteroposterior canal from the choana rim to the posteroexternal rim of the palatal vacuity.   Probably this transmitted the palatine artery and nerve (a branch of V_2, but its posterior course beyond this canal cannot be clearly traced), and the anterior opening, on the vacuity rim, may be functionally a palatine foramen although not strictly in the palate itself.

The choanae are separated by a vertical median plate of bone, presumably vomer (or parasphenoid), as in monotremes, cynodonts, and some higher mammals.

ZYGOMA

The zygomata are stout—their apparent frailty in previous figures was caused by their very incomplete preservation in Gidley's specimen. They arise opposite P^{3-4} and are moderately expanded, widest posteriorly.   The whole anterior root is formed by the maxilla, and the inferior part of this extends back almost to the glenoid surface.   Gidley and

Broom both considered this posterior extension as belonging to the jugal (the most probable assumption as long as permitted by imperfect material) but in my better specimens it seems almost certain that there is no suture between this and the maxilla. The squamosal sends forward a strong zygomatic process, lapping outside and above that of the maxilla. There is no postorbital process on these bones, which must have been very much as in my restoration. It is still conceivable that there was also a small jugal that lay above them, and it is tempting so to identify a small element that lies loose in the matrix near the zygoma in American Museum No. 35490, but this is so doubtful that is seems unwarranted to introduce it into the restoration. On this interpretation, the arch is distinctly monotreme-like, perhaps the only definite character exclusively suggestive of such affinities. Aside from its rather superficial and, in view of other profound differences, contradictory nature, however, the value of this item of evidence is doubtful in the extreme as long as we do not know what really happened to the jugal in the multituberculates. For instance, it might merely be fused with the maxilla, in which case the arch is fundamentally as in marsupials and almost all other mammals and allied reptiles.

The glenoid process stands well out from the cranium, to which it is attached by a constricted pedicle. The articular surface is nearly flat, with very slightly raised outer rim, and is rounded-triangular, slightly longer than wide. It is peculiarly non-rodent-like in view of the rodent-like habitus characters in the dentition and, to a slight extent, elsewhere.

CRANIAL ROOF

Each frontal has a roughly triangular, but detailedly complex, form. Anteriorly a median point projects between the nasals, and lateral to this is a curved emargination for the nasal, then a short oblique suture against the maxilla. The frontal forms the superior border of the orbit and a very slight supraorbital process. Posteriorly the two frontals are prolonged far towards the occiput into an acute point inserted between the parietals. The dorsal surface of the frontal is almost flat and featureless.

Each parietal is characterized by a long anterior process, lateral to the frontal, extending nearly to the supraorbital process. In this genus it does not, however, reach the nasal or the maxilla. Posteriorly the parietals form almost the whole cranial roof, probably ending at the lambdoid crest, although the suture cannot be made out, nor can that between the two parietals. Broom shows a hypothetical or doubtful interparietal bone, but I see no evidence for this—its existence is, of course,

possible or even probable, but if so it is probably fused with neighboring elements and the hypothesis is not worthy of further consideration until some evidence for it is observed.   The temporal crests are feeble anteriorly and follow the parieto-frontal sutures to unite in the sagittal crest posterior to the frontals.   The sagittal crest is definite but not very high. The lambdoid crest is more strongly developed.

The squamoso-parietal suture is identified with probability only on the lambdoid crest, but it appears that the squamous part of the squamosal is small and that this element has almost no part in the cranial roof.

OCCIPUT

The occiput is not well preserved in any specimen and no reconstruction of it has been attempted.   Its few interesting characters are not well shown.   It was apparently nearly as high as broad, and roughly semicircular in outline, with low, indistinct relief.   There is a prominent mastoid foramen in the usual position (presumably venous; relations to a possible mastoid bone are not evident).   I cannot certainly identify any sutures.   A slightly imperfect condyle is present on U. S. N. M. No. 6076, from which its probable complete form has been shown in the restorations.

ORBIT AND INTERORBITAL WALL

The moderate-sized orbit is widely open posteriorly and the other boundaries are formed by the frontal above and the maxilla anteriorly and below.   The orbit strictly speaking, or its outer part, has no floor, as it is above the anterior part of the large temporal opening.   More medially the alveolar (molar) process of the maxilla forms a rounded swelling, not very distinct as a floor or ledge.   The interorbital wall can be studied to advantage only in U. S. N. M. No. 6076 and is there imperfect but reveals important characters.   Above the maxillary process containing the roots of M^1 there appears to be a large, discrete, roughly quadrate, vertical, anteroposteriorly elongated element, perhaps the orbitosphenoid. Near its anteroventral corner there is a foramen at the bottom of a funnel-shaped depression.   At the posterior edge of the orbitosphenoid, between it and the following element (doubtless alisphenoid) there is a somewhat similar but much larger foramen.   These two foramina are widely separated, the more anterior above the anterior end of M^2 and the more posterior above the posterior end of M^2.   At first sight the more anterior foramen might be taken for the optic foramen, but this cannot be correct; it is far anterior to the postorbital constriction (which is always the

approximate point of origin of the optic nerve) and in the floor of the anterior part of the orbit. Although it has not been followed through, its general anatomical relations are such that it must almost necessarily lead into the nasal cavity near the posterior end of the palatal vacuity, and it is therefore the sphenopalatine (= internal orbital) foramen, transmitting part of the naso-oral innervation from V_2. Except for its large size, it is not particularly distinctive from many other mammals.

The larger, more posterior foramen must in any case be the sphenorbital fissure (= foramen lacerum anterius of some authors), and evidently the optic foramen was either confluent with this or barely (and not clearly in the specimen) separate. No specimen permits a categorical statement regarding the foramen rotundum, but it was also probably confluent with the sphenorbital fissure, or nearly so. The observation is uncertain, but there seems to be a very small foramen dorsal to the sphenopalatine foramen, in the frontal just below the postorbital process. If real, this must be the sphenethmoid (or ethmoid) foramen for the nasociliary nerve.

Aside from the possible large orbitosphenoid, as mentioned above, the anterior part of the orbital wall seems to be formed by the maxilla, the superior part by the frontal, and the posterior part by alisphenoid and parietal. The palatine seems to have little, if any, exposure in this surface. This unusual feature may be illusory or may be correlated with the unusually heavy alveolar and zygomatic development of the maxilla.

As far as can be judged from the material now known, this whole region shows very little differentiation. It is basically mammalian but with no marked peculiarities, and differs from the advanced reptilian condition only in being more completely ossified.

BASICRANIUM AND EAR

In U. S. N. M. No. 6076 much of the basicranium appears to be present, but on closer study it is so poorly preserved and so misleading that it is hardly possible to identify any structure except by comparison with better material.[1] Yet it helps materially in orienting more fragmentary but clearer material, and also shows the condyle and the (almost featureless) basioccipital, not otherwise known. American Museum No. 35490 has this region broken into several fragments and dis-

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[1] Gidley mentioned only the possible presence of an alisphenoid canal and bulla, both of which now appear to be absent. Broom doubted the presence of an alisphenoid bulla, correctly identified the cochlea and the hypoglossal foramen, and suggested the presence of two foramina in the alisphenoid region: one of these is here described as the foramen ovale inferius and is one of the few definite landmarks in this part of this skull; the other is an artifact.

arranged, yet the isolated fragments are for the most part very well pre-
served.   It is, of course, possible that features that lay along the edges of
these parts, or between them, are lost, and also that their reassembling
has not been at exactly correct angles, since their are no good contacts,
yet the structure cannot have been very different from that shown.
American Museum No. 35491 is very fragmentary and does not have any
of the actual basicranium, but has been of some assistance as regards the
ear region.

The principal element to be described is a fragment including the
whole posterolateral part of the basicranium, from the condylar pedicle
to the edge of the jugular foramen and anteriorly to the region of the
foramen ovale, with most of the basicranial foramina and the whole ear
region, as well as part of the occiput.   This should include squamosal,
alisphenoid, periotic, and occipital elements, at least, but they seem to be
coössified, or at least I cannot make out any sutures with sufficient
probability to warrant their description.   This region is present on both
sides of our best specimen and in each case has broken away as a unit
under crushing, without itself being much distorted.   On the left side it
has been left as found, nearly in place but rotated by rushing while that
from the right side has been dissected out and thoroughly prepared under
a microscope, but without sectioning or dissection of the fragment itself.

Anteriorly there is a prominent oval foramen, and from U. S. N. M.
No. 6076 this appears to have been faced almost straight ventrally and
to have been in a low triangular eminence in which the pterygoid crest
terminates posteriorly.   Dorsal to this and slightly anterolateral is
another smaller foramen, directed laterally, and separated from the first
by a bony plate or bridge—this can also be confirmed on U. S. N. M.
No. 6076 with our specimen as a control.

The presence of two foramina in the region of the foramen ovale, one
facing antero-inferolaterally and one almost straight ventrally was long
a serious stumbling block in the study of this skull.   The obvious alterna-
tives, that these are the foramina ovale and rotundum or that they
are the foramina ovale and caroticum are both untenable.   The more
anterior foramen can hardly be the foramen rotundum, for its relation-
ships both within and outside the skull are all but impossible for the
maxillary nerve.   Nor is it reasonable to suppose that the more ventral
foramen is for any part of the carotid, in the first place because the posi-
tion and relationships would be extremely aberrant and all but inexpli-
cable and in the second because there is a large foramen, certainly for a
branch of the carotid, in the basisphenoid and it seems highly unlikely

that there should be another even larger and distant foramen to share this function.   Reference to some rodents seems to offer a probable interpretation.   In these, as first shown by Hill (1935), the mandibular nerve issues from the skull through two openings, and in some cases comparison with rodent skulls has shown an almost exact agreement with *Ptilodus*. The more anterior foramen, facing antero-inferolaterally, gives passage
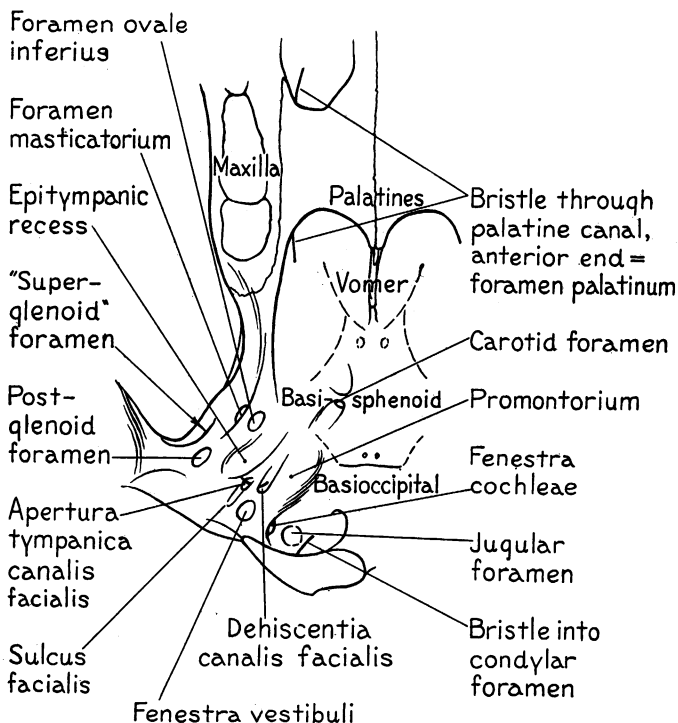

Fig. 7. *Ptilodus montanus*. Interpretation of the structure seen in the basicranial region in Fig. 6.

to the masticatory nerve, while the more posterior, facing ventrally, gives passage to the inferior ramus (= posterior trunk) of the mandibular nerve, which, soon after leaving the skull, divides into the lingual and inferior alveolar nerves.   Hill called this latter foramen in rodents the foramen ovale and gave the anterior opening the new name masticatory foramen.   In fact, the two openings together, and not the posterior alone, are homologous with the foramen ovale as that term has always

been strictly used. In order to preserve this important distinction, I propose to call the more posterior and ventral foramen the inferior oval foramen (foramen ovale inferius) in rodents, and so apply that name to the opening in the multituberculate skull that I believe to be homologous. The qualification "inferior" is descriptively correct, and also refers to its transmitting the inferior ramus of V_3.

The masticatory nerve of recent mammals has motor branches to the external pterygoid, masseteric and temporal muscles and a small sensory branch (the buccinator nerve) to the buccinator muscle, skin of the cheek and mucous membrane of the mouth. The structural parallel that seems to exist between the multituberculates and most rodents in the presence of a separate and relatively large foramen for this nerve may thus reasonably be correlated with the equally striking structural parallel in the great development and in the general arrangement of the muscles which the nerve chiefly serves. In rodents, the development of this foramen is closely associated with the alisphenoid canal, but the latter is apparently lacking, and at least shows no such association, in *Ptilodus*, nor does *Ptilodus* seem to have any other character in the foramina that is specifically rodent-like. This testifies to the probability that this one resemblance is, in fact, convergence related to analogous development of the jaw musculature.

Immediately posterior to the foramen ovale inferius the ear region begins, occupying a disproportionately large part of the remarkably small basicranium. As far as shown, the middle ear is completely open, its roof (or superomedial wall) about on a level with the rest of the basicranium, and not marked off by crests or processes. The most lateral feature is a well-marked concavity which must represent the epitympanic recess. Medial or posteromedial to the posterior part of this recess is a small foramen, directed posterolaterally, separated by a feeble rod of bone from a larger, more medial, slit-like opening, both leading into an elongated cavity which appears to have a connection with the upper part of the auditory meatus.[1] This seems most probably to be the canalis facialis, and the smaller, more lateral foramen the apertura tympanica canalis facialis. The homologies and function of the other, larger opening are not clear. It may, indeed, be simply a defect in ossification, as its slit-like nature also suggests. It is probably not a true hiatus facialis, for it certainly opens into the middle ear, and there is no evident probable way by which the superficial petrosal nerve, if it issued here, reached the

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[1] It has been dissected through, but in cleaning hard matrix from such a very minute canal (about .10–.15 mm. in diameter) it is sometimes possible to pierce a still thinner bone partition accidentally, so that I do not make the assertion unreservedly.

middle fossa of the skull or the sphenopalatine ganglion. Nor can it be an aperture of the canalis prooticus such as occurs in monotremes, for it is medial, not lateral, to the apertura tympanica canalis facialis and does not seem to (although it could conceivably) lead to the sulcus sinus transversus, and, as will be shown below, there is definitely a normal and non-monotreme venous drainage from the sulcus. In position and character it is analogous with the dehiscentia canalis facialis of *Tachyglossus*[1] and perhaps homologous, and it may in any case be given that non-committal
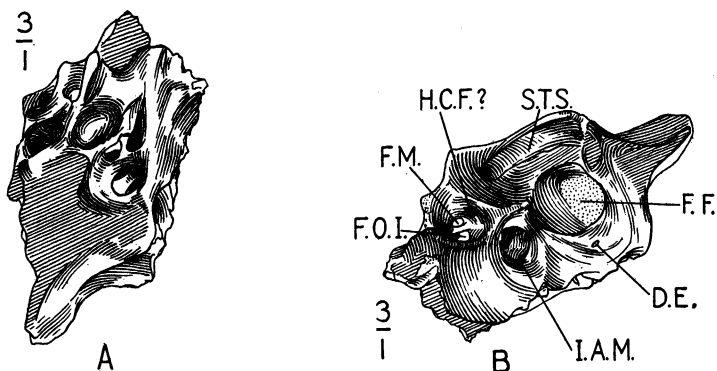

Fig. 8. *Ptilodus montanus.* Amer. Mus. No. 35490, right ear region, dissected away from the skull and drawn as preserved, without restoration except in slight details visible on the left side of the same specimen. A, somewhat oblique ventral view; for orientation and identification of structures see Figs. 6 and 7. B, somewhat oblique internal (endocranial) view.

DE, endocranial aperture of the endolymphatic duct. FF, floccular fossa. FM, foramen masticatorium. FOI, foramen ovale inferius. HCF?, hiatus canalis facialis? IAM, internal auditory meatus. STS, sulcus of transverse sinus. Three times natural size.

name. The cavity in the floor of which this opening occurs is larger than a normal facial canal and may have lodged a strongly developed genicular ganglion. Posterolateral to this opening and immediately medial to the faintly impressed sulcus facialis there is a large oval opening facing infero-anterolaterally in the most probable orientation. This must be the fenestra vestibuli. It is separated by a stout convex bar of bone from a slightly larger, nearly circular opening, facing posteromedially into what was probably a large shallow depression. This must be the fenestra cochleae and its relations are strikingly like those of *Ornithorhynchus,*

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[1] For details of the monotreme ear see Simpson, 1937, in which I have recorded a detailed study made in the course of the present comparisons.

almost equally like the cynodont reptiles (except for the purely super-
ficial difference in degree of ossification) and quite unlike higher mam-
mals.   There is no canalis craniotympanalis and this region is, on the
whole, more reptilian than monotreme-like.   Medial to the fenestra
cochleae, along the broken edge of the bone as preserved, is part of the
rim of what must have been a rather prominent and probably more
rounded than slit-like opening into the cranial cavity, surely the jugular
foramen.

The fenestrae vestibularis and cochleae lead into the two sides of a
single cavity, the vestibule, which appears to be small.   A gentle swell-
ing on the basicranium runs anteromedially for a short distance from
here, medial to the dehiscentia canalis facialis.   This is the promonto-
rium and contains the cochlea, a cast of which is visible on U. S. N. M.
No. 6076 as Broom correctly noted long ago (1914).   In our speci-
men the slit-like area cribrosa (= spiralis, but not spiral in this form)
can be seen in the roof of the cochlear fossa beginning above and between
the fenestrae, leaving no doubt as to identification.   The cochlear fossa
is relatively stout and short and is nearly straight, but is slightly curved
so as to be more convex ventro-posteromedially.   It is monotreme-like,
and even more cynodont-like.[1]

In the recess above the condyle in U. S. N. M. No. 6076 is a single
small hypoglossal foramen—this is double in at least some cynodonts
and usually in marsupials, generally single in placentals and absent
(confluent with the jugular foramen) in monotremes.   It is probably al-
most directly posterior to the jugular foramen, but the two are not shown
on any one specimen.

Lateral to the ear region or more specifically to the epitympanic
recess, on the pedicle of the glenoid process and medial to the posterior
part of the glenoid surface, there is a large foramen opening downward.
This leads into a canal running dorsoposteriorly which could not be fol-
lowed but is inferred to communicate with the mastoid foramen on the
occiput and another running almost straight dorsally which was followed
and which opens into the sulcus sinus transversus on the endocranial sur-
face.   The foramen is thus functionally a postglenoid foramen, although
the name is descriptively incorrect—indeed *Ptilodus* has no postglenoid
region.   A smaller foramen dorsoanterior to this opens forward from the
same canal.   Descriptively and functionally this is a supraglenoid fora-

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[1] For this and other comparisons with cynodonts, see Simpson, 1933.   It still seems quite
possible that mammals, all or part, did arise eventually from cynodonts, and even if they did not,
comparison in these details must be with cynodonts, for we do not know the details in forms perhaps
closer to the mammals, and they must have been nearly like the cynodonts in this region.

men, although it does not necessarily follow that it is literally homologous with that variable opening in higher mammals. In monotremes this transverse sinus system is largely associated with the middle ear (see Simpson, 1937) and it is striking that *Ptilodus* has a very different arrangement and one more nearly approaching the marsupials and placentals.

The inferior margin between glenoid and condyle is not perfectly preserved in any case, but it seems that no auditory notch or groove is present and surely there is no definite bony external meatus. This meatus must then have been cartilaginous and must have passed under the lower jaw, as in monotremes, or, as the relative positions of the pertinent structures make more likely, under the posterolateral edge of the skull, behind the jaw, as in cynodonts, although it does not appear to have grooved the skull as in the latter

The basisphenoid is mostly preserved in American Museum No. 35490. Aside from two pairs of tiny probable nutritive foramina, it has a pair of large lateral foramina, into each of which a groove leads anteromedially. These must be carotid foramina,[1] which thus retain the primitive position as in cynodonts, monotremes and most marsupials, variously modified in higher mammals. Anterior to them on each side is a depressed and rough area which I take to be a collapsed sinus.

ENDOCRANIUM

It has been possible to reconstruct a dorsal view of the braincast with reasonable accuracy. The olfactory bulbs and anterior part of the cerebral hemisphere are visible in U. S. N. M. No. 9710, much of the cerebrum and cerebellum in U. S. N. M. No. 6076, almost all of the cerebellum and part of the cerebrum in American Museum No. 35491, and a few additional or confirmatory details in American Museum No. 35490. There is thus no part of the dorsal surface of the braincast that has not been observed in one specimen or another, and the only probable sources of error are occasional obscurity due to crushing or discrepancies of proportion in reduction to a common size.

Like most of the rest of its structure, the cast thus reconstructed for *Ptilodus* is extraordinarily different from those known in any other groups of mammals. It is evidently primitive, in a general way, but shows no particular resemblance to cynodont reptiles, on one hand, or to monotremes, marsupials, insectivores or rodents on the other.

The olfactory bulbs are enormous, relatively larger than in any other

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[1] They have been followed into the endocranium, have the correct relationships for the carotids and are not the ends of a transverse canal.

mammalian brain known to me.   The length of the post-olfactory region cannot be measured on any one specimen, but it can hardly have been as great as twice the length of the olfactory bulbs.   The latter are completely exposed dorsally and are also peculiar in shape, being pyriform but with the greatest width anterior.   The olfactory foramina are proba-
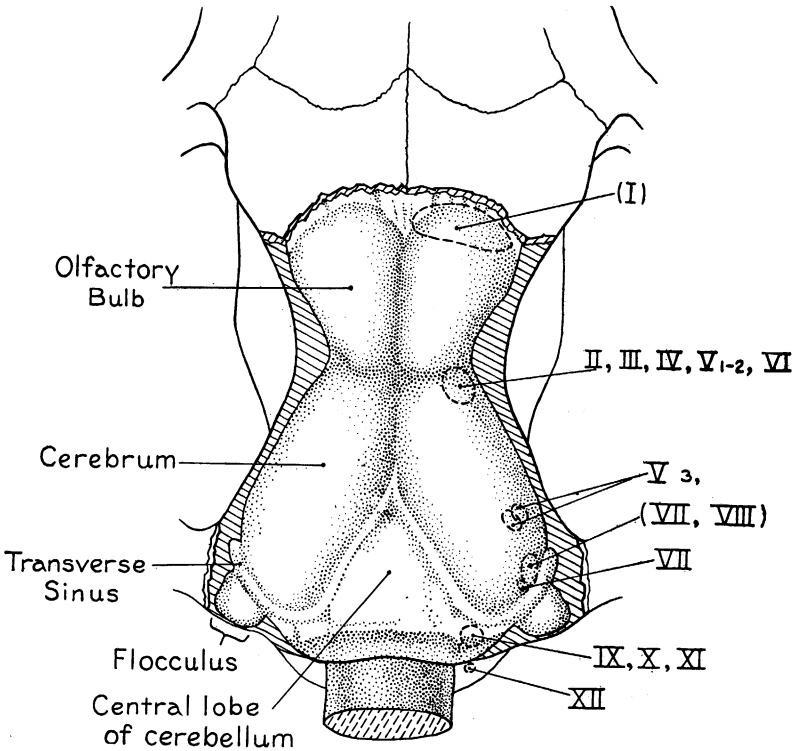

Fig. 9. *Ptilodus montanus.*   Composite reconstruction of part of the skull dorsal view, with the cranial roof represented as cut away to show the endocranial cast.   The Roman numerals correspond with the cranial nerves and the broken lines foramina (not visible in dorsal view of the endocranial cast) through which they pass.   For the Roman numerals in parentheses these foramina are endocranial, for the others external.   Orientation with respect to the whole skull may be seen by comparison with Fig. 5.   About three times the size of an average individual.

bly multiple, unlike *Ornithorhynchus*, and more anterior than ventral, unlike *Tachyglossus*, but this is not quite certain.   The two lobes are closely appressed along the midline, but distinguished by a deep median groove.

The dorsal surface of each hemisphere of the cerebrum is somewhat irregularly elliptical. The two hemispheres are closely appressed anteriorly, but posteriorly they diverge widely. They almost reach the occiput, and they overlie part of the cerebellum posterolaterally. The overlapping of the cerebellum by the cerebrum is generally a progressive character among higher mammals, denoting an expansion of the neopallium and associated higher mental capacities, but it seems quite clear that such an interpretation cannot apply to *Ptilodus*, that its cerebrum is not expanded beyond an extremely primitive, even reptilian, stage, but that on the contrary the cerebellum has in some sense been folded under, and in part pushed into it. This is correlated, again, with the excessively short cranium, but just how such a condition arose or what its functional significance may be, is not clear.

The dorsal surface of the cerebrum is entirely smooth. There may have been (doubtless was) a rhinal fissure, but it must have been lateral or even ventral and barely or not visible in dorsal view.

The triangular central lobe of the cerebellum, which likewise shows no convolutions on the cast, is relatively large and is deeply inserted between the posterior ends of the cerebral hemispheres, which apparently did not here overlap it but simply separated to receive it between them. A large and well-marked transverse venous sinus departs from the sagittal fissure and on each side courses between the hemisphere and the central lobe of the cerebellum, around the posterior end of the hemisphere, then curves forward, looping over the flocculus, and turns downward into the proötic canal, to issue from the postglenoid foramen. The central lobe of the cerebellum is sharply bounded posteriorly, where it turns at an abrupt angle into the nearly vertical occipital surface. There was apparently a very small lateral dorsal exposure of the cerebellum posterior to the cerebrum, and this shows some vague signs of differentiation, but is not clear. There are large and sharply differentiated flocculi projecting posterolaterally from the cerebellum beneath the posterior ends of the cerebral hemispheres. Their distal ends are covered only by a thin film of bone on the occiput. The greatest width of the brain is across these floccular lobes. A small fragment with American Museum No. 35491 bears the bony impression of a tract with a lobulated, or descriptively floccular, surface, but the lobe does not make contact with the probably associated *Ptilodus* skull fragment and I have not been able to place it. It must represent part of the region posterior or posteromedian to the flocculus.

In the lower part of the skull, the internal bony surface is known for the ear region (the united elements described externally on a previous page) and part of the basisphenoid. Posterolaterally the most prominent feature is the large and deep, approximately circular floccular fossa, which has the rim slightly elevated all around. The sulcus sinus transversus is prominent above and around this, and enters the endocranial orifice of the proötic canal anterior to it. Near the inferior lip of the floccular recess and anteromedial to it is a small bony projection medial to which is the internal auditory meatus, which is nearly circular and does form a true meatus but is not deep. The minute opening of the endolymphatic duct can be seen on the raised rim of the floccular recess, about at its most posteromedial part.

Anterior to the internal auditory meatus in the most anterior part of the bone complex as preserved, is a well-marked pit, intermediate in size between the meatus and the floccular recess. Its dorsal, posterior, and ventral borders are rather sharp, but anteriorly it is less distinctly bounded and passes into a shallow groove. It is from the outer part (or fundus) of this pit that the foramen masticatorium and foramen ovale inferius, already described from their external aspect, depart, and it seems probable that the pit lodged the semilunar ganglion, or part of it, and associated structures. Such a fossa is developed in many groups of mammals, being quite distinct in the opossum, for instance, but is not commonly as sharply defined as here, which may be correlated with the hypertrophy of V_3 in *Ptilodus*. If my tentative interpretation of this region in *Ptilodus* is correct, its trigeminal nerve is more literally quadrigeminal, because four nerves, rather than three, left this fossa: the ophthalmic and the maxillary, departing from the more dorsal, median, and anterior part of the ganglion and running forward within the endocranial cavity to the sphenorbital fissure, and the masticatory and the inferior trunk (of the mandibular, common trunk of the lingual and the inferior alveolar nerves) arising from the more external part of the ganglion and leaving the fossa through their respective foramina in its bottom. In the posterior wall of the fossa there is a small depression probably representing a foramen although it could not surely be followed through. There is some probability that this leads to the canalis facialis and is the true hiatus canalis facialis.

The endocranial surface of the basisphenoid has a low transverse crest, homologous with the dorsum sellae, shortly anterior to the suture against the basioccipital, forming the anterior boundary of the ill defined basilar groove and the posterior boundary of the more distinct but broad and

shallow hypophyseal fossa.   The entocarotid canals open into the lateral parts of this fossa.

MANDIBLE

The lower jaws of various multituberculates, including *Ptilodus*, have been so often and well described that there is nothing to add.   The principal features are the short, open symphysis; long collar-like alveolar process for the incisor; oblique, rodent-like horizontal ramus; small, recurved pointed coronoid process; sessile condyle; large temporal and masseteric fossae; and the prominent, flange-like pterygoid crest which does not form a true angular process.

SUMMARY OF FORAMINA

The principal known cranial canals and foramina in *Ptilodus* are here listed in more convenient form for reference.   It is understood that some of the identifications are tentative, as suggested in the previous description.

NASAL FORAMINA.—Two or more vascular foramina in the dorsal surface of each nasal.

INFRAORBITAL FORAMEN.—A single opening of moderate size in the facial part of the maxilla on the lower part of the zygomatic root.   The canal and posterior opening, within the orbit, have the usual relationships.

ANTERIOR PALATAL FORAMEN OR INCISIVE FORAMEN.—On the palate, between premaxilla and maxilla, large, pyriform, with a deep pit perhaps for Jacobson's organ in its posterior rim.   At least one small foramen leads from the vascular (and nervous) canals of the maxilla into this pit.

PALATAL VACUITY.—In the palatal process of the maxilla, similar to the structure in marsupials.

POSTERIOR PALATINE FORAMINA.—Apparently not present or distinct as such, but there are very minute foramina in the posterior part of the palatine.

PALATINE FORAMEN.—The homologue of the foramen palatinum, strictly speaking, is probably an opening within the posterolateral part of the rim of the vacuity, the anterior end of a longitudinal canal in the lateral part of the palatine.

MASTOID FORAMEN.—There is an opening on the occiput in the usual position of this foramen, probably communicating with the proötic canal.

SPHENOPALATINE OR INTERNAL ORBITAL FORAMEN.—A large foramen at the level of the anterior end of M^1 leading from the floor of the orbit into the nasal cavity near the posterior end of the palatal vacuity.

SPHENORBITAL FISSURE OR FORAMEN LACERUM ANTERIUS.—A large fissure in the interorbital wall opposite the posterior end of M^2.   It probably transmitted cranial nerves II, III, IV, V_{1-2}, and VI, the foramen opticum and foramen rotundum being little or not differentiated from it.

FORAMEN OVALE.—Represented by the following two foramina.

FORAMEN MASTICATORIUM.—Directed more or less laterally in about the usual

position of the foramen ovale. Probably transmitting the masticatory branch of V₃.

FORAMEN OVALE INFERIUS.—Immediately ventral to the preceding, directed ventrally, and probably transmitting the rest of V_3.

APERTURA TYMPANICA CANALIS FACIALIS.—A small opening medial to the posterior part of the epitympanic recess. There is no stylomastoid foramen.

DEHISCENTIA CANALIS FACIALIS.—Medial to the preceding, larger and slit-like.[1]

HIATUS CANALIS FACIALIS.—Not certainly observed, but possibly opening into the posterior wall of the fossa for the semilunar ganglion.

FENESTRA VESTIBULI.—Large, oval, between the sulcus facialis and the posterior end of the promontorium.

FENESTRA COCHLEAE.—Large, nearly circular, facing posteromedially and separated from the fenestra vestibuli by a bridge of bone continuous with the promontorium.

JUGULAR FORAMEN.—Only part of the rim preserved, but evidently large, free, not slit-like.

HYPOGLOSSAL FORAMEN.—Small, circular, single, in a recess above the condyle.

POSTGLENOID FORAMEN.—Internal to the posterior part of the glenoid surface, on the ventral aspect of the glenoid pedicle. It is the principal external opening of the proötic canal, which runs from the lateral end of the sulcus sinus transversus almost straight ventrally, anterolateral to the ear region as a whole into this foramen.

SUPRAGLENOID FORAMEN.—Dorsoanterior to the preceding, opening forward, and also leading to the proötic canal. It does not correspond exactly with the supraglenoid of the type description by Cope (1890) and may or may not be homologous, the name being applied descriptively.[2]

CAROTID FORAMEN.—In the basisphenoid, much as in cynodonts, monotremes, most marsupials, and some placentals; there is no transverse canal, unlike marsupials and rodents.

POSITION OF *PTILODUS* AMONG THE MULTITUBERCULATA

It is a permissible assumption that the same broad laws of evolution apply to multituberculates as to other vertebrates, that the Jurassic forms are on the whole more primitive than their later allies that could mechanically be derived from them, that structures shared with ancient or primitive mammals of other groups or with advanced mammal-like reptiles are likely to be primitive for the multituberculates, and that characters common to all of them are probably ancient within the group. On this basis, *Ptilodus* must be judged to be definitely more primitive in the known skull structure than are *Taeniolabis* or *Djadochtatherium*, despite the fact that these are both older than *Ptilodus*. *Ptilodus* doubtless

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[1] Since this paper was written Prof. D. M. S. Watson has kindly examined the material and he agrees with my tentative identification of this dubious foramen.

[2] The external openings from the various venous sinuses and canals in this general region are extremely variable among mammals, both individually and by the apparently independent origin of more or less typical conditions in various particular groups. With the possible exception of the postglenoid foramen, when correctly identified as the primitive and usually the principal foramen of this system, strict homology among all mammals probably does not exist. There are sometimes as many as six or seven separate foramina functionally similar to the often single postglenoid, and on the other hand true foramina surely of this group may be lacking, as they are essentially in the monotremes.

will prove to have various generic peculiarities in skull structure, but on the whole it seems warranted to conclude that it is typical of late Cretaceous and early Paleocene multituberculates and that it is rather primitive, or at least not markedly aberrant or strongly specialized, within this group.

The degree to which knowledge of *Ptilodus* will prove to be applicable to the vastly older Jurassic plagiaulacids is more difficult to judge. In the dentition, there are pronounced changes from the plagiaulacids to *Ptilodus*. One cheek tooth is lost in the upper jaw, two or three in the lower, and the shear is concentrated on a single opposing pair of teeth instead of on two in the upper and two or three in the lower dentition on each side. M_1^1 become large relative to M_2^2, the cusp numbers increase, and their form becomes more complicated. Both upper molars acquire an imperfect third row of cusps. These changes are surprisingly slight for such a long interval, and homologous teeth and still more strongly the dentition as a whole retain the clearest evidence of close affinity. The dentition of *Ptilodus* is about as much like that of *Ctenacodon* as it is like that of its near contemporary *Taeniolabis*, which again shows *Ptilodus* as a member of a conservative line within the Multituberculata. The lower jaws of the Upper Jurassic genera and of *Ptilodus* are not markedly different in any respect, and this is also true of the little that is known of the osteology of the skull in the earlier forms. On the whole it seems improbable that any of the important, basic characters of the Jurassic multituberculates are profoundly obscured or modified in *Ptilodus*, which is thus acceptable, unless definite contrary evidence is later discovered, as a representative of the whole group (Plagiaulacoidea) in considering its affinities.

As regards *Tritylodon*, the case is very different. *Tritylodon* shows hardly any apparently reliable or diagnostic special resemblance either to *Ptilodus* or, as far as they are known, to any other plagiaulocoids. Even in the dentition almost the only resemblances are the presence of enlarged incisors and of cheek teeth with longitudinal cusp rows. Experience has shown that such evidence of supposed relationship, without other reënforcement, has no practical value. In the known skull structure the resemblance is equally distant. There seems to be no good evidence that *Tritylodon* and its allies, the Tritylodontoidea, really belong to the Multituberculata, and they are placed there only hypothetically and because there is no more natural position for them in the established system and inadequate basis for erecting a new major division for them.

The true multituberculates, the Suborder Plagiaulacoidea, form a

clearly natural group, despite their diversity, as is confirmed by what is now known of the skull structure.	Conclusions as to broader affinities based on *Ptilodus*, as a typical representative of this natural group, are presumptive evidence as regards the whole suborder, but not as regards the whole Order Multituberculata if the Tritylodontoidea also be placed here.

NEW EVIDENCE ON MULTITUBERCULATE AFFINITIES

Previous evidence on the affinities of the Multituberculata has already been summarized and discussed in sufficient detail (especially Simpson, 1929; Granger and Simpson, 1929), and need not be repeated. New evidence in this paper relates chiefly to the skull foramina, ear, basicranium and endocranium.	It is important because it adds greatly to the number of characters available for comparison, and particularly because it concerns structures which are frequently the best evidence of ordinal and higher affinities.

The general bearing of these new facts may already be apparent from the occasional comparisons made in describing them.	At first sight it appeared that the monotreme basicranium would provide a key to that of *Ptilodus*, and a very detailed point by point comparison was made, after all the structures on *Ornithorhynchus* and *Tachyglossus* had been examined and identified (Simpson, 1937).	The result, however, was unexpectedly unfavorable.	The resemblance is superficial and the monotreme and multituberculate basicranium do not really appear to be built on the same plan, aside from the most fundamental mammalian characters.	The resemblances seem almost without exception to be either characters of the advanced mammal-like reptiles or of the most primitive mammals generally, and hence in either case not good evidence of relationships within the Mammalia.	The basisphenoid entocarotid entrance, the widely open middle ear, the shape of the cochlea, the relations of the fenestra cochleae, the evidently loose tympanic and absence of a bony external meatus, the large flocculus (absent, however, in *Tachyglossus*), the exposed olfactory bulbs and smooth cerebral hemispheres (but the latter, again, not true of *Tachyglossus*), and some other characters give the cranium of *Ptilodus* a monotreme-like aspect, but there is nothing specific or really characteristic in them.	At most they indicate a similar degree of evolution, very low among Mammalia, and not a common heritage within the Mammalia.	The characters that are truly peculiar or diagnostic in this region for the monotremes do not occur in *Ptilodus:* witness the absence of the craniotympanal canal, presence of

a separate hypoglossal foramen, very different drainage of the venous sinuses, distinctive development of the foramen ovale, epitympanic sinus and facial canal (most distinctive from *Ornithorhynchus*, but also from *Tachyglossus*), very different form and relations of olfactory bulbs and of the cerebellum, and numerous other characters.

The peculiar basicranial proportions in *Ptilodus* seem at first sight to be similar to those of cynodonts and of monotremes, and hence primitive like most of the characters shared with the monotremes. This is probably true to some extent, yet the endocranial relationships now suggest that in multituberculates these proportions have been retained or accentuated by an aberrant development not paralleled in monotremes, as if the cerebellum had been telescoped into the posterior end of the cerebrum.

Whatever may be true of that character, it is evident that there are many structural specializations or aberrations, on a low plane, in *Ptilodus*, and that few of these appear in the monotremes.

In spite of these facts, it might be maintained that profound transformation, partial reversal, differential evolution and general structural upheaval during the long span of the Tertiary might have transformed the multituberculates into monotremes, but the possibility is not now worthy of serious consideration. Aside from the fact that nature does not seem to have wrought any such complete structural remodelings during the Tertiary, it is unreasonable to maintain such a radical view in the absence of good evidence for it. The hypothesis was the most reasonable one when first advanced and when it was so judicially supported by Broom, because most of the resemblances to monotremes and few of the basic differences were then known, but every later accretion of knowledge has made this view less and less probable, until the relatively satisfactory data now in hand seem to make it untenable. We now know most of the characters which were anticipated as the crucial test, and they do not tend to link multituberculates and monotremes, despite the fact that a serious effort has been made to fit these into that hypothesis.

As regards marsupial relationships the situation is similar but even clearer. I see no possibility of correlating the multituberculate cranial structure with that of marsupials, and in this case the evidence is still more conclusive for we know that typical marsupials, rather less like the multituberculates than are some living forms, had long been in existence when *Ptilodus* lived.

It was previously concluded (Granger and Simpson, 1929, and elsewhere) that the limb structure of the multituberculates, at least in the

Paleocene, was metatherian in evolutionary grade but not in taxonomic relationships. It now appears, somewhat unexpectedly in view of that observation, that the cranial structure is prototherian in evolutionary grade but not in a taxonomic sense. There is thus an interesting sort of crossing-specialization, prototherian cranium against metatherian limbs, which in itself would militate against reference taxonomically either to the Prototheria or to the Metatheria, aside from the apparently reliable and quite consistent detailed evidence.

The hypothesis is still sometimes advanced, in apparent seriousness, that the multituberculates were ancestral or closely related to some or to all placental mammals. If the evidence already available were not enough, the new observations here presented would seem in themselves such sufficient refutation of this belief as to make detailed analysis supererogatory.

The result of this increased knowledge is to strengthen the growing conviction toward which all the recent accretions of data on the multi-tuberculates have contributed, that these animals were not the ances-tors of or closely related to monotremes, marsupials, or placentals, that any phyletic connection between them and the latter three groups must have been far back toward the origin of the Mammalia, possibly even be-fore that artifically delimited event, and that taxonomically this means that the Multituberculata form a separate subclass, Allotheria.

Some years ago I remarked that triconodonts might be remotely re-lated to the multituberculates, perhaps only in their pre-mammalian ancestry (Simpson, 1928). This possibility, for which the evidence was (and still is) considered inadequate, was based chiefly on the dentition and mandible. The dorsal braincast, basisphenoid, internal aspect of the periotic, and palate are known in part in triconodonts, and now that they are known in a multituberculate a comparison may be made. Both have palatal vacuities, but the palates are otherwise very different, and even the vacuities differ in the absence of a median bar in tricono-donts (or in the genus *Priacodon*). In the latter the choanae are very narrow, the palatines are not applied to the alveolar process, and there is a broad groove, on the maxilla, internal to the latter. The zygoma also was quite different in triconodonts.

The dorsal aspect of the braincast in *Triconodon* has a generally primi-tive aspect that could give rise to that of *Ptilodus*, but does not in fact approach the particular characters of the latter. The olfactory bulbs are large, but not as large as in *Ptilodus* and more generalized in form. Each cerebral hemisphere is similar in form and smooth, but the two do

not diverge posteriorly. There is a large, triangular central lobe of the cerebellum, but it is not inserted between the cerebral hemispheres and there is a long dorsal cerebellar exposure. There are large flocculi, but so are there in cynodonts and many primitive mammals of several subclasses and orders.

The basisphenoid in *Triconodon* has apparent entocarotid foramina as in *Ptilodus*, but these again seem to be primitive for all mammals. Lateral to each of them is a large foramen, probably in the alisphenoid, perhaps the foramen ovale, and in any case quite unlike *Ptilodus*. The internal aspect of the periotic in *Triconodon* has a large floccular recess, a simple circular meatus and another recess anterior to this, more or less as in *Ptilodus*, and the cochlea is similarly uncoiled but even straighter and relatively small. The sulcus sinus transversus and proötic canal, if present in *Triconodon*, must have been in a different position from *Ptilodus*. On the whole this region is like that of *Ptilodus*, if only higher mammals are compared on the other hand, but all the resemblances were part of the advanced reptilian heritage and hence they really speak neither for nor against special relationship.

There seems to be nothing conclusive or even particularly suggestive of triconodont-multituberculate affinities in these various respects, and the hypothesis remains as such, unsupported by any worthy evidence, but not inherently improbable. The failure of this new evidence to provide any good support for the hypothesis, however, tends to push the possible connection between the two groups far back in mammalian, or probably into pre-mammalian history, as was, indeed, anticipated when the hypothesis was first stated.

REFERENCES

Only papers explicitly cited in the text are listed. Simpson, 1928*a* and 1929, and Granger and Simpson, 1929, provide a nearly complete bibliography of the Multituberculata.

ABEL, O. 1911. 'Grundzüge der Palaeobiologie der Wirbeltiere.' E. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele), Stuttgart. [*Ptilodus.*]

BROOM, R. 1905. 'On the affinities of *Tritylodon.*' Trans. S. African Phil. Soc., XVI, pp. 73–77.

    1910. 'On *Tritylodon* and on the relationships of the Multituberculata.' Proc. Zool. Soc. London, 1910, pp. 760–768.

    1914. 'On the structure and affinities of the Multituberculata.' Bull. Amer. Mus. Nat. Hist., XXXIII, pp. 115–134. [*Tritylodon, Ptilodus, "Polymastodon" = Taeniolabis.*]

COPE, E. D.   1890.   'On the foramina perforating the posterior part of the squamosal
bone of the Mammalia.'   Proc. Amer. Phil. Soc., XVIII, pp.
452–461.

GIDLEY, J. W.   1909.   'Notes on the fossil mammalian genus *Ptilodus* with de-
scriptions of new species.'   Proc. U. S. Nat. Mus., XXXVI,
pp. 611–626.

GREGORY, W. K.   1910.   'The orders of mammals.'   Bull. Amer. Mus. Nat. Hist.,
XXVII, pp. 1–524.   [*"Polymastodon"* = *Taeniolabis.*]

GRANGER, W., AND SIMPSON, G. G.   1929.   'A revision of the Tertiary Multi-
tuberculata.'   Bull. Amer. Mus. Nat. Hist., LVI, pp. 601–676.
[*Taeniolabis.*]

HILL, J. E.   1935.   'The cranial foramina in rodents.'   Jour. Mammalogy, XVI,
pp. 121–129.

OSBORN, H. F.   1887.   'No parietal foramen in *Tritylodon.*'   Science, (2) IX, p. 538.
[See also pp. 92 and 114 of the same volume.]

OWEN, R.   1884.   'On the skull and dentition of a Triassic mammal (*Tritylodon
longaevus*) from South Africa.'   Quart. Jour. Geol. Soc. London,
XL, pp. 146–152.

PETRONIEVICS,   B.   1917.   'On the skull of *Tritylodon longaevus* Owen.'   Ann.
Mag. Nat. Hist., (8) XX, pp. 283–289.

1922.   'Note on root division in the molar teeth of *Tritylodon.*'   Ann.
Mag. Nat. Hist., (9) X, pp. 216–217.

SCOTT, W. B.   1913.   'A history of land mammals in the Western Hemisphere.'
The Macmillan Co., New York.   [*Ptilodus.*]

SEELEY, H. G.   1895.   'The reputed mammals of the Karroo formation of Cape
Colony.'   Phil. Trans. Roy. Soc. London, CLXXXV, B, pp.
1019–1028.   [*Tritylodon.*]

SIMPSON, G. G.   1925.   'A Mesozoic mammal skull from Mongolia.'   Amer. Mus.
Novitates, No. 201, pp. 1–11.   [*Djadochtatherium.*]

1926.   'Mesozoic Mammalia. IV. The multituberculates as living
animals.'   Amer. Jour. Sci., (5) XI, pp. 228–250.   [*Ctenacodon,*
etc.]

1928a.   'A catalogue of the Mesozoic Mammalia in the Geological Depart-
ment of the British Museum.'   British Museum (Natural His-
tory), London.   [*Tritylodon, Bolodon.*]

1928b.   'Further notes on Mongolian Cretaceous mammals.'   Amer.
Mus. Novitates, No. 329, pp. 1–14.   [*Djadochtatherium.*]

1929.   'American Mesozoic Mammalia.'   Mem. Peabody Mus., Yale
Univ., III, Pt. I, pp. i–xvi, 1–236.   [*Ctenacodon, Psalodon.*]

1933.   'The ear region and the foramina of the cynodont skull.'   Amer.
Jour. Sci., (5) XXVI, pp. 285–294.

1937.   'Osteography of the ear region in monotremes.'   American Mus.
Novitates [in press].

[In press.]   'The Fort Union of the Crazy Mountain Field, Montana, and
its mammalian faunas.'   Bull. U. S. Nat. Mus.   [*Ptilodus.*]