First Evidence of Tooth Replacement in the Subclass Allotheria (Mammalia)

BY FREDERICK S. SZALAY[1]

INTRODUCTION

Multituberculates (the only known order of the subclass Allotheria) are abundantly represented in Mesozoic and Paleocene mammal localities. Of the relatively large number of multituberculate mandibles and maxillae known up to the summer of 1963, not one showed a tooth in the process of replacement. Young specimens were known with less fully erupted teeth (Jepsen, 1940, p. 245; Clemens, 1963, p. 34), but it has not been possible before to demonstrate diphyodonty in multituberculates.

With a now-standardized washing technique used for obtaining vertebrate microfossils (Hibbard, 1949; McKenna, 1962), a vertebrate paleontology field party of the American Museum of Natural History collected a large assemblage of vertebrate fossils during the summer of 1963. The collection was of approximately Torrejonian age from the eastern part of the Washakie Basin in southern Wyoming.[2] Among the large number of multituberculates represented, a fragmentary left mandible (A.M.N.H. No. 83003) is one of the two specimens described in the present paper that supply the first direct evidence of allotherian tooth replacement. The deciduous lower incisor is still present in the mandible,

and the incisor is in the process of being replaced by a barely erupting homologous tooth. For comparison, other mandibles of the same species from the same quarry were also studied (A.M.N.H. Nos. 83000, 83001, and 83002). Another specimen showing tooth replacement, a fragmentary right maxilla of *Cimolodon* sp. with three teeth (S.D.S.M. No. 63716), was graciously lent to me for study by Dr. Robert W. Wilson, of the South Dakota School of Mines and Technology. It was collected in the Hell Creek Formation (Latest Cretaceous) approximately 12 miles southwest of Buffalo, South Dakota. The exact locality is V637 of the Museum of Geology, South Dakota School of Mines and Technology.

In this paper the designation of multituberculate teeth as premolars and molars is based on morphology. I realize that the distinction of teeth based on adaptive differences may not be a good criterion. At the present time, however, there is no sufficient evidence by which to differentiate allotherian teeth into premolars and molars on the basis of replacement or lack of it, as is done in the Theria. The following brief definitions, as suggested by M. C. McKenna (personal communication), attempt to give a clarity and preciseness of meaning to the terms "deciduous" versus "permanent" and "premolar" versus "molar" as used in the present paper. The third and fourth lower premolars, when written out, mean the peg and the blade, respectively, without an implication of replacement. DP_3 and dP_4 refer to the peg and the blade, respectively, that have been replaced by P_3 and P_4 in ontogeny. P_3 and P_4 hence depict teeth that replaced dP_3 and dP_4. DP^1 is the tooth behind the incisors that is replaced by P^1. DP^2 is the second tooth posterior to the diastemata that separate the first premolar and the last incisor. P^2 is the tooth that replaces dP^2. A replacement tooth is one that replaces a deciduous tooth.

Were the third and fourth premolars not replaced in ontogeny, these teeth might be considered part of the molar series by persons who choose to apply the same criteria to the allotherians as those by which therian cheek teeth are differentiated.

Simpson's (1926) analysis of the multituberculates as living animals is an outstanding contribution to the understanding of the natural history of this group. An important treatment of the allotherian shoulder girdle with a general discussion of multituberculate affinities was recently published by McKenna (1961). An excellent study of the late Cretaceous multituberculates by Clemens (1963) defined the state of published knowledge of the order. Sloan and his colleagues (in preparation) have extensive new evidence on the osteology, ecology, and evolution of this important order of mammals from the uppermost Cretaceous strata of Montana.

ACKNOWLEDGMENTS

DESCRIPTION

The juvenile specimen of *Ptilodus* cf. *P. wyomingensis*[1] (A.M.N.H. No. 83003) is a fragmentary left mandible. The inferior portion of the horizontal ramus, and the ascending ramus and the posterior portion of the jaw behind the alveolus of P_4, are lacking (see fig. 1). The teeth present in the jaw are the root of dI, I, and the third and fourth premolars.

The tip of the gently arching incisor is entirely unworn (it may not have pierced the gum by the time of death), and the tooth projects out of the broken bone approximately 2 mm. (fig. 2). The visible portion of the incisor is completely covered with enamel, and it is oriented in the way (but not yet positioned) in which it would have been fixed in the adult. Such positioning means that the somewhat medially flattened left and right incisors would be in close contact with each other, forming a single pointed device.[2] The permanent incisor extends backward under the blade where it had been broken off by postmortem damage prior to fossilization. The inferior (or, more precisely, anterior) portion of the posteriorly exposed segment of the incisor has a band of well-formed

---

[1] It appears to me that the oblique extension of the crista coronoidea under the anterior root of the fourth premolar in all *P. montanus* specimens examined and the extension of this crest only under the posterior root of the same tooth in *P. wyomingensis* as illustrated by Jepsen (1940) may be of diagnostic value between the two species.

[2] Simpson (1926) remarked: "The lower incisors are procumbent, and with the jaws closed their main axis forms an angle about 90° with that of the upper incisors." He noted that the orientation of the incisors in the adult is like that in modern diprotodont marsupials. The orientation is similar, but the function of the multituberculate incisors oriented in this fashion was probably somewhat different from that of the shovel-like incisors of modern diprotodonts, as suggested below.

enamel. The large diameter of the broken end permits the conclusion that the incisor must have extended backward at least to the posterior root of M_1. The antero-external surface of the exposed anterior portion is smoothly covered with enamel, much thicker on the anterior surface than on the medial and superior ones. The result of differential enamel distribution is the folding of the enamel into a crest medially and superiorly, producing a slight depression at the labial edges of both medial and superior surfaces. The medial and superior surfaces of the incisor form an angle of approximately 110 degrees, producing a ridge. The
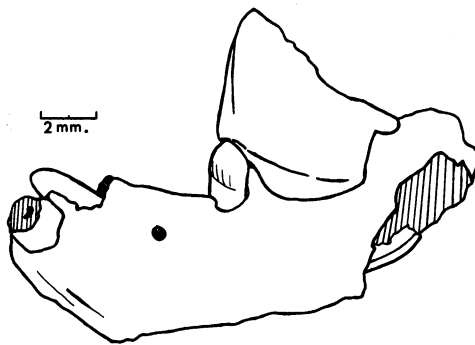

FIG. 1. Lateral view of the fragmentary left lower mandible of *Ptilodus*, cf. *P. wyomingensis* (A.M.N.H. No. 83003), illustrating the deciduous and permanent incisors in the process of replacement. Inferior and posterior portions of the mandible are broken off. The crown of dI and part of the crown of P_4 are missing. Note backward extension of the permanent incisor where it is broken off. Hatched areas represent broken surfaces. ×3.75.

ridge is directed somewhat medially at the tip of the tooth (see fig. 2B). The medial surface of the incisor is wider than the superior one (see fig. 3). Incisors with unequal surfaces, juxtaposed along the wider surface, are a more efficient piercing device than incisors with juxtaposed medial and superior surfaces that are equally wide. The two lower incisors, then, formed a very efficient, three-sided, equilateral, dagger-like, piercing tool, probably for puncturing and slicing open fruits with resistant or slippery coverings, or both.

The root of dI, still firmly implanted in the jaw, is clearly visible, anterolabial to the erupting incisor (see fig. 1). The blade, as indicated by the remaining inferior portion, is fully erupted, although it may not have fully emerged from the gum. The erupting incisor is inferior to the blade; the anterior root of the latter is pushed out laterally to accom-

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF FOUR SPECIMENS OF *Ptilodus* CF. *Ptilodus wyomingensis*[a]

	A.M.N.H. No. 83000	A.M.N.H. No. 83001	A.M.N.H. No. 83002	A.M.N.H. No. 83003 Juvenile
Length of P_4[b]	8.35	7.8	8.8	—
Width of P_4	3.2	2.3	3.15	3.3
Crown height of P_4	7.0	6.95	7.6	—
Jaw width below crown of P_4 at rim of alveolus of anterior root	2.75	2.9	3.0	3.25
Jaw width below crown of P_4 at rim of alveolus of posterior root	2.6	2.6	2.7	2.75
Greatest jaw width at anterior root of P_4	3.45	3.7	3.7	4.55
Lingual striations	11	11–12	12–14	—
Labial striations	13	12–14	12–15	—

[a] Owing to heavy wear on the adult specimens and breakage on the juvenile one, accurate serration counts cannot be given.

[b] Measurement taken as suggested by Jepsen (1940).

modate the tooth below. The comparative measurements taken of the specimens illustrate the lateral spread of the anterior root of the fourth premolar of the juvenile *Ptilodus*. A.M.N.H. No. 83003 has a remarkably greater jaw width (4.55 mm.) at the anterior root of the blade, than the three specimens with which it was compared (see table 1). The posterior half of the fourth premolar is raised high so that the posterior root is superior to the incisor below; the root is probably not fully calcified until the incisors are replaced. The replacing incisor is not wedged between the roots of the obliquely oriented blade.

The fragmentary mandibles of three adult individuals (as inferred from tooth wear) from the same quarry have also been studied. Measurements taken for all four specimens of *Ptilodus* are presented in table 1.

I tentatively refer the specimen from the Hell Creek Formation to *Cimolodon* sp. on the basis of general size range and the morphology of the teeth. As Clemens (1963) remarked, *Cimolodon nitidus* (as the species is known at present) may be taxonomically heterogeneous.

S.D.S.M. No. 63716 (the specimen was dissected for detailed examination) was a fragment of the right maxilla, with three premolars in the bone and part of the hard palate preserved (see figs. 4 and 6). The most anterior tooth, P^1 (length, 1.4 mm.; width, 1.4 mm.), was erupting at

the time of death; the roots were only partially ossified. This tooth is three-cusped, the cusps forming an equilateral triangle. P^1 is positioned in the bone so that one cusp is buccal and the remaining two cusps line up behind each other lingually. The first premolar is very likely a replacement tooth. It has partially erupted, and its roots are only partially formed. Since dP^2 (length, 1.5 mm.; width, 1.2 mm.) is in the process of replacement by P^2, P^1 probably shoved out dP^1 from the maxilla.

As noted above, P^2, of which only the enamel cap was preserved, was replacing dP^2 at the time of death (see figs. 4 and 6). Figure 4 illustrates how the crown of the replacement tooth was pushing against the root of the deciduous one. During excision from the bone the brittle enamel cap

FIG. 2. Anterior portion of the left lower mandible of *Ptilodus,* cf. *P. Wyomingensis* (A.M.N.H. No. 83003). The deciduous incisor is in the process of being pushed out by the barely erupting permanent one. Hatched areas represent broken surfaces. A. Superior view. B. Superior and somewhat lingual view. × 3.75.
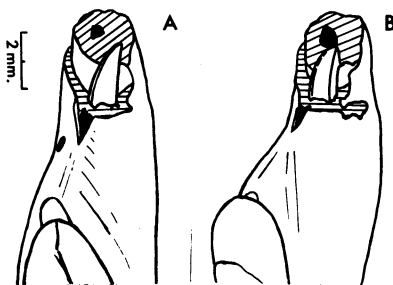
separated into two halves. Both parts of the broken cap were fitted together, and it is evident that the crown pattern of P^2 is quite unlike that of dP^2. The three-cusped crown of P^2 is more like that of P^1; it has no resemblance to its deciduous counterpart (see fig. 5). There is no doubt, however, that P^2 (as interpreted by me) was replacing dP^2 inferior to it and not P^1.

DISCUSSION

Clemens (1963, p. 34, fig. 7) illustrated a fragmentary left lower jaw of *Mesodma formosa,* a ptilodontine from the Lance Formation of Wyoming, in which the P_4 is still erupting. He wrote of this specimen (p. 35): "At the time of death of this individual the formation of enamel was not completed and the roots were not calcified. The incisor root is lingual to P_4 and the alveolus for dP_3 is anterior and slightly linguad to the anterior edge of P_4. X-rays and partial dissection of the mandible did not conclusively demonstrate the presence of a replacement tooth anterior to the crypt for P_4. Certainly a well calcified P_3 is not present." A fragmentary left mandible of *Meniscoessus robustus* was figured by Clemens (1963,

p. 86, fig. 40) showing a partially erupted incisor. The alveoli of the jaw are free of teeth but indicate the presence of the post-incisor series at the time of eruption of the incisor.

When the direct evidence described in the present paper and the additional information cited from Clemens are considered it is clear that in multituberculates a deciduous dentition preceded the replacement one. In addition, some conclusions can be drawn about the eruption and replacement sequence, especially in the Ptilodontidae. Unfortunately the specimen of *Cimolodon* indicates only that dP^1 and P^1 erupted earlier than P^2. The eruption and replacement sequence of the first and second premolars to the more posterior cheek teeth can only be conjectured. Jepsen
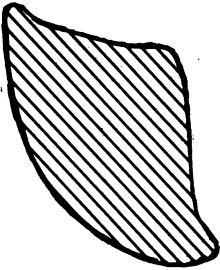

Fig. 3. Cross section of the permanent left lower incisor of *Ptilodus* cf. *P. wyomingensis* (A.M.N.H. No. 83003) approximately 2 mm. from the tip, posterior view. The right side is the medial surface, and the upper side is the superior one. Approximately ×26.

(1940, p. 246) noted the way the peg fitted under the basal concavity of the blade and suggested that the third premolar must have erupted either after the growth of the fourth or synchronously with it, but not before.[1] In the alveolus in front of the blade of the individual of *Mesodma* cited by Clemens, a peg was present that he interprets as a deciduous one. This dP_3 may have been lost before the death of the individual; it is not necessarily a postmortem factor. Clemens reasons, concerning the P_4, and I agree, that it is a permanent tooth because of its late eruption. Hence a fully erupted peg anterior to P_4 would very probably have been a dP_3 for the reasons cited above.

X-ray photographs taken of A.M.N.H. No. 83003 do not contradict the following suggested replacement sequence in *Ptilodus* and what is likely in other ptilodontids. I suspect, although the evidence is indirect,

---

[1] I agree with Jepsen. Conceivably, owing to forward rotation of the fourth premolar, the third one may come in first. I have no confidence in this possibility. Eruption of the blade may not involve so much rotation as first thought. Judged from the figure of *Mesodma formosa* in Clemens (1963, p. 34, fig. 7), first the anterior portion of the blade emerges from the jaw. This emergence, I believe, is followed by the raising of the entire crown at a more or less even level and rate, involving only a very minimum, if any, of further rotation. The entire process is probably further complicated by the growth of the mandible.

that the first to erupt in the mandible is dP_4, followed by, or at the same time as, the eruption of dP_3. It seems probable to me that the large majority of multituberculates had altricial young (newborn that are not fully developed at the time of birth and are dependent on the mother's milk and care for a prolonged period). The assumption is that the multituberculates occupied niches presumably similar to those occupied at the present time by therian cricetids, murids, and sciurids. In these groups of rodents the young are mostly altricial. In multituberculates the early presence of forward-projecting lower incisors would have been probably a handicap in suckling.[1] On the other hand, it is conceivable that during the period of active dependence on the mother dP_4 and dP_3 had already erupted. The deciduous incisor was implanted after the eruption of dP_4 and dP_3. Although it is postulated here that the peg and the blade are replaced in ontogeny, the actual sequence of tooth replacement is doubtful. The blade in A.M.N.H. No. 83003 (the juvenile individual) does not seem to differ in its dimensions or morphology from the great majority of presumed replacement P_4's from the quarry sample. In this specimen the peg and the blade are interpreted to be replacement teeth. The eruption of dI then preceded the replacement of dP_4 and dP_3 by P_4 and P_3. Following the latter events (we know nothing about the eruption of molars) the permanent incisors could move forward to replace the deciduous ones. The evidence presented in this paper is open to possible alternative interpretations, although at present I find the above-postulated replacement sequence the most convincing one.

The molars probably erupted once the blade and peg were in place, but there is not even indirect evidence that the molars were replaced. No homology is implied, however, between the molars of allotheres and those of therian mammals. Butler (1939) noted that the morphological transition of the premolar into the molar pattern can take place along varied positions of the tooth row in different groups of therian mammals or in the same group during different times of their phylogeny. This statement would imply that the premolar-molar transition is not necessarily linked on genetic grounds with tooth replacement in any way. The prob-

---

[1] This point is highly speculative. No evidence contradicts the possibility that allotherians were not viviparous, had no means of lactating the young, or that the young hatched from eggs. Dr. W. A. Clemens remarked (personal communication), in relation to the procumbent incisors and suckling in multituberculates, that in murids the deciduous incisors splay out laterally, encircling the nipple, thus reducing the danger of cutting the mother. The suggestion is an excellent one, and I consider it just as possible as my tentative explanation. Unfortunately the number of juvenile specimens is few, and in the known ones it cannot be determined whether there was any splaying of the incisors or not.

lem of molar replacement in allotherians would probably depend on some adaptive advantage either way, rather than on the premolar-molar differentiation.

The differences between dP^2 and P^2 of *Cimolodon* demonstrate the fundamental dissimilarities that can exist between homologous deciduous and permanent multituberculate teeth (see fig. 5). I believe that the non-grinding and non-occluding three anterior upper premolars of ptilodontids are more prone to variation than are the remaining teeth,
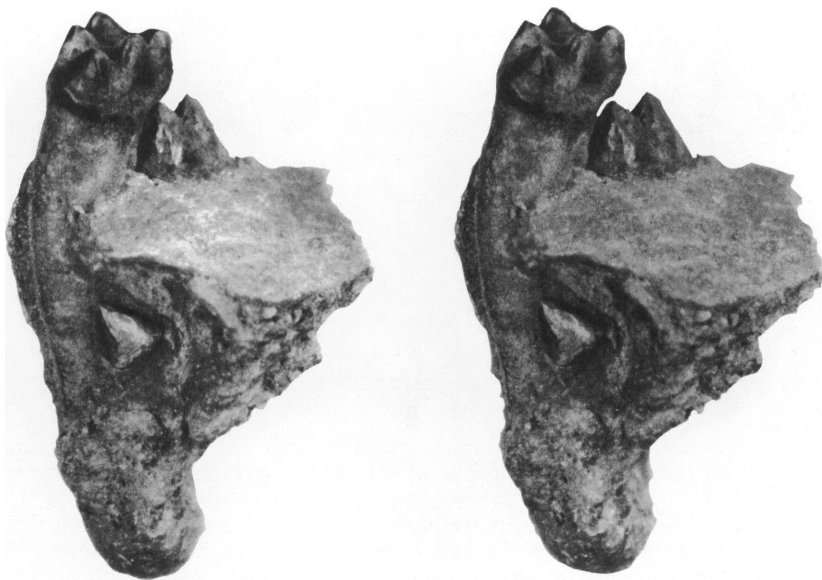

FIG. 4. Stereophotograph of right maxilla of *Cimolodon* sp. (S.D.S.M. No. 63716), with P^1, dP^2, and P^2 in place. The deciduous second premolar is shown in the process of being replaced by P^2 which is superior (inferior on the photograph) and medial to dP^2. The sequence of teeth from left to right is dP^2, P^2 (embedded in bone), and P^1. $\times 12$.

owing to loss of their original function which very likely involved occlusion. In spite of the great morphological variation exhibited by the deciduous and replacement second upper premolars, it seems remarkable that the more anterior upper premolars in ptilodontids kept their primitive crown pattern as consistently as they did. The three upper premolars undoubtedly have some advantage, probably to hold food in the buccal cavity. Curiously, however, the teeth in question, which probably evolved for a chewing function somewhat similar to that of the more posterior

and occluding last premolar and molars, generally retained their primitive crown pattern. The genetic factors that probably controlled and maintained the morphogenetic field of the occluding and chewing teeth also continued to influence and preserve the primitive morphology of the non-occluding premolars. This fact suggests that there was no selective pressure either for the loss of the anterior premolars in the maxilla or for their transformation into other types of teeth. In other words, the non-occluding upper premolars could adequately anchor food. Whenever
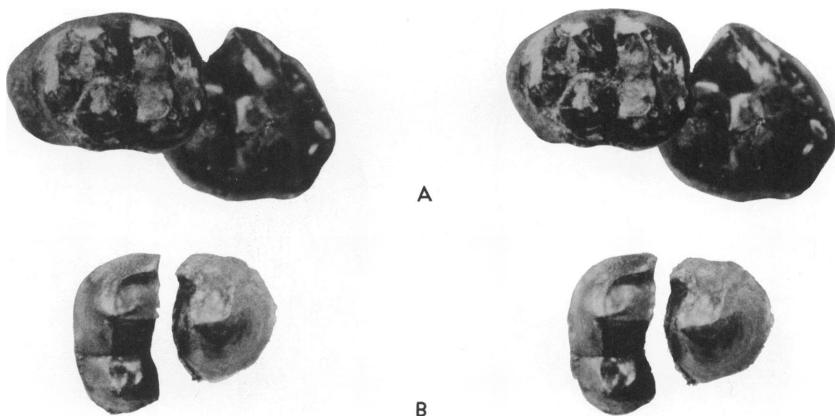

FIG. 5. Stereophotographs of dP^2 (and P^1) and P^2, respectively, of *Cimolodon* sp. (S.D.S.M. No. 63716). The differences between dP^2 (left tooth on A) and dP^2 (B, the two parts of the enamel cap are fitted together as they were in the maxilla) demonstrate the fundamental dissimilarities that can exist between homologous deciduous and replacement teeth of ptilodontid multituberculates. Both A and B are crown views. All ×15.

genetic factors affected the crown pattern of any of the anterior upper premolars, this resulting aberrant crown pattern was not so rigidly selected against as that of the occluding posterior teeth. Consequently, we may find a greater morphological variation between homologous deciduous and replacement anterior (1–3) premolars, and among various homologous specimens of any one of these teeth, than we find among occluding cheek teeth.

Regardless of the correctness of the above explanation of great variation in the non-occluding premolars, future taxonomic studies of multituberculate species must allow for the probable differences between homologous teeth (deciduous versus replacement and replacement versus replacement from another individual) in the allothere dentition.
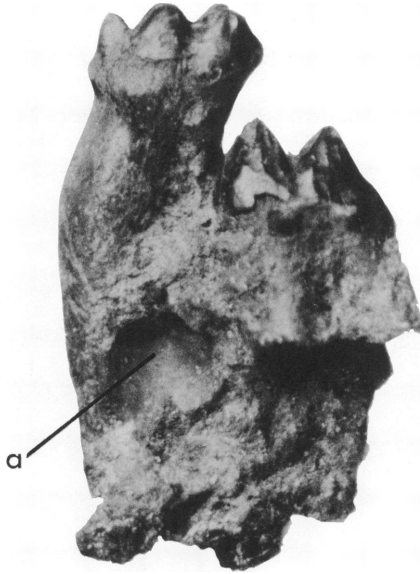
Fig. 6. S.D.S.M. No. 63716, after P² has been dissected from cavity under dP² (depression marked with a). Teeth from left to right are dP² and P¹. Lingual view. ×15.

REFERENCES

BUTLER, P. M.
  1939. Studies of the mammalian dentition. Differentiation of the post-canine dentition. Proc. Zool. Soc. London, vol. 109B, pp. 1–36, figs. 1–28.
CLEMENS, W. A.
  1963. Fossil mammals of the type Lance Formation, Wyoming. Part I. Introduction and Multituberculata. Univ. California Publ. Geol. Sci., vol. 48, pp. 1–105, figs. 1–51, tables 1–10.
HIBBARD, C. W.
  1949. Techniques of collecting microvertebrate fossils. Contrib. Mus. Paleont. Univ. Michigan, vol. 8, no. 2, pp. 7–19, pls. 1–4.
JEPSEN, G. L.
  1940. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Proc. Amer. Phil. Soc., vol. 83, no. 2, pp. 217–340, figs. 1–23, pls. 1–5, tables 1–20.
McKENNA, M. C.
  1961. On the shoulder girdle of the mammalian subclass Allotheria. Amer. Mus. Novitates, no. 2066, pp. 1–27, figs. 1–6, table 1.
  1962. Collecting small fossils by washing and screening. Curator, vol. 5, no. 3, pp. 221–235, figs. 1–6.

SIMPSON, G. G.
    1926. Mesozoic Mammalia. IV: The multituberculates as living animals. Amer. Jour. Sci., ser. 5, vol. 11, pp. 228–250, figs. 1–8.
SWAIN, B. W.
    [M.S.] Fort Union Formation, west flank of the Sierra Madre, Carbon County, Wyoming. Laramie, University of Wyoming, Master's thesis, 1957.