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# Deciduous Dentition of the Early Tertiary Phenacodontidae (Condylarthra, Mammalia)

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## INTRODUCTION

Isolated deciduous teeth are frustrating and often confusing finds for mammalian paleontologists. Accurate identification and interpretation of these teeth depend upon positive association with permanent teeth. Unfortunately deciduous teeth commonly are found separately, because they were either shed by the living animal in the course of maturation or they were lost after the death of a subadult individual. Additionally, rapid wear often removes most of their distinguishing features early in life, so many are virtually featureless, whereas permanent teeth, at a similar age, retain much of the surface topography.

In the process of a study of the Paleocene to Eocene condylarth family Phenacodontidae, I encountered a large number of deciduous teeth both isolated and in jaws and frequently associated with at least one permanent tooth. The present paper describes and illustrates the deciduous premolar dentitions, as far as known, of three common genera of phenacodont condylarths (*Tetraclaenodon, Phenacodus,* and *Ectocion).*

The presence of some deciduous teeth in place in jaws allows examination of their relationships with one another and with the permanent teeth. It is also possible, under favorable circumstances, to postulate the sequence of replacement of deciduous teeth and eruption of the permanent teeth.

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All measurements are given in millimeters, and the important features of the deciduous teeth are shown in the outline drawing (fig. 1). The following abbreviations are used:

A.C.M., Amherst College Museum
A.M.N.H., the American Museum of Natural History, Department of Vertebrate Paleontology
C.M., Carnegie Museum
F.M.N.H., Field Museum of Natural History
M.C.Z., Museum of Comparative Zoology, Harvard University
P.L., Mr. Pierre Louis, via Muséum National d'Histoire Naturelle, Paris
P.U., Princeton University
U.C.M.P., University of California Museum of Paleontology, Berkeley
U.S.N.M., United States National Museum, Smithsonian Institution
Y.P.M., Peabody Museum of Natural History, Yale University

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## PREVIOUS WORK

Cope (1884, p. 489) first mentioned phenacodont deciduous teeth and briefly described $dP_4$ and $dP^4$ of *Tetraclaenodon puercensis* (then referred to *Phenacodus*) from the "basal Eocene Puerco beds" (now the middle

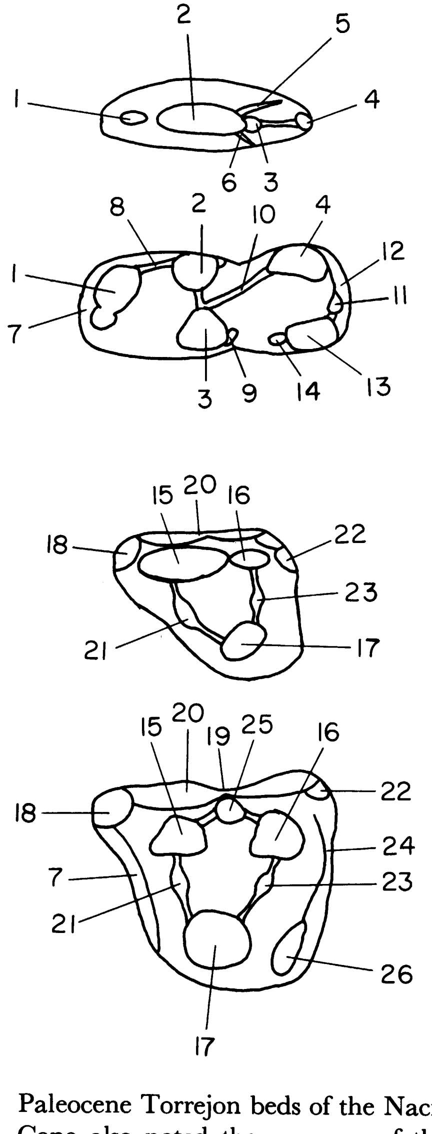


FIG. 1. Diagrammatic representation of phenacodont deciduous third and fourth premolars. Top to bottom: Right $dP_3$ and $dP_4$, left $dP^3$ and $dP^4$. Anterior ends are directed to the left, buccal sides to the top. 1, paraconid; 2, protoconid, with position of internal doubling indicated (this is position of crestlike paralophid in *Ectocion* molars); 3, metaconid; 4, hypoconid; 5, posteroexternal crest; 6, posterointernal crest; 7, anterior cingulum; 8, protolophid; 9, metastylid; 10, cristid obliqua; 11, hypoconulid; 12, posterior cingular ramp; 13, entoconid; 14, entostylid; 15, paracone; 16, metacone; 17, protocone; 18, parastyle; 19, ectoflexus; 20, external cingulum; 21, protoconule; 22, metastyle; 23, metaconule; 24, posterior cingulum; 25, mesostyle; 26, hypocone. Nomenclature adapted from Van Valen, 1966.

Paleocene Torrejon beds of the Nacimiento Formation) of New Mexico. Cope also noted the presence of the second and third deciduous premolars in the specimen A.M.N.H. No. 940. Osborn and Earle (1895, p. 65, fig. 19) illustrated $dP^4$ of *Tetraclaenodon puercensis,* (then called *Euprotogonia;* see West and Baird, 1970), with a notation in the figure legend, but no text discussion. In 1897 Matthew (p. 310, fig. 13) described *Euprotogonia minor* (now regarded as *Tetraclaenodon pliciferus*) from the early Torrejonian of New Mexico. The type specimen, A.M.N.H. No. 3897, includes a worn $dP_4$ which was measured and figured.

Matthew (1937, pl. 53, figs. 1–3), in his review of the San Juan Basin Paleocene faunas, illustrated deciduous teeth of *Tetraclaenodon puercensis*, but omitted mention of them in the text. In his illustration of A.M.N.H. No. 16719 (pl. 53, fig. 1) he called the teeth $M^1$–$M^3$ in the legend; they are actually $dP^3$, $dP^4$, and $M^1$. In figures 2 and 3 of the same plate he illustrated A.M.N.H. No. 16725, which has the third and fourth lower deciduous premolars, but he did not identify the teeth in the legend. He also repeated (1937, p. 362) the 1897 illustration of *Tetraclaenodon pliciferus*.

A *Phenacodus primaevus* maxillary fragment containing $dP^4$–$M^2$ was discussed and illustrated by Simpson (1942, pp. 132–133, fig. 1) in connection with its unique occurrence on the floor of a pre-Columbian pit house in New Mexico. He was concerned primarily with its connotations for aboriginal fossil collecting, and did not mention the presence of a deciduous tooth.

Butler (1952) analyzed the milk teeth of perissodactyls, utilizing the phenacodonts illustrated by Matthew as examples of the primitive perissodactyl condition. Butler based his discussion and illustrations of the milk teeth of *Tetraclaenodon puercensis* on casts of A.M.N.H. Nos. 16719 and 16725 (misnumbered 16735 by Butler, p. 792).

McKenna (1960, p. 100, fig. 53c) described an isolated $dP^4$, referred to *Phenacodus brachypternus,* from the early Wasatchian of northwestern Colorado. More recently a $dP^4$ of *Phenacodus* cf. *P. teilhardi* was found in a Sparnacian collection from the Paris basin of France (Rich, In press).

## MATERIAL AND SYSTEMATICS

In the course of the present investigation, 164 specimens of phenacodont deciduous teeth were studied (see Appendix). Most were placed in the known taxa either by direct association with permanent teeth or by comparison with other milk teeth so associated. Others were referred, with less confidence, on the basis of size and provenance. No material appears to represent species not known from permanent teeth.

The systematics of the Phenacodontidae are currently under study; therefore they will be mentioned here only briefly. Four genera are at present included in the family: *Tetraclaenodon,* ranging through the Torrejonian (middle Paleocene) and into the early Tiffanian (early late Paleocene) of North America; *Phenacodus,* ranging from early Tiffanian to late Bridgerian (late middle Eocene), and occurring in both North America and Europe; *Ectocion,* ranging from early Tiffanian to late Wasatchian (late early Eocene) of North America; and a new genus from the late Tiffanian (late late Paleocene) Plateau Valley local fauna of Colorado, initially recognized by Bryan Patterson. The first three genera are represented by deciduous as well as permanent teeth. In the ensuing discussion *Gidleyina* is considered congeneric with *Ectocion,* and *Desmatoclaenus* synonymous with the arctocyonid *Loxolophus.* The details of these synonymies and the systematic review of the Phenacodontidae will be included in a subsequent publication.

The most abundant deciduous tooth material is of *Phenacodus primaevus* and *Ectocion osbornianum,* but *Tetraclaenodon puercensis* is also well represented. These three species are over-all the most common phenacodonts in existing collections. Other taxa are considerably less abundant, both over-all and as deciduous teeth. All taxa are illustrated in the following pages. The full listing of the studied deciduous tooth material is given in the Appendix.

## DESCRIPTIONS

### General

Deciduous teeth may be identified as such by several rather constant features. Identification to particular taxon is, of course, considerably more difficult if comparative material or associated adult teeth are not available.

An isolated deciduous tooth is usually quite low crowned (fig. 2) and has weak, often splayed, roots, if any are present. If the tooth were lost normally, the root structure would have largely disappeared. Deciduous teeth are often heavily worn, and in many cases are lighter in color than other teeth from the same locality, as noted by Simpson (1951, p. 8). This may be related to the extent of replacement mineralization or to thinner enamel than that in permanent teeth. When found in a jaw with permanent molars deciduous teeth are easier to recognize than are isolated deciduous teeth, and this positive identification then allows isolated teeth to be taxonomically allocated with greater certainty.

Only deciduous premolars are considered here. The incisors and canines are not positively known, and their lack of distinguishing characters does not allow identification of isolated anterior milk teeth. No recognized deciduous incisors and canines were encountered preserved in jaws along with deciduous premolars.

In the present paper the deciduous teeth are designated after their permanent successor teeth. This has no functional meaning for the deciduous fourth premolars, as they function as molars in the deciduous series, and are replaced by premolariform teeth. Only nonreplaced

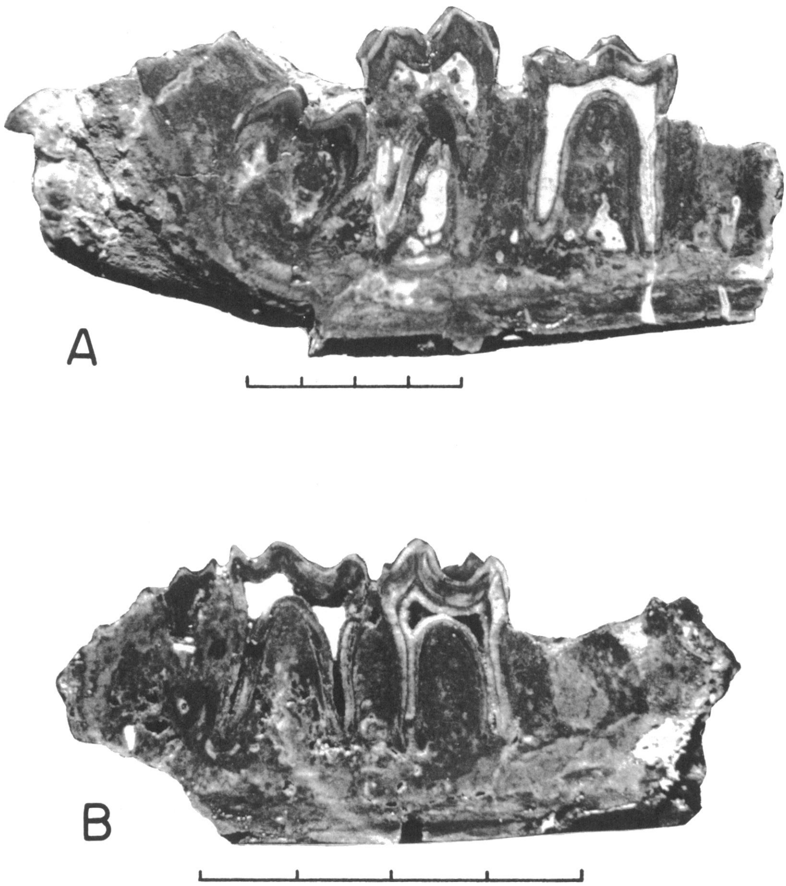

FIG. 2. Saggital sections of phenacodont dentaries, showing lower fourth deciduous premolars and first molars. A. A.M.N.H. No. 15303, *Phenacodus primaevus*, $dP_4$—$M_1$, with $M_2$ forming within the bone. B. A.M.N.H. No. 4294, *Ectocion osbornianum*, $dP_4$—$M_1$. Each scale unit equals 5 mm.

posterior teeth are here referred to as molars, although in some eutherians, such as most modern ungulates, some premolars are as molariform as molars. The numbers designate the positions of the deciduous teeth with respect to their permanent replacements. There are only three replaced premolars in phenacodonts, but they occupy the positions of permanent premolars 2 through 4, and are so numbered 2 through 4 rather than 1 through 3. The first premolar actually may be ontogenetically part of the initial, deciduous series, but as it probably is not replaced, it is here designated as a permanent premolar. This means, without considering eruption sequence, that the initial phenacodont tooth series includes $P_1$, $dP_2$, $dP_3$, $dP_4$, $M_1$, $M_2$, and $M_3$, and the replacement series includes $P_2$, $P_3$, and $P_4$.

The deciduous premolars of all members of the Phenacodontidae retain a similar structure (fig. 1). Their pattern does not change as substantially phylogenetically as does the pattern of the permanent premolars and molars.

The phenacodont $dP_2$ is a simple, trenchant tooth, with no development of accessory cusps on the single, high main cusp. The two-rooted tooth has some cresting on the posterior flank of the protoconid extending toward the somewhat flattened talonid area. Some later species have a small talonid cusp. This tooth, usually little worn, closely resembles the permanent second premolar.

$DP_3$ is also a trenchant tooth, with linearly arranged cusps. The high protoconid is flanked anteriorly by a low, sharp paraconid, and two or more crests extend down the back of the protoconid toward the single-cusped talonid, the widest part of the tooth. Later species have larger paraconids and some display a small metaconid high on the postero-internal side of the protoconid. The double-rooted $dP_3$ is rather similar to its permanent successor and is seldom heavily worn except on the posterior flank of the protoconid.

The molariform $dP_4$ is often heavily worn. The forwardly placed paraconid is large and may be multiple, producing a strikingly squared-up trigonid. The metaconid and protoconid are about equal in size, with the metaconid usually placed slightly posterior to the protoconid. This low trigonid, much lower than the main cusp of $dP_3$, makes up more than half the length of $dP_4$. Both the hypoconid and the entoconid are large cusps, swelling the talonid into the widest part of the double-rooted tooth. The median posterior hypoconulid is the smallest of the talonid cusps. Stylids frequently are present on either or both the entoconid and metaconid. $DP_4$ does not presage the configuration of the permanent fourth premolar.

No crowns of the phenacodont $dP^2$ are known. It is, however, a double-rooted tooth, as shown by P.U. No. 17498 (*Tetraclaenodon puercensis*).

$DP^3$ is triangular with a strong parastyle at the anterior end of the tooth. The high paracone is the largest cusp; the metacone is situated on its posterior flank and is better developed in later species. The protocone is posteriorly situated internal to the metacone and is the lowest major cusp. There is no mesostyle at the small ectoflexus, and a small metastyle is present at the posteroexternal corner of the tooth. The posterior part of the tooth, much wider than the anterior, is the more molariform. $DP^3$ has three roots, one above each major cusp, and is considerably smaller than $dP^4$. It rather closely resembles the permanent third upper premolar.

The molariform $dP^4$ is a distorted reflection of the permanent molars. The anteroexternal area is greatly enlarged due to the presence of a large parastyle. A well-formed mesostyle is present in all phenacodont species except *Tetraclaenodon pliciferus*. The hypocone is variably developed although it is usually more prominent in the later species. Intermediate conules are usually present. The cingula of the three-rooted $dP^4$ are weaker than those of the permanent molars. The distorted molariform pattern of $dP^4$, the juvenile functional molar, does not reflect the structure of the permanent fourth premolar, but does predict the general appearance of the permanent molars.

### GENUS *TETRACLAENODON*

*Tetraclaenodon pliciferus* (FIG. 3): Torrejonian to early Tiffanian, New Mexico and Montana. $DP_4$ shows the typical phenacodont structure and is differentiated from that of *T. puercensis* by its smaller size. The molar paraconid of *T. pliciferus* is relatively smaller than that of *T. puercensis*; this distinction is not apparent in $dP_4$ of *T. pliciferus*.

The third upper deciduous premolar has a large anterior parastyle. A metacone is absent, although there is a slight cresting between the paracone and metastyle. The small conical protocone is low and posterior to the main cusp. The posterior half of the tooth is much wider than the anterior half. $DP^4$ is unique among the phenacodonts in the absence of a mesostyle. A small hypocone is positioned somewhat more posteriorly than in $M^1$. The large parastyle is aligned with the paracone. There is a large, well-developed external cingulum. The jaw above this tooth is rather corroded in A.M.N.H. No. 3897, and there is no indication of a developing $P^4$, but the slight wear on $dP^4$ suggests that it may not have been emplaced for very long.

*Tetraclaenodon puercensis* (FIGS. 4, 5): Torrejonian of Texas, New Mexico, California, Wyoming, Montana, North Dakota, and Alberta, Canada. $DP_2$ is a simple trenchant tooth as described above. The paraconid of the elongate $dP_3$ is small, and there is no metaconid. $DP_3$ is slightly simpler than $P_3$, with fewer crests on the main cusp and a more posteriorly placed hypoconid. $DP_4$ has a single triangular paraconid at the anterior end of the elongate trigonid. The low cristid obliqua is cuspidate. Both the entoconid and the hypoconid are large, creating a bulbous talonid; the hypoconulid is displaced slightly toward the hypoconid.

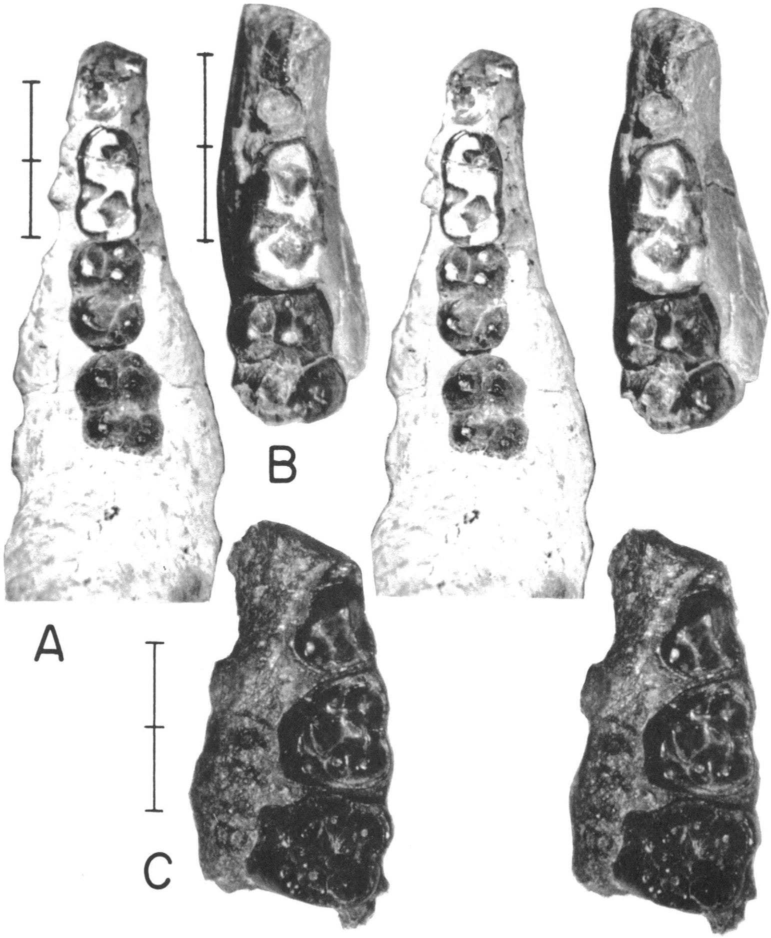


FIG. 3. Deciduous teeth of *Tetraclaenodon pliciferus*. A. A.M.N.H. No. 3897, type specimen of *T. minor* (Matthew), lower Torrejon, San Juan Basin, New Mexico, left $dP_4$—$M_2$. B. A.M.N.H. No. 35429, Ft. Union Formation, Loc. 25, Crazy Mountain Field, Montana, left $dP_4$—$M_1$. C. A.M.N.H. No. 16648, lower Torrejon, San Juan Basin, New Mexico, left $dP^3$—$M^1$. Each scale unit equals 5 mm.

This tooth does not show the reduced paraconid of the molars.

$DP^3$ is dominated by the large paracone behind the elongate parastyle. There is no mesostyle or metacone, but a small metastyle occupies the posteroexternal corner of the tooth. The posteriorly displaced protocone is small. $DP^4$ is much larger than $dP^3$, and has the typical distorted

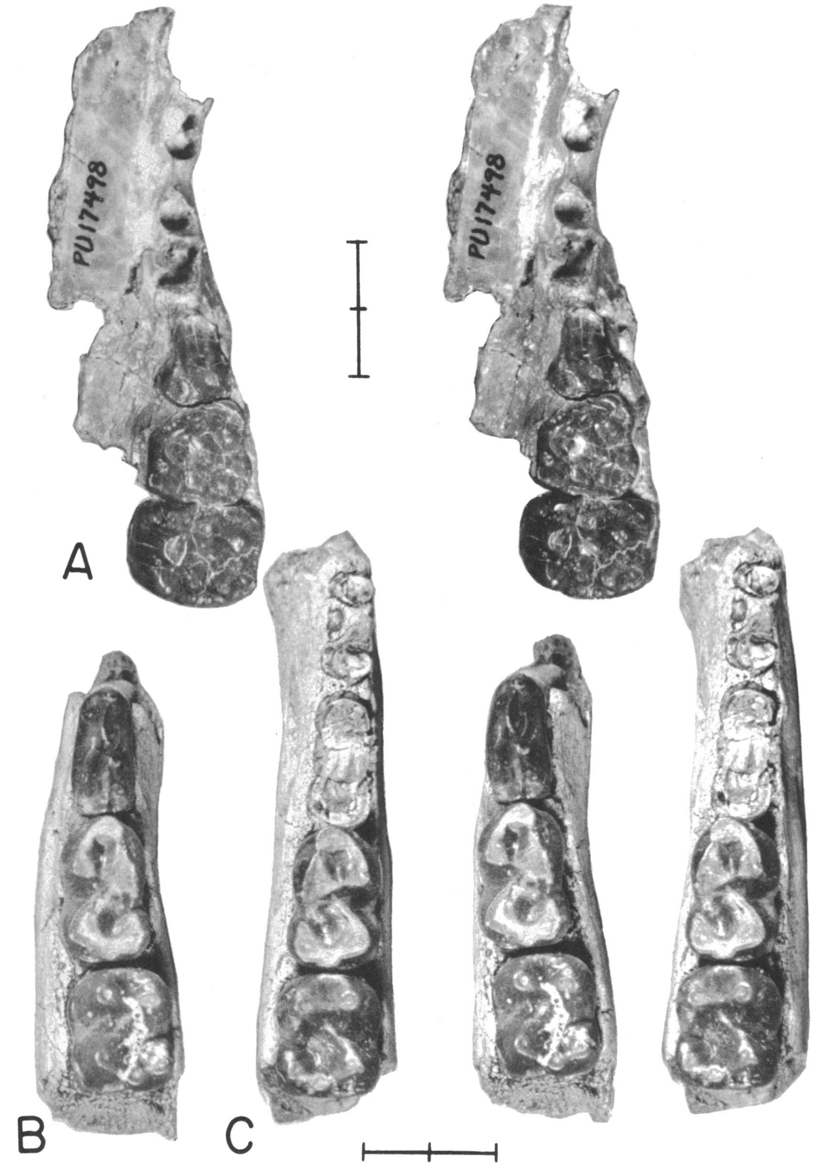


FIG. 4. Deciduous teeth of *Tetraclaenodon puercensis*. A. P.U. No. 17498, Torrejonian, Bighorn Basin, Wyoming, left dP$^3$—M$^1$. B, C. A.M.N.H. No. 16725, Torrejonian, San Juan Basin, New Mexico, left dP$_3$—M$_1$ and right dP$_4$—M$_1$. Each scale unit equals 5 mm.

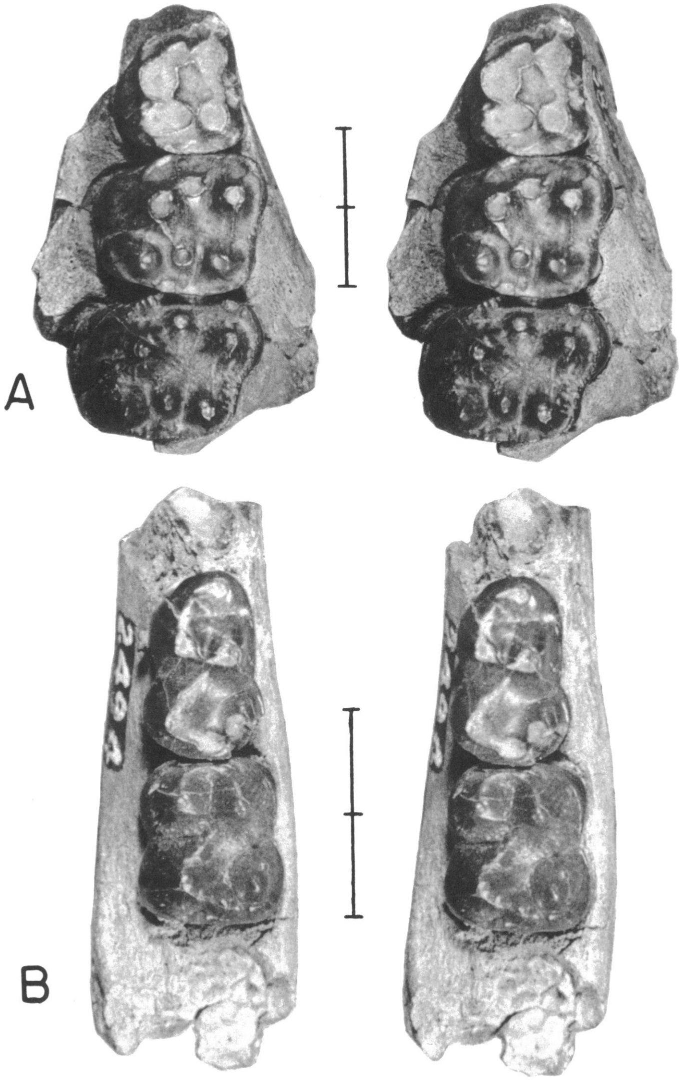


FIG. 5. Deciduous teeth of *Tetraclaenodon puercensis*. A. A.M.N.H. No. 3841, Torrejonian, San Juan Basin, New Mexico, left $dP^4$—$M^2$. B. A.M.N.H. No. 2494, Torrejonian, San Juan Basin, New Mexico, left $dP_4$—$M_1$. Each scale unit equals 5 mm.

molariform topography. In contrast to $P^4$ of *T. pliciferus*, there is a well-formed mesostyle. The two intermediate conules are relatively smaller

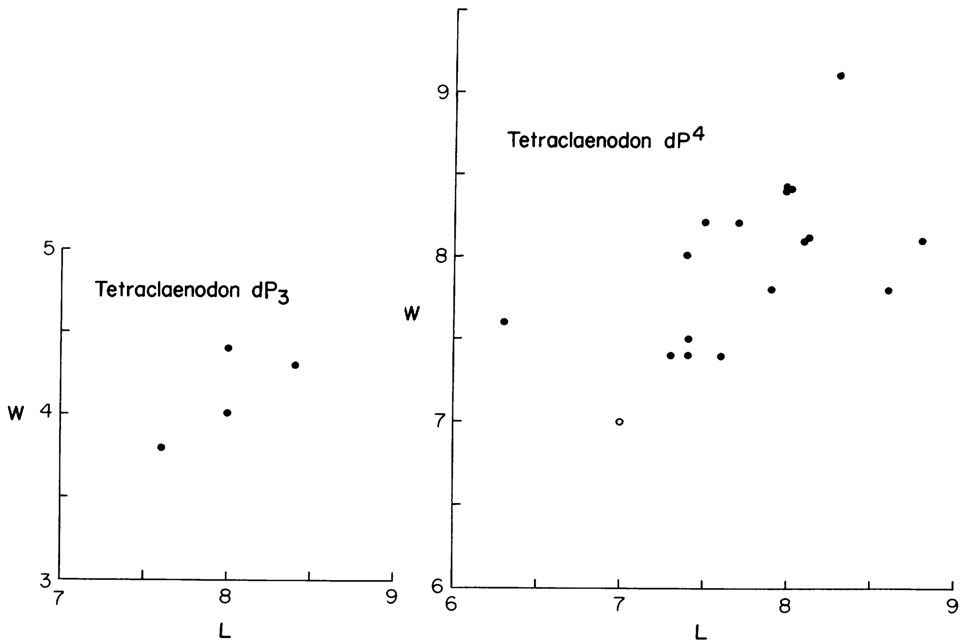


FIG. 6. Scatter diagrams indicating dimensions, in millimeters, of upper deciduous teeth of *Tetraclaenodon*.
*Symbols:* ●, *T. puercensis;* ○, *T. pliciferus.*

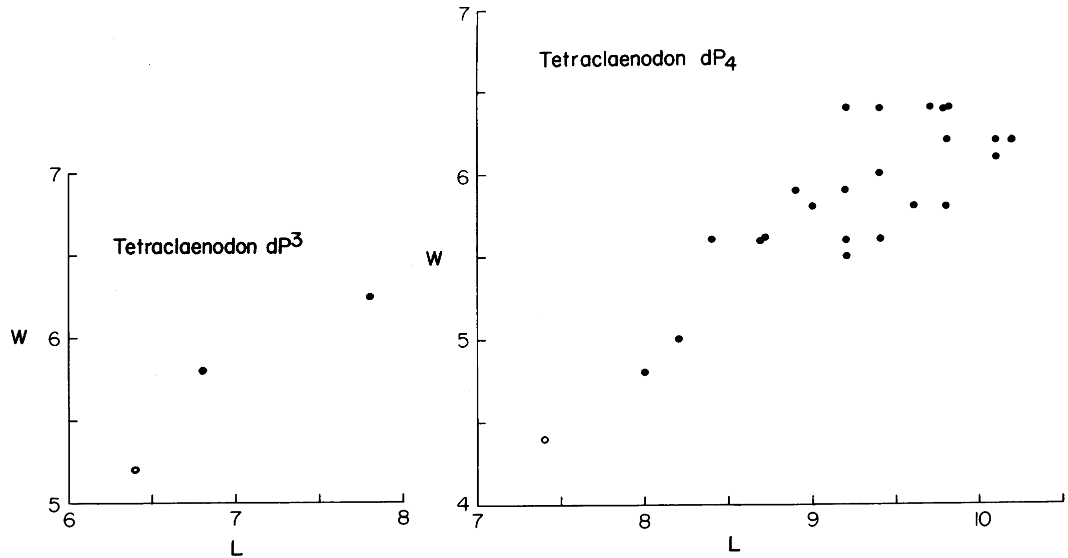


FIG. 7. Scatter diagrams indicating dimensions, in millimeters, of lower deciduous teeth of *Tetraclaenodon.*
Symbols as in figure 6.

than in $M^1$. The hypocone is small, as it is in *T. puercensis* molars.

The scatter diagrams, figures 6 and 7, show the sizes of the various *Tetraclaenodon* deciduous teeth.

## GENUS *PHENACODUS*

*Phenacodus bisonensis* (FIG. 8C): Early Tiffanian, Wyoming and Montana. $DP_4$ is almost identical to that of *P. grangeri,* distinguished mainly by smaller size. Its single paraconid is large, and there are anterior and posterior stylids on the metaconid, as well as an entostylid. The cristid obliqua is cuspidate.

The fourth upper deciduous premolar of *P. bisonensis* has a markedly reduced hypocone and no metaconule. The protoconule is large. Otherwise the tooth is similar to $dP^4$ of *P. grangeri.*

*Phenacodus grangeri* (FIG. 9): Tiffanian, Colorado and Wyoming. The single known $dP_4$ (P.U. No. 19584) is well worn. It has the elongate trigonid and large paraconid typical of the family. Stylids are present on both the entoconid and the metaconid. The talonid is the widest part of the tooth.

$DP^3$ shows differentiation from the *Tetraclaenodon* condition in the presence of a discrete metacone posterior to the paracone. The posteriorly placed protocone is larger and the posterior end of the tooth is relatively wider than in *Tetraclaenodon.* Small conules are present, and there is no hypocone or mesostyle. $DP^4$ of *P. grangeri* is much the same as that of *Tetraclaenodon puercensis*, with large styles, relatively small conules, and a relatively accessory hypocone.

*Phenacodus almiensis* (FIG. 8A, B): Late Tiffanian, Wyoming. This species is tentatively retained as a separate taxon, although it is very similar to *P. vortmani.* The single known $dP_4$ (U.S.N.M. No. 26236) has a triple-lobed paraconid, with the median lobe the largest. Large stylids are present on both entoconid and metaconid in strong contrast to their slight development on $dP_4$ of *P. vortmani.* The cristid obliqua is weakly cuspidate.

$DP^4$ has well-developed conules and a small hypocone. It is more similar to the corresponding tooth in *P. vortmani* than is the lower milk tooth.

*Phenacodus brachypternus* (FIG. 10): Early Wasatchian of New Mexico, Colorado, and Wyoming. $DP_4$ is represented by a single isolated specimen, Y.P.M. No. 17575. The lack of direct association with permanent teeth makes this assignment tentative. This tooth is more massive and slightly larger than $dP_4$ of *Ectocion osbornianum.* It shows several structural differences, especially in the median, independent location of the hypo-

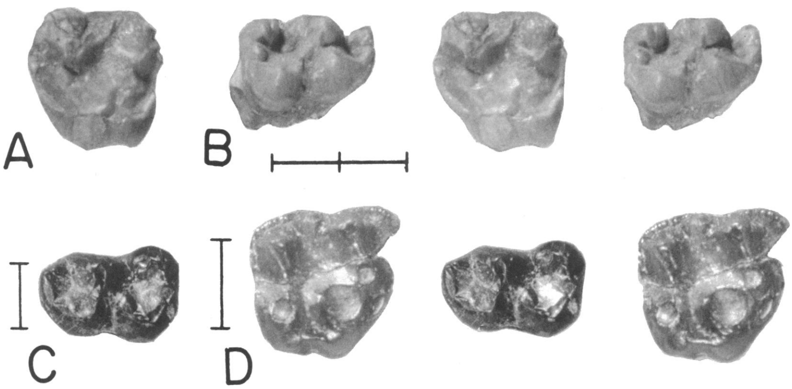


FIG. 8. Deciduous teeth of *Phenacodus*. A. U.S.N.M. No. 26327, *P. almiensis*, Tiffanian, Buckman Hollow, Wyoming, left $dP^4$. B. U.S.N.M. No. 26326, *P. almiensis*, Tiffanian, Buckman Hollow, Wyoming, right $dP_4$. C. U.S.N.M. No. 26325, *P. bisonensis*, Tiffanian, Bison Basin, Wyoming, left $dP_4$. D. P.L. No. 196 Mu, *P.* cf. *P. teilhardi*, Sparnacian, Paris Basin, France, right $dP^4$. Each scale unit equals 5 mm.

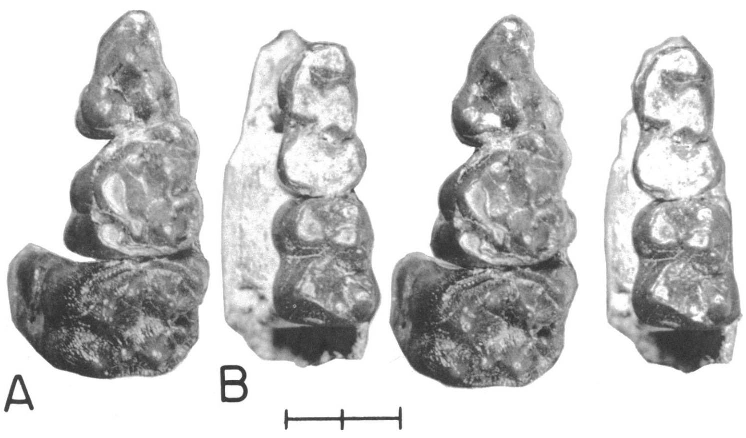


FIG. 9. Deciduous teeth of *Phenacodus grangeri*. A. P.U. No. 19561, Tiffanian, Bighorn Basin, Wyoming, left $dP^3$—$M^1$. B. P.U. No. 19584, Tiffanian, Bighorn Basin, Wyoming, left $dP_4$—$M_1$. Each scale unit equals 5 mm.

conulid and the junction of the cristid obliqua and protoconid-metaconid crest midway between the latter two cusps. It has a strong anteroexternal cingulum, a slightly doubled paraconid, a small accessory cuspule on the posteroexternal slope of the protoconid, and a prominent entostylid. The metaconid is broken away. As is the case with the upper deciduous teeth of *P. brachypternus,* $dP_4$ is not conspicuously lengthened.

$DP^3$ (P.U. No. 13115) is narrow, but not as elongate as $P^3$. Wear has removed any possible indication of a metacone. $DP^4$ of P.U. No. 13115 is much more worn than is $dP^3$. U.C.M.P. No. 46172, much less worn, is a normal *Phenacodus* $dP^4$, although it is smaller than the corresponding

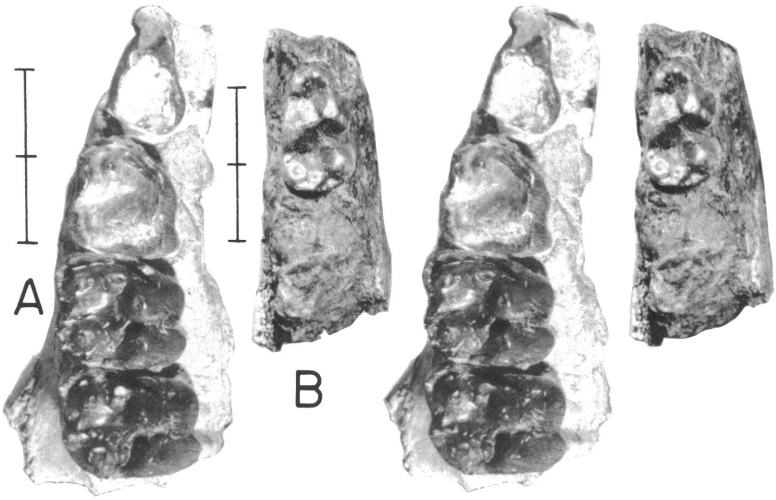


FIG. 10. Deciduous teeth of *Phenacodus brachypternus.* A. P.U. No. 13115, lower Willwood Formation, Bighorn Basin, Wyoming, right $dP^3$—$M^2$. B. Y.P.M. No. 17595, lower Willwood Formation, Bighorn Basin, Wyoming, left $dP_4$. Each scale unit equals 5 mm.

tooth in other species of *Phenacodus.* The hypocone is relatively larger than that of $dP^4$ in the Tiffanian species of *Phenacodus*, and the mesostyle is posteriorly placed. The adult molars of *P. brachypternus* are strikingly elongate; this specific character is not reflected in the milk teeth.

*Phenacodus vortmani* (FIG. 11): Wasatchian of Colorado and Wyoming. $DP_3$ is a long, narrow trenchant tooth with a small, discrete paraconid and no metaconid. The metaconid is not present in even the latest, Lost Cabin, specimens. $DP_4$ shows considerable variation in paraconid shape, which is single, although laterally elongate in some specimens, whereas in others it is double. The stylids in *P. vortmani* $dP_4$ are usually small, and the cristid obliqua is cuspidate.

$DP^4$ has the normal phenacodont appearance. Both conules are present with the paraconule somewhat larger than the metaconule. The hypo-

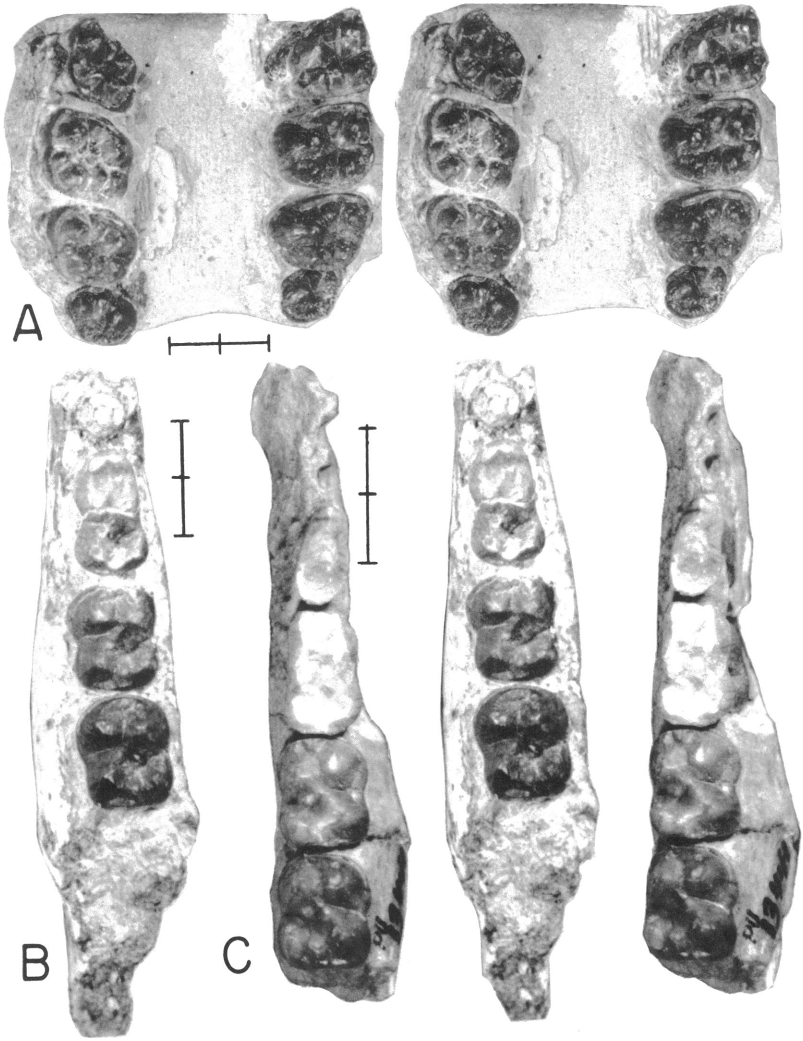

FIG. 11. Deciduous teeth of *Phenacodus vortmani.* A. A.M.N.H. No. 15763, lower Willwood Formation, Bighorn Basin, Wyoming, right and left $dP^4$—$M^3$. B. A.M.N.H. No. 4382, lower Willwood Formation, Bighorn Basin, Wyoming, left $dP_4$—$M_2$. C. P.U. No. 13441, upper Wind River Formation, Wind River Basin, Wyoming, right $dP_3$—$M_2$. Each scale unit equals 5 mm.

cone is smaller than the protocone. Cingula on $dP^4$ are weaker than on the permanent molars.

*Phenacodus primaevus* (FIGS. 12, 13): Late Tiffanian, Wasatchian and


FIG. 12. Deciduous teeth of *Phenacodus primaevus*. A. A.M.N.H. No. 4377, lower Willwood Formation, Bighorn Basin, Wyoming, right $dP_3$—$M_3$. B. U.S.N.M. No. 20070, lower Willwood Formation, Bighorn Basin, Wyoming, left c, $P_1$, $dP_3$—$M_2$. Each scale unit equals 5 mm.

Bridgerian, Texas, New Mexico, Colorado, and Wyoming. This species herein includes Eocene material separated by various authors as *P. robustus*, *P. intermedius*, and *P. hemiconus*, as well as the larger *Phenacodus* specimens from the late Paleocene beds of the Fort Union Formation in the Bighorn Basin of Wyoming.

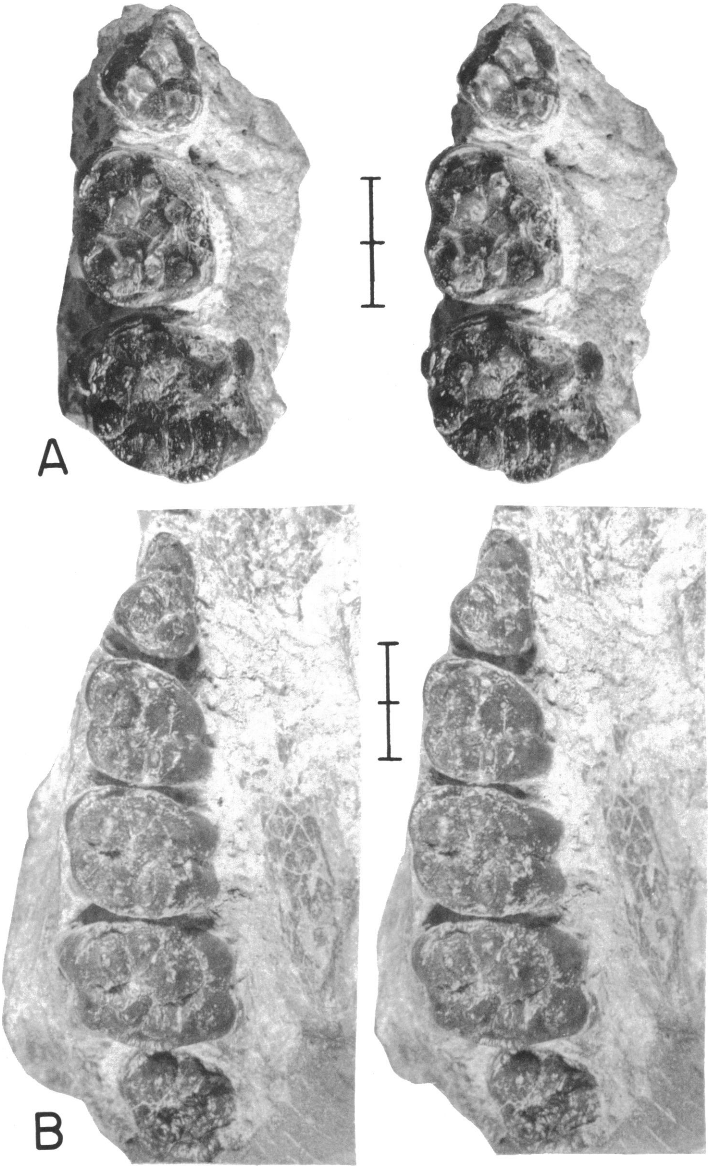


FIG. 13. Deciduous teeth of *Phenacodus primaevus*. A. P.U. No. 13048, lower Willwood Formation, Bighorn Basin, Wyoming, right $dP^3$—$M^1$. B. U.S.N.M. No. 20070, lower Willwood Formation, Bighorn Basin, Wyoming, right $dP^3$—$M^3$. Each scale unit equals 5 mm.

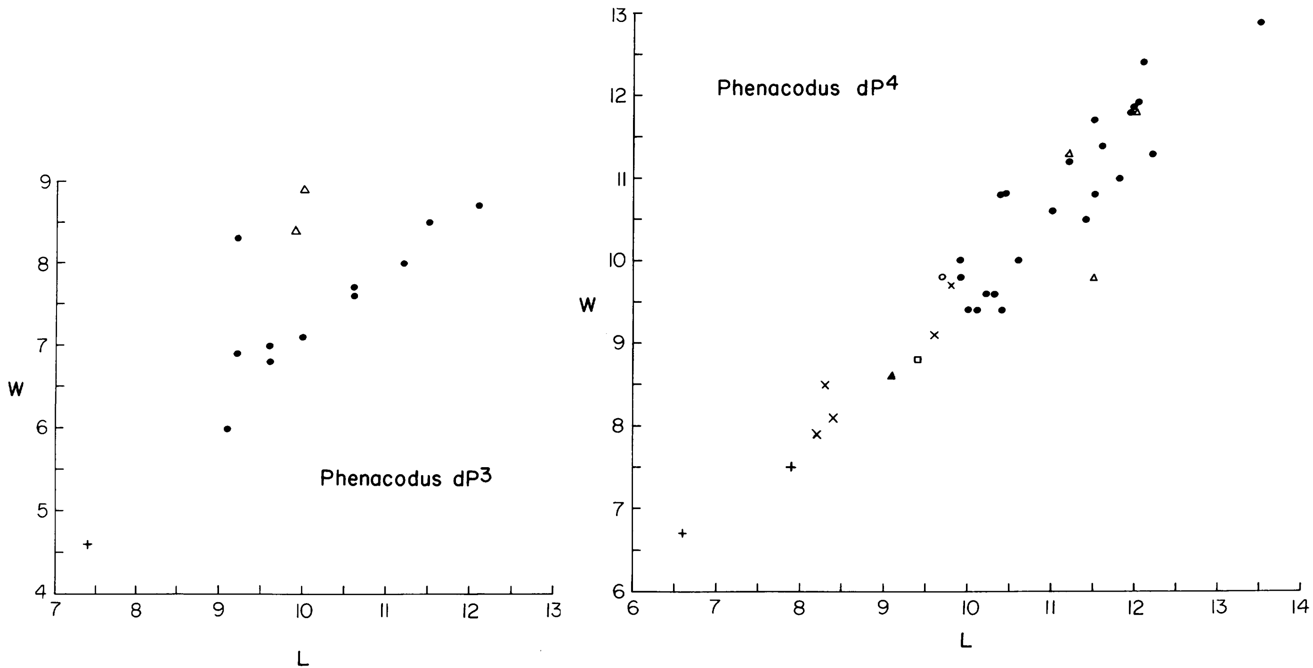


FIG. 14. Scatter diagram indicating dimensions, in millimeters, of upper deciduous teeth of *Phenacodus*.
*Symbols:* ●, *P. primaevus;* ○, *P. almiensis;* ▲, *P. bisonensis;* △, *P. grangeri;* □, *P.* cf. *P. teilhardi;* ×, *P. vortmani;* +, *P. brachypternus.*

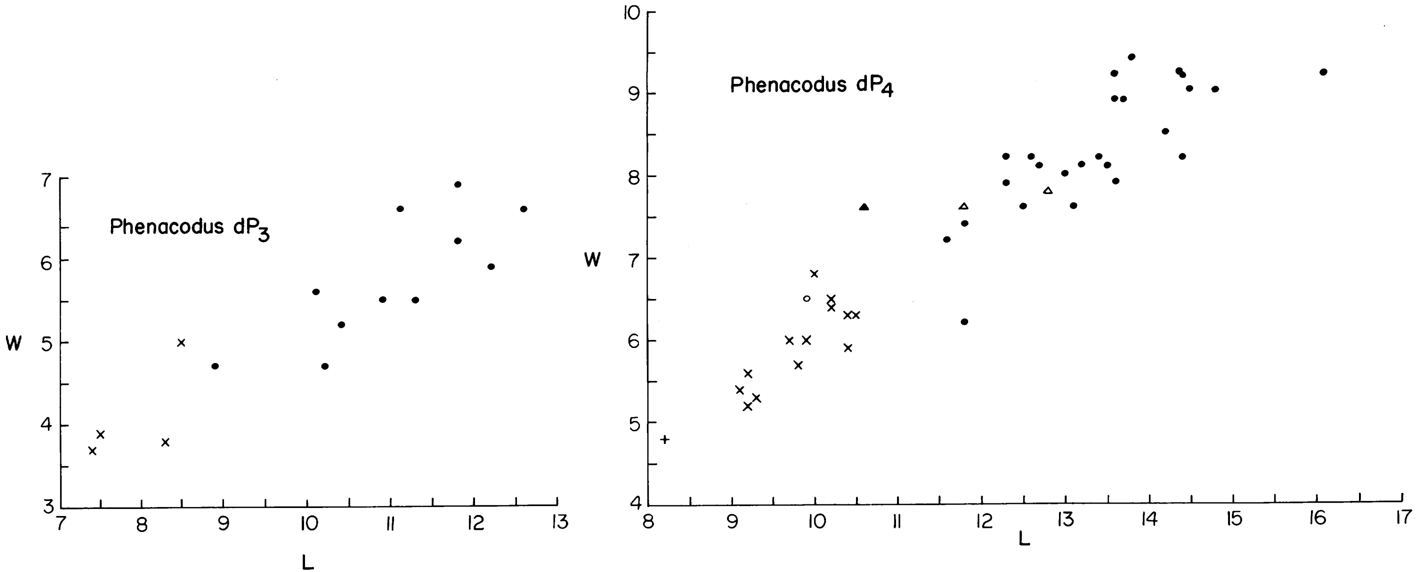


FIG. 15. Scatter diagrams indicating dimensions, in millimeters, of lower deciduous teeth of *Phenacodus*. Symbols as in figure 14.

$DP_2$ of *P. primaevus* is a simple trenchant tooth with no accessory cusps. The third lower deciduous premolar is also a trenchant tooth. In addition to the prominent anterior paraconid, it has a small metaconid on the flank of the protoconid. There is a small talonid basin. $DP_4$ usually has a doubled paraconid which results in a square trigonid. The stylids are commonly small, in contrast to their strong development in the molars. The talonid is the widest part of the tooth, and the trigonid is more than 50 per cent of the total tooth length.

$DP^3$ is triangular in outline. The metacone is well developed, although it is partially united with the paracone. The large protocone is displaced posteriorly; low crests from the protocone to the metacone and paracone enclose a small, shallow basin. The fourth upper deciduous premolar is much the same as in other phenacodonts. The conules vary greatly, as is the case in the permanent molars where the metaconule is frequently entirely lacking. The hypocone is larger than in $dP^4$ of any other species of *Phenacodus*.

*Phenacodus* cf. *P. teilhardi* (FIG. 8D): Sparnacian to Lutetian, France and Spain. One European species of *Phenacodus* is represented by a deciduous tooth. $DP^4$ of *P.* cf. *P. teilhardi* (P.L. No. 196 Mu) has several distinctions from those of North American *Phenacodus* while retaining the basic phenacodont pattern. The large paraconule is far forward and there is no metaconule. The mesostyle is placed farther anteriorly than in the American species. The protocone is much larger than the hypocone; the small hypocone plus the absence of the metastyle creates a rather contracted posterior part of the tooth.

The scatter diagrams (figs. 14, 15) indicate the sizes of the various *Phenacodus* deciduous teeth.

## GENUS *ECTOCION*

*Ectocion montanensis* (FIG. 16): Tiffanian of Montana. $DP_3$ is a simple trenchant tooth with a small anterior cusp high on the anterior slope of the protoconid. There is no metaconid development. The single paraconid of $dP_4$ is transversely elongate, almost semicircular, and rounds the anterior end of the trigonid. Strong stylids are present on either side of the metaconid and also on the anterior slope of the entoconid. The hypoconulid is medially located.

$DP^4$ is a normal phenacodont milk tooth. The mesostyle is relatively small. The metaconule is the smaller of the two conules, and the hypocone is smaller than the protocone.

*Ectocion wyomingensis* (FIG. 17): Tiffanian of Colorado and Wyoming.

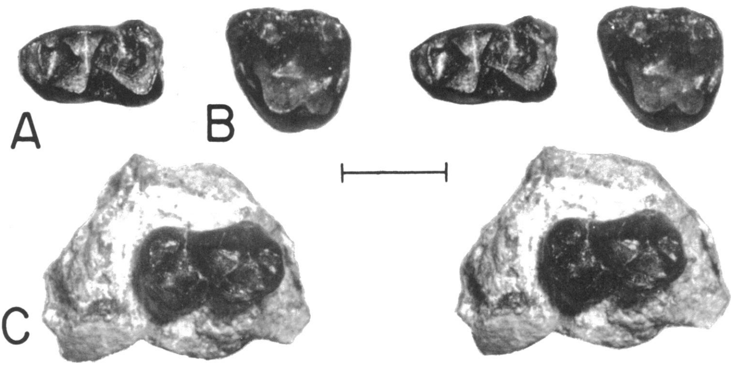


FIG. 16. Deciduous teeth of *Ectocion montanensis*. A. P.U. No. 20426, Tiffanian, Ft. Union Formation, Montana, left $dP_4$. B. P.U. No. 20428, Tiffanian, Ft. Union Formation, Montana, left $dP^4$. C. P.U. No. 20417, Tiffanian, Ft. Union Formation, Montana, right $dP_4$. Each scale unit equals 5 mm.

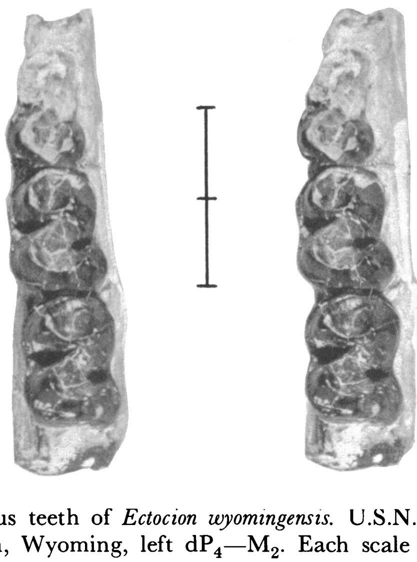

FIG. 17. Deciduous teeth of *Ectocion wyomingensis*. U.S.N.M. No. 21264, Tiffanian, Fossil Basin, Wyoming, left $dP_4$—$M_2$. Each scale unit equals 5 mm.

The trenchant $dP_3$ is progressive with a discrete anterior cusp and a small metaconid. The crests on the posterior flank of the protoconid are quite strong. $DP_4$ has a single, triangular paraconid. There is a well-developed metastylid but no entostylid. The cristid obliqua is slightly cuspidate and high. The hypoconulid is equidistant from both the ento-

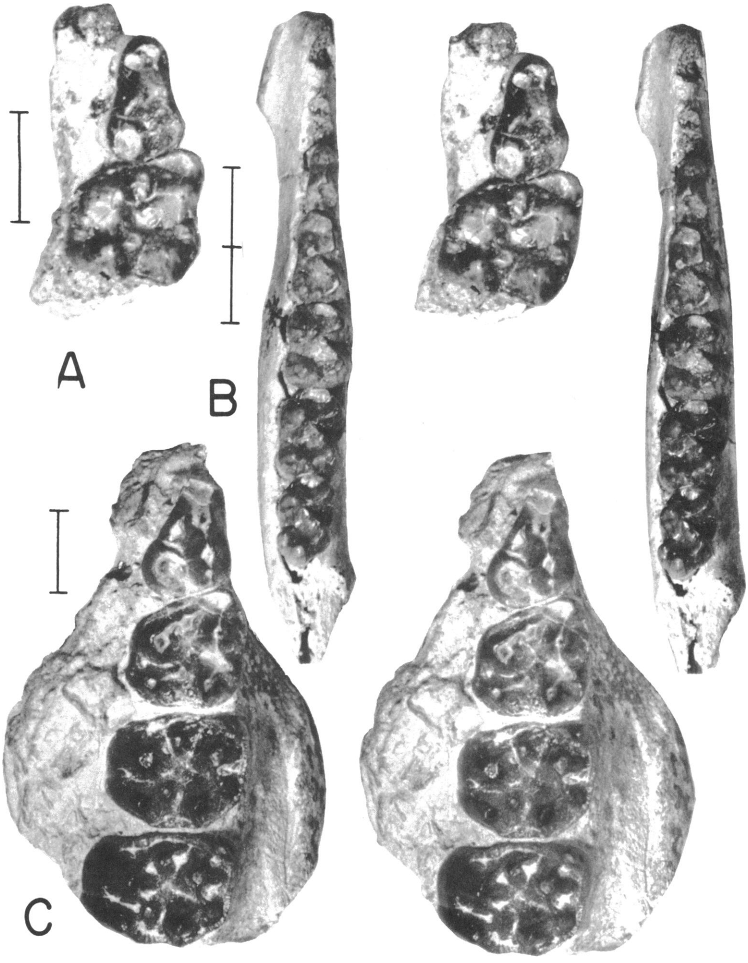


FIG. 18. Deciduous teeth of *Ectocion osbornianum*. A. P.U. No. 17813, Tiffanian, Bighorn Basin, Wyoming, left $dP^3$—$dP^4$. B. P.U. No. 17757, Tiffanian, Bighorn Basin, Wyoming, right $dP_3$—$M_3$. C. P.U. No. 13325, Wasatchian, Bighorn Basin, Wyoming, left $dP^3$—$M^2$. Each scale unit equals 5 mm.

conid and hypoconid; in the adult tooth it is closer to the entoconid. $DP_4$ does not suggest the depression of the paralophid, a diagnostic feature of adult *Ectocion* lower molars.

*Ectocion osbornianum* (FIG. 18): Late Tiffanian and Wasatchian of Colorado and Wyoming. This species contains material often separated as *E. ralstonensis* (Guthrie, 1967). The second lower deciduous premolar is a simple trenchant tooth with no accessory cusps. $DP_3$ has a high, pointed paraconid and a relatively prominent metaconid. It is trenchant and does not differ materially from the $dP_3$ of *Phenacodus* except in size. $DP_4$ of *E. osbornianum* has a single triangular paraconid. There is no indication of the strongly depressed molar paralophid. The $dP_4$ paraconid is well developed. Stylid development is usually strong on the metaconid, and some entostylids are present in Wasatchian specimens. The hypoconulid of late Paleocene *E. osbornianum* is slightly closer to the entoconid than to the hypoconid; by Wasatchian time it had migrated and $dP^4$ shows a talonid condition similar to that of the adult teeth, with entoconid and hypoconulid virtually connate. The paralophid of *Ectocion* $dP_4$ is higher and sharper than that of $dP_4$ of *Phenocodus*.

$DP^3$ of *E. osbornianum* is quite advanced, as the metacone is independent of the paracone and the protocone is large. A central basin is enclosed by the lateral crests from the protocone to the metacone and paracone. Incipient conules are present. $DP^4$ is more typical of the phenacodont pattern. The conules are large and variable, and the hypocone is small but high. The parastyle is not as extended as in *Phenacodus*.

The scatter diagrams in figures 19 and 20 show the sizes of the *Ectocion* deciduous teeth considered in this study.

## Phenacodont Ancestors

The phenacodont condylarths might have evolved from forms resembling the *Protogonodon-Loxolophus* complex of Puercan and early Torrejonian arctocyonids (Gazin, 1941; Van Valen, 1969). Information on the deciduous teeth of these forms is severely limited, but A.M.N.H. No. 16397, the type specimen of *Protogonodon kimbetovius* from the Puercan of New Mexico (Matthew, 1937, p. 56, fig. 9), has $dP_4$ preserved in both dentaries, as well as the roots of $dP_3$, the emerging tip of $P_2$, and emerging $M_3$.

$DP_4$ of *Protogonodon kimbetovius* (fig. 21) is quite similar to that of the phenacodonts discussed above, differing primarily in the shape of the paraconid and the development of the hypoconulid. The paraconid is a conical cusp, less anteriorly flattened than in phenacodonts, and situated on the anterolingual corner of the tooth. The protoconid is lower than the metaconid, and is situated slightly forward of it. There is no metastylid. The talonid is short, less than 50 per cent of the length of the tooth. There is a large hypoconid and somewhat smaller entoconid. The hypoconulid is much smaller than in *Tetraclaenodon,* and is in a medial position.

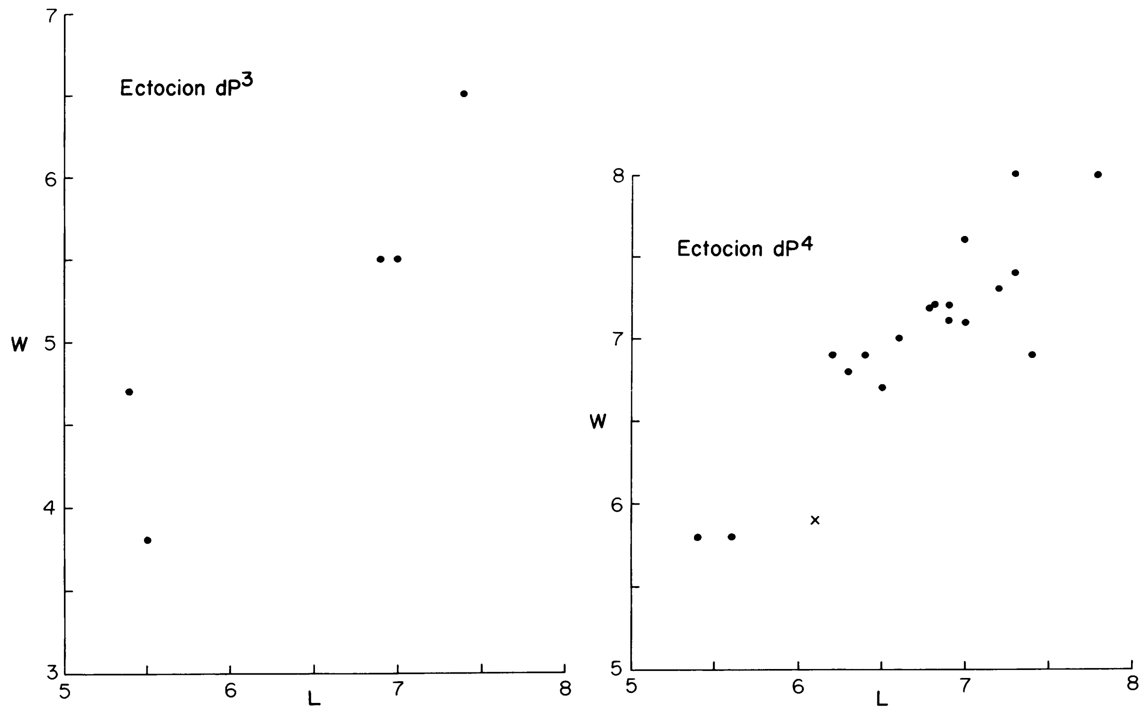


FIG. 19. Scatter diagrams indicating dimensions, in millimeters, of upper deciduous teeth of *Ectocion*. *Symbols:* ●, *E. osbornianum;* △, *E. wyomingensis;* ×, *E. montanensis.*

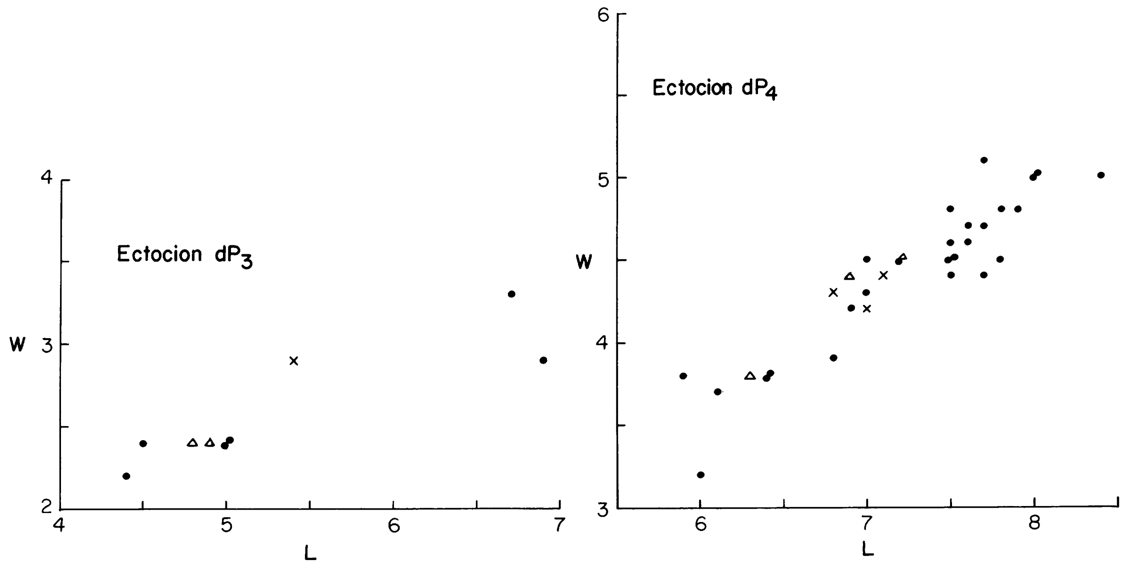


FIG. 20. Scatter diagrams indicating dimensions, in millimeters, of lower deciduous teeth of *Ectocion*. Symbols as in figure 19.

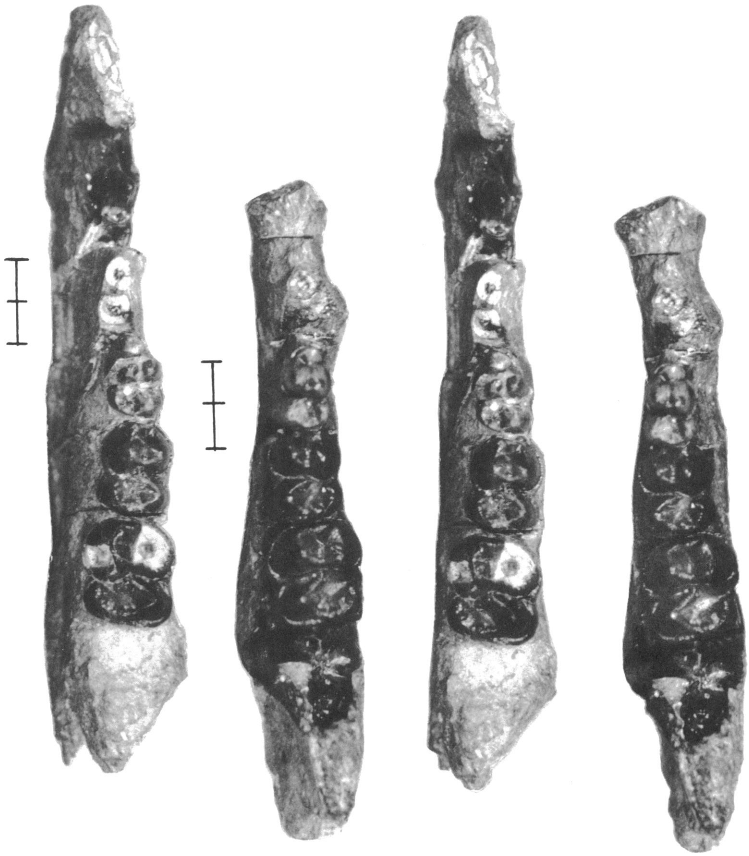

FIG. 21. Deciduous teeth of *Protogonodon kimbetovius,* A.M.N.H. No. 16397, Puercan, San Juan Basin, New Mexico, right $dP_3$—$M_2$, left $dP_4$—$M_3$. Each scale unit equals 5 mm.

## EVOLUTIONARY TRENDS

Despite the lack of striking changes, several trends may be noted in the deciduous dentition of the Phenacodontidae. The protocone and metacone of $dP^3$ increase in size and importance from *Tetraclaenodon* to *Phenacodus* and *Ectocion.* The metastyle is somewhat reduced in later species. There is a general increase in the molariformity in this tooth, although without development of a mesostyle or hypocone.

$DP^4$ changed less than $dP^3$ through the phylogeny of the phenacodonts, as it is completely molariform in the earliest phenacodonts. It shows a considerable amount of variability, especially in the relative size of the hypocone, which tends to be larger and more important in the later North American *Ectocion* and *Phenacodus,* while remaining quite small in the French *P.* cf. *P. teilhardi.* All species except *T. pliciferus* have a well-formed mesostyle. The intermediate conules of $dP^4$ are reduced in later taxa, and the metaconule is entirely lost in some specimens of *Phenacodus;* this loss is also noted in some later *Phenacodus* molars.

$DP_3$ shows considerable increase in complexity from the Torrejonian to the Wasatchian. There is increasing development of the paraconid and metaconid, producing more molariform teeth in later *Phenacodus* and *Ectocion* than in *Tetraclaenodon* and earlier species of *Phenacodus* and *Ectocion.*

There is relatively little change in $dP_4$. Later species of *Phenacodus* tend to have a multiple paraconid which squares up the anterior end of the trigonid, whereas later species of *Ectocion* shows the characteristic proximity of the hypoconulid and entoconid, a feature which is not present in earlier species. Stylids are variable in $dP_4$, although they generally reflect the generic distinction of little to no entostylid in *Ectocion* and both entostylid and metastylid in most individuals of *Phenacodus.* The protoconid-metaconid crest becomes progressively weaker in *Phenacodus,* especially the larger species; this crest remains high and strong in *Ectocion.*

## TOOTH SUCCESSION

The phenacodont deciduous dentition presumably included three incisors, one canine, and three premolars in each quadrant. Of these, only the three premolars are retained in any known specimens.

The sequence of emplacement of the phenacodont deciduous premolars is not definitely known. $DP^4_4$ are frequently heavily worn; this may indicate that the teeth were emplaced in the jaw and functioning prior to the eruption of the less worn $dP^3_3$ and $dP^2_2$. Alternatively, $dP^4_4$ may have been emplaced simultaneously with or shortly after the anterior milk teeth, with the excessive wear resulting from the more extensive occlusal abrasion on that molariform tooth. Unfortunately no specimens of young individuals are available to verify one or the other of the above possibilities. The youngest stage represented is P.U. No. 16170, *Ectocion osbornianum,* which shows a worn $dP_4$ in place at the time of eruption of $M_1$, certainly an indication of a considerable temporal gap between the eruption of $dP_4$ and $M_1$, but no help in the interpretation of the deciduous sequence.

$DP^4_4$ show considerable variation in the amount of wear at the time of loss. Some teeth were worn practically smooth while still in the functioning dentition (figs. 3, 5, 8, 10, 11), and others apparently were shed while they were still distinctly cusped. This appears to be largely individual variation, as there is no systematic order to the degree of wear. It cannot be determined whether this is primarily a function of diet, dependent on local vegetation, or the result of some other factors.

Modern ungulates display remarkable diversity in their deciduous dentition eruption sequences. Examples may be cited for both early and late eruption of $dP^4_4$. In *Sus scrofa* $dP_4$ is the initial lower milk tooth to erupt, whereas $dP^3$ slightly precedes $dP^4$. On the other hand, the collared peccary (*Dicotyles tajacu*) has a $dP^3_3$, $dP^2_2$, $dP^4_4$ sequence (Kirkpatrick and Souls, 1962, p. 216). Among the perissodactyls, more direct descendents of the phenacodonts, the tapir has a $dP^1_1$, $dP^2_2$, $dP^3_3$, $dP^4_4$ sequence, rhinoceroses a $dP^3_3$, $dP^4_4$, $dP^2_2$, $P^1_1$ pattern (B. Slaughter, personal commun., April 15, 1970), and horses have a complete deciduous premolar set at birth (Peyer, 1968, p. 321).

Positive delineation of the phenacodont sequence thus cannot be based on comparison with modern ungulates; it awaits discovery of very young individuals that have the deciduous teeth in the process of eruption.

After the emergence of the deciduous series, phenacodont permanent molars erupted in a front to back sequence (fig. 22). A number of specimens adequately indicate this process. The permanent premolars also erupted anterior to posterior, with $P_2$ appearing at about the same time as $M_3$. U.S.N.M. No. 20070, *Phenacodus primaevus*, has $P_1$, $dP_2$, $dP_3$, and $dP_4$ in place while the permanent canine is erupting. U.S.N.M. Nos. 19997 and 20066 and A.M.N.H. No. 15298 show $P_2$ erupting while $dP_3$ and $dP_4$ are still in place. *Phenacodus vortmani*, A.C.M. No. 4380, has a $dP_4$ in place during the eruption of $P_3$. The fourth permanent premolar is the final tooth to emerge and is shown in a great many specimens. This phenacodont succession pattern is shown diagrammatically in figure 22.

The sequence of eruption of permanent premolars in *Protogonodon kimbetovius* also appears to have been $P_2$, $P_3$, $P_4$, with $P_2$ and $M_3$ erupting simultaneously. $DP_4$ in A.M.N.H. No. 16397 was not particularly worn at the time of eruption of $M_3$.

The sequence of eruption of the permanent premolars varies greatly in both modern and fossil mammals (Ziegler, 1967; Slaughter, personal commun.). Ongoing studies by a number of workers may reveal a pattern to the seemingly random differences.

Although the permanent premolars were emplaced anterior to posterior, the tooth buds do not appear to form in that sequence. X-rays, longitudinal sections, and careful preparations of phenacodont dentaries

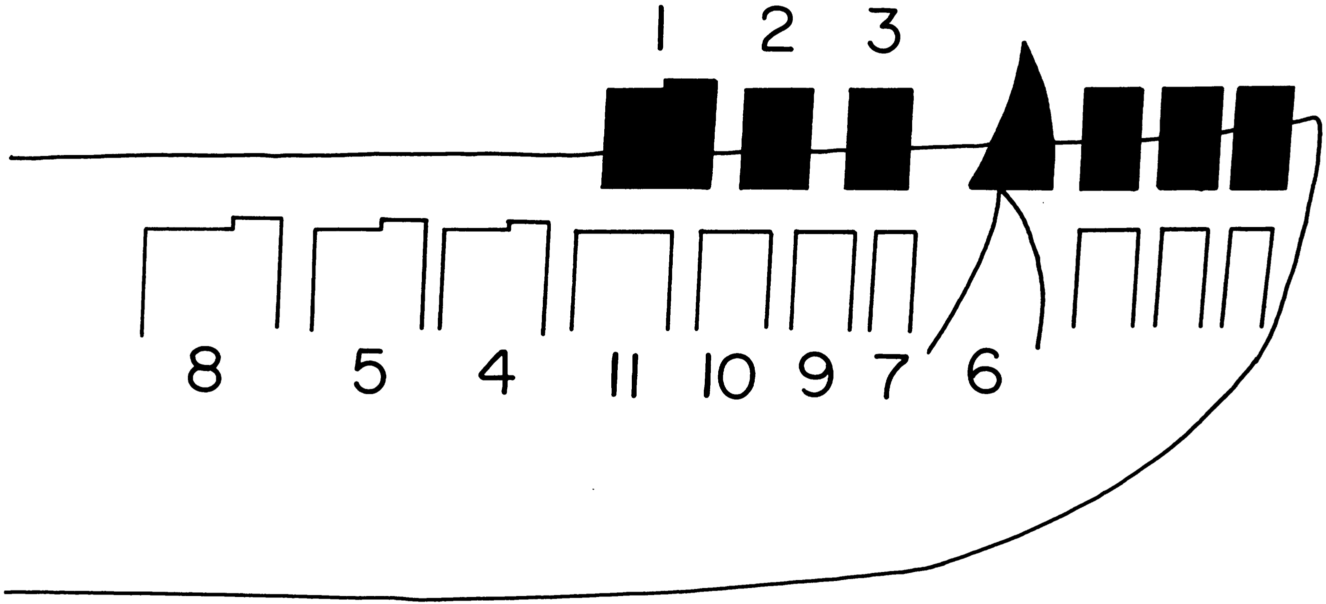


FIG. 22. Presumed eruption sequence of phenacodont premolars and molars. Deciduous teeth are indicated by solid areas, permanent teeth by outlines. The numbers indicate the order of emplacement, assuming that $dP_4$ is the first deciduous tooth to erupt. If the deciduous teeth are emplaced front to rear, numbers 1—3 would be reversed.

(fig. 23) show that the bud of $P_4$ is the first to calcify, and that of $P_3$ the second. This differential between eruption and calcification sequences may be explained as the result of the greater complexity of $P_4$ requiring more development time within the jaw.

This successional pattern, involving an early eruption of $dP^4_4$, has a likely selective advantage. It is beneficial for this omnivorous animal to have crushing teeth early in life, and consequently the deciduous premolar row was quickly completed. While the emerging molars lengthened the crushing dentition, the permanent premolars erupted, providing a more slicing anterior dentition. $DP^4_4$ remained until the last, as it was apparently initially more important for effective slicing teeth to be present than for the molariform $dP^4_4$ to be eliminated.

FIG. 23. X-ray positive of dentary of *Phenacodus primaevus,* A.M.N.H. No. 15298. The calcified bud of $P_4$ is visible beneath $dP_4$, but there is no indication of calcifying $P_3$. Natural size.

## SUMMARY AND CONCLUSIONS

Mammalian posterior milk teeth have been said to either preserve dental features characteristic of their ancestors (be "conservative") or to precede the molars and replacement premolars in adapting to changing conditions (be "progressive") (Von Koenigswald, 1967, pp. 780–782).

The phenacodont fourth deciduous upper premolars are initially progressive teeth, as are the milk teeth of the succeeding perissodactyls, whose condition Von Koenigswald used in framing his concept of progressiveness. At first $dP^4$ was predictive of future adult conditions, as in *Tetraclaenodon puercensis* it possesses a well-formed mesostyle; this feature did not become characteristic of phenacodont upper molars for several million years after its appearance in $dP^4$. This predictive nature of $dP^4$

did not continue, however. $DP^4$ of both *Phenacodus* and *Ectocion* retain the mesostyle, but seem not to have gained new characters predictive of future molar conformations. $DP_4$ is not nearly so progressive. Throughout the history of the phenacodonts $dP_4$ had a large, often multiple paraconid; the progressive loss of this cusp is a feature of the permanent molars of the phenacodonts. Although a small molar paraconid is present in both species of *Tetraclaenodon,* in *Phenacodus* it was absorbed into the metaconid, leaving only a semicircular crest at the anterior end of the trigonid. *Ectocion* lost the molar paraconid altogether, retaining only a lingually sloping paralophid. On the other hand, the proximity of the hypoconulid and entoconid is a feature of *Ectocion* molars that is increasingly apparent through time in *Ectocion* $dP_4$.

The anterior deciduous teeth are less instructive than the posterior ones. $DP\frac{3}{3}$ appear to represent the anterior end of the molarization field in the phenacodonts, as the posterior parts are much more molariform than the anterior parts.

The progressive nature of $dP\frac{4}{4}$, suggested by the early development of a mesostyle, and the increasing molariformity of the permanent fourth premolar, suggests that the later phenacodonts had at least some genetic potential for premolar molarization so successfully developed by the perissodactyls, an early product of the phenacodont lineage (Radinsky, 1966). The Phenacodontidae died out before they had the opportunity to utilize this potential. $P\frac{4}{4}$ of the phenacodonts never became truly molariform. The molars did not become lophodont and hypsodont as perissodactyl molars did, and there is little suggestion in the milk teeth that this was possible.

## APPENDIX

### Deciduous Tooth Material Studied

#### ARCTOCYONIDAE

*Protogonodon*

*P. kimbetovius*

A.M.N.H. No. 16397 (type), right and left $dP_4$–$M_2$; lower Puerco beds, Nacimiento Fm., San Juan Basin, New Mexico.

#### PHENACODONTIDAE

*Tetraclaenodon*

*T. puercensis*

A.M.N.H. Nos. 940, R $dP_4$–$M_2$; 2474, L $dP^4$; 2494, L $dP_4$–$M_1$; 2559, R $dP_4$; 3831, L $dP_4$–$M_1$; 3841, L $dP^4$–$M^2$; 3849, L $dP_3$–$M_1$; 3850, L $dP_4$–$M_2$; 3875, L $dP_4$–$M_1$; 3917, R $dP_4$–$M_1$; 3919, L $dP_4$; 3953, R $dP_4$–$M_2$; 3969, R $dP^4$–$M^1$; 3970, R $dP_4$–$M_1$, L $dP_4$–$M_1$, R $dP_4$; 4008a, L $dP^4$; 16656, L $dP_3$–$M_2$; 16719,

R $dP_4$–$M_1$; 16725, L $dP_2$–$M_1$, R $dP_4$–$M_1$; Torrejon beds, Nacimiento Fm., middle Paleocene, San Juan Basin, New Mexico.
U.C.M.P. No. 36513, R $dP_4$–$M_1$, Blanco Divide, upper Nacimiento Fm., middle Paleocene, San Juan Basin, New Mexico.
A.M.N.H. Nos. 87604, right and left $dP^4$; 87626, R $dP_4$; Swain Quarry, Ft. Union Fm., middle Paleocene, Washakie Basin, Wyoming.
A.M.N.H. No. 35425, L $dP^4$–$M^1$; upper Lebo Mem., Ft. Union Fm., late Paleocene, Crazy Mountain Field, Montana.
U.S.N.M. No. 22144, L $dP^4$–$M^2$; Lebo Mem., Ft. Union Fm., middle Paleocene, north of Livingston, Montana.
U.S.N.M. No. 6181, R $dP^4$; Loc. 51, Lebo Mem., Ft. Union Fm., middle Paleocene, Crazy Mountain Field, Montana.
P.U. Nos. 13947, L $dP_3$–$M_1$; 17498, L $dP^3$–$M^1$; 17641, L $dP_3$–$M_1$; 20340, R $dP^4$(4); 20341, L $dP^4$(3); 20358, R $dP^4$; Rock Bench Quarry, Ft. Union Fm., middle Paleocene, Bighorn Basin, Wyoming.

*T. pliciferus*
A.M.N.H.Nos. 3897 (type), L $dP_4$–$M_2$, R $M_1$–$M_2$; 16648, L $dP^3$–$M^1$; lower Torrejon beds, Nacimiento Fm., middle Paleocene, San Juan Basin, New Mexico.
A.M.N.H. No. 35429, L $dP_4$–$M_1$; Loc. 5, upper Lebo Mem., Ft. Union Fm., late Paleocene, Crazy Mountain Field, Montana.

*Phenacodus*

*P. bisonensis*
U.S.N.M. No. 26325, L $dP_4$; Ft. Union Fm., late Paleocene, Bison Basin, Wyoming.
P.U. No. 14634b, R $dP^4$; Douglass Quarry, Lebo Mem., Ft. Union Fm., late Paleocene, Crazy Mountain Field, Montana

*P. grangeri*
P.U. Nos. 19465, $dP^3$–$M^1$; 19561, L $dP_4$–$M_1$; 19584, L $dP^3$–$M^1$; 20254, L $dP^4$; 20290, L $dP_4$; Cedar Point Quarry, Ft. Union Fm., late Paleocene, Bighorn Basin, Wyoming.

*P. almiensis*
U.S.N.M. Nos. 26236, R $dP_4$; 26327, L $dP^4$; Buckman Hollow, Evanston Fm., late Paleocene, Green River Basin, Wyoming.

*P. brachypternus*
P. U. No. 13115, R $dP^3$–$M^2$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.
Y.P.M. No. 17595 R $dP_4$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.
U.C.M.P. No. 46172, R $dP^4$; West Alheit Pocket, Hiawatha Mem., Wasatch Fm., early Eocene, Moffat Co., Colorado.

*P. vortmani*
A.M.N.H. No. 4382, L $dP_4$–$M_2$; 15763, R & L $dP^4$–$M^3$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.
P.U. Nos. 16146, L $dP_4$–$M_2$; 20260, R & L $dP^4$; Willwood Fm., early Eocene, Bighorn Basin, Wyoming.
U.S.N.M. Nos. 19991, L $dP_4$–$M_1$; 19997, R $dP_3$–$M_1$; 19998, R $dP^4$–$M^2$; 20013, L $dP_4$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.
Y.P.M. Nos. 17695, R $dP_4$–$M_1$; 17597, R $dP_3$–$M_1$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

A.C.M. No. 4380, R & L $dP_4$; Lysite Mem., Wind River Fm., early Eocene, Wind River Basin, Wyoming.

A.M.N.H. No. 15652, L $dP_4$–$M_1$, R $dP_4$–$M_2$; Lysite Mem., Wind River Fm., early Eocene, Wind River Basin, Wyoming.

P.U. No. 13441, R $dP_3$–$M_2$; Lysite Mem., Wind River Fm., early Eocene, Wind River Basin, Wyoming.

Y.P.M. Nos. 17689, L $dP_4$–$M_1$; 22979, R $dP_4$–$M_1$; Lysite beds equivalent, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

A.M.N.H. No. 55229, L $dP_4$–$M_2$; Huerfano B beds, Huerfano Fm., early Eocene, Huerfano Basin, Colorado

M.C.Z. No. 3444, R $dP_4$–$M_2$; Lost Cabin Mem., Wind River Fm., early Eocene, Wind River Basin, Wyoming.

*P. primaevus*

P.U. Nos. 17955, R $dP^3$–$dP^4$; 17987, R $dP^4$; 18937, L $dP_4$–$M_1$; 18953, R $dP_4$–$M_1$; 19009, R $dP^3$–$M^1$; 20363, R $dP^4$; Silver Coulee beds, Ft. Union Fm., late Paleocene, Bighorn Basin, Wyoming.

A.M.N.H. No. 32660, R $dP^4$–$M^2$; unknown level, probably early Eocene (floor of kiva), northwestern New Mexico.

A.M.N.H. Nos. 1779, L $dP_4$–$M_1$; 4296, L $dP_4$–$M_1$; 4377, R $dP_3$–$M_3$, L $dP_4$–$M_2$; 14791, R & L $dP^4$–$M^1$; 15060, L $dP_4$–$M_1$; 15298, L $P_2$, $dP_3$–$M_3$; 15299, L $dP_3$–$M_2$; 15307, L $dP_4$–$M_1$; 15308, L $dP_3$–$M_1$; 15312, L $dP^3$, L $dP^4$, R $dP^3$–$dP^4$; 15753, L $dP_4$–$M_2$, L $dP^4$–$M^3$; 15760, R $dP^3$–$M^2$, L $dP^4$–$M^2$, L $dP_3$–$M_1$, R $dP_4$–$M_1$; 16188, R $dP^3$–$M^1$; 21865, R $dP_4$(2); Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

U.S.N.M. Nos. 19994, R $dP_4$–$M_1$; 20014, L $dP^3$–$M^1$; 20053 R $dP_4$–$M_2$, L $dP_4$; 20066, R $dP_3$–$M_2$; 20067, L $P_2$ $dP_3dP_4M_1M_2$; 20070, R & L $dP^3$–$M^3$, R $dP_4$–$M_2$, L $dP_3$–$M_2$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

P.U. Nos. 13035, R & L $dP^4$–$M^3$, L $dP_2$–$M_3$, R C–$M_2$; 13040, R $dP^3$–$M^1$; 13044, L $dP_4$–$M_2$; 13208, L $dP^3$–$M^1$, L $dP_3$–$dP_4$; 16201, $dP_3$ $M_1$, $M_2$; 16200, L $dP_4$–$M_2$; 16202, L $dP_4$–$M_1$; 17883, R $dP^4$; 20113, R $dP^4$–$M^3$; 20152, R $dP_4$–$M_2$, L $dP_4$; 20155, L $dP^4$–$M^1$, R $dP^4$–$M^1$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

A.C.M. No. 4377, $dP_3$–$M_2$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

Y.P.M. Nos. 23105, L $dP_4$–$M_1$; 17598, L $dP^4$–$M^1$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

M.C.Z. No. 17994, L $dP^4$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

C.M. No. 15–52, R $dP^4$–$M^1$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

F.M.N.H. No. P15681, L $dP_4$–$M_3$; Shire Mem., Wasatch Fm., early Eocene, Piceance Creek Basin, Colorado.

*P.* cf. *P. teilhardi*

P.L. No. 196–Mu, R $dP^4$; Mutigny, early Eocene, Paris Basin, France.

*Ectocion*

*E.* cf. *E. wyomingensis*

U.S.N.M. No. 21264, L $dP_4$–$M_2$, Twin Creeks, Evanston Fm., late Paleocene, Fossil Basin, Wyoming.

P.U. Nos. 19966, L $dP_3$–$M_2$; 20291, L $dP_3$–$dP_4$; Cedar Point Quarry, Ft. Union Fm., late Paleocene, Bighorn Basin, Wyoming.

F.M.N.H. No. P15532, R $dP^3$–$dP^4$, Atwell Gulch Mem., Wasatch Fm., late Paleocene, Piceance Creek Basin, Colorado.

*E. montanensis*

P.U. Nos. 20417, R $dP_4$, R $dP_3$, L $M_3$; 20426, L $dP_4$(2), 20428, L $dP^4$, Douglass Quarry, Lebo Mem., Ft. Union Fm., late Paleocene, Crazy Mountain Field, Montana.

*E. osbornianum*

P.U. Nos. 13938, R $dP_3$–$M_3$; 13945, R $dP^3$–$M^1$, 13963, R $dP_4$–$M_1$; 14247, R $dP^3$–$dP^4$; 14858, L $dP_2$–$M_2$; 14969, L $dP_4$; 17717, L $dP_4$; 17756, L $dP_3$–$M_2$; 17757, R $dP_3$–$M_3$; 17759, L $dP_3$–$M_3$; 17813, L $dP^3$–$dP^4$; 18095, L $dP^4$; 18595, L $dP_4$–$M_2$; 18975, L $dP_4$–$M_1$; 18977, L $dP^4$–$M^3$; 18988, L $dP^4$; 19123, L $dP^4$; 19132, R $dP^4$–$M^1$; Silver Coulee beds, Ft. Union Fm., late Paleocene, Bighorn Basin, Wyoming.

U.S.N.M. No. 20468, R $dP_4$–$M_2$; Buckman Hollow, Evanston Fm., late Paleocene, Green River Basin, Wyoming.

A.M.N.H. No. 88155, R $dP^4$; JO Loc., Indian Meadows Fm. equivalent, latest Paleocene or earliest Eocene, Purdy Basin, Mt. Leidy Highlands, Wyoming.

A.M.N.H. No. 15854, L $dP_4$–$M_1$; "Clark Fork beds," Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

P.U. No. 17901, L $dP^4$–$M^2$; "Clark Fork beds," Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

A.M.N.H. Nos. 1780, R $dP^4$–$M^1$; 4293, L $dP^4$–$M^2$; 4294, R $dP_4$–$M_1$; 4690, L $dP_4$–$M_2$; 16132, R $dP^3$–$M^1$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

P.U. Nos. 13225, L $dP^3$–$M^2$; 13226, R $dP_4$–$M_3$; 13228, R $dP^4$; 16149, R $P_2dP_3dP_4$; 16170, R $dP_4$; 19592, L $dP_4$–$M_2$; 19821, R $dP_4$, L $dP_4$–$M_1$; 20182, L $dP_4$–$M_1$, L $dP_3$–$dP_4$; 20204, R $dP_4$–$M_1$, 20212, R $dP_4$–$M_1$, R $dP^4$; 20456, L $dP^4$–$M^2$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

A.C.M. No. 10052, R $dP_4$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

Y.P.M. Nos. 17596, R $dP_4$; 22980, L $dP_4$–$M_1$; Greybull beds, Willwood Fm., early Eocene, Bighorn Basin, Wyoming.

A.M.N.H. No. 56304, $dP^4$; unnamed beds, early Eocene, Powder River Basin, Wyoming.

## REFERENCES

Butler, P. M.

1952. The milk-molars of Perissodactyla, with remarks on molar occlusion. Proc. Zool. Soc. London, vol. 121, pt. 4, pp. 777–817, 16 figs.

Cope, E. D.

1884. Tertiary Vertebrata. Vol. III. Rept. U. S. Geol. Surv. Terr., 1009 pp., 38 figs., 75 pls.

Gazin, C. L.

1941. The mammalian faunas of the Paleocene of central Utah, with notes on the geology. Proc. U. S. Natl. Mus., vol. 91, no. 3121, 53 pp., 29 figs.

GUTHRIE, D. A.
1967. The mammalian fauna of the Lysite Member, Wind River Formation, (early Eocene) of Wyoming. Mem. Southern California Acad. Sci., vol. 5, 53 pp., 36 figs., 29 tables.
KIRKPATRICK, R. D., AND L. K. SOULS
1962. Age determination of the collared peccary by tooth-replacement pattern. Jour. Wildlife Management, vol. 26, no. 2, pp. 214–217, 1 fig., 1 table.
MCKENNA, M. C.
1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. California Publ. Geol. Sci., vol. 37, no. 1, pp. 1–130, 64 figs.
MATTHEW, W. D.
1897. A revision of the Puerco fauna. Bull. Amer. Mus. Nat. Hist., vol. 9, art. 2, pp. 259–323, 20 figs.
1937. Paleocene faunas of the San Juan Basin, New Mexico. Trans. Amer. Phil. Soc., new ser., vol. 30, pp. 1–510, 85 figs., pls. 1–65.
OSBORN, H. F., AND C. EARLE
1895. Fossil mammals of the Puerco beds. Bull. Amer. Mus. Nat. Hist., vol. 7, art. 1, pp. 1–70.
PEYER, B.
1968. Comparative odontology. Chicago, Univ. Chicago Press, 347 pp., 220 figs., 8 pls.
RADINSKY, L. B.
1966. The adaptive radiation of the phenacodontid condylarths and the origin of the Perissodactyla. Evolution, vol. 20, no. 3, pp. 408–417, 5 figs.
RICH, T. H.
[In press.] Deltatheridia Carnivora and Condylarthra from the early Eocene, Paris Basin, France. Univ. California Publ. Geol. Sci.
SIMPSON, G. G.
1942. The beginnings of vertebrate paleontology in North America. Proc. Amer. Phil. Soc., vol. 86, no. 1, pp. 130–188, 23 figs.
1951. American Cretaceous insectivores. Amer. Mus. Novitates, no. 1541, pp. 1–19, 7 figs.
VAN VALEN, L.
1966. Deltatheridia, a new order of mammals. Bull. Amer. Mus. Nat. Hist., vol. 132, art. 1, pp. 1–126, 17 figs., 8 pls., 26 tables.
1969. Multiple origins of the placental carnivores. Evolution, vol. 23, no. 1, pp. 118–130, 11 figs.
VON KOENIGSWALD, G. H. R.
1967. Evolutionary trends in the deciduous molars of the Hominoidea. Jour. Dent. Res., vol. 46, no. 5, pt. 1, pp. 779–786, 6 figs.
WEST, R. M., AND D. BAIRD
1970. *Protogonia subquadrata* Cope, 1881 (Mammalia): Proposed suppression of generic and specific names under the plenary powers. Bull. Zool. Nomenclature, vol. 26, pts. 5, 6, pp. 230–232.
ZIEGLER, A. C.
1967. Dental ontogeny of the mole *Scapanus latimus* (Bachman) and its evolutionary importance. Ph. D. dissertation, University of California, 375 pp., 72 figs.